EXOTIC GRASS INVASION INCREASES [FORAGE] PRODUCTIVITY AND REDUCES DIVERSITY OF A [HIGH ALTITUDE] MESIC GRASSLAND.

T Weaver and S Bao.
Ecology and Land Resources Departments,
Montana State University. Bozeman Mt 59717.

February 2021

.

ABSTRACT

Mesic temperate rangeland, e.g. from the North American mixed grass prairie, Rocky Mountain grasslands and southern hemisphere continents is being invaded by the exotic rhizomatous grasses, *Poa pratensis* and *Bromus inermis*. To project the effects of their invasion on one grassland, we compared community properties in- and outside of clones invading a level environmentally homogeneous meadow representative of our high altitude fescue grasslands. Yields increased from native vegetation dominated by *Festuca idahoenis* (Feid, x= 96 gm/m2) through exotic vegetation dominated by Poa (x= 158 gm/m2) to Brome (x= 258 gm/m2) with little difference in forage quality (protein content). Some, e.g. a grazier, might therefore view the change as beneficial. Measurement of community composition in the three communities showed a considerable impoverishment of the native fescue (Feid) community by exotic invasion, an impoverishment understated by measured reduction in species richness [i.e. from Feid (16-12 species per 1.13m2) through *Poa* (11) to Brome (4); species evenness (Simpson) [i.e. from 88-84 to 81 to 42]; and life-form evenness (%forb) [i.e, Feid (42-34%) through Poa (23%) to Brome (5%). The impoverishment probably resulted **first**, from competitive exclusion of natives by lack of soil resources captured by exotics (whose entry surely demonstrated a superior capacity to acquire water and nutrients) and **second**, for natives associated with taller Brome, from a reduction of ground-level light, a deficiency confirmed by etiolation of the natives. Conservationists will surely decry the losses. Due to the inexorable rhizomatous spread of Poa and Brome and the resultant impossibility of controlling them, we deduce that managers should accept the foresee-able [vegetation] type-conversion and develop methods for managing/using the new vegetation- - a resigned reaction paralleling the response necessary for other anthropogenic factors: urbanization, N-supplementation, pollution and climate change. We expect parallel responses in other mesic grasslands. Sampling and statistics completed 2014-20l5. 1st draft reviewed 2016.

Key words: Exotic invasion. Mesic grasslands: mixed grass prairie, mountain meadows. *Festuca idahoensis, Poa pratensis, Bromus inermis,* forage production, vegetation composition (richness & evenness), management.

INTRODUCTION

Humans now dominate the earth's ecosystems spatially, bio-geochemically, hydrologically and biologically **(**Vitousek et al 1997*).* Invasions by exotic plants represent a major component of the biological change (Vitousek et al., 1996). To plan their response to such exotic invasion, range managers need information about the effects of invasion on grasslands, in particular on resultant changes in forage production, forage quality, and community composition.
First, the fact that exotic grasses often dominate natives suggests that they may out-produce the natives and thus that invasion may yield a desirable increase in forage production. While papers considering effects of grass invasion on range/grassland production are almost non-existent (e.g. Toledo et al 2014 for Poa pratensis), a few papers show production increases associated with forb invasion (e.g. Cook-Patton and Agrawal 2014, Maron et al 2014)
Second, we find no discussion of effects of grass invasion on forage quality and thus our study. There are obvious effects of invading forbs (e.g. Euphorbia, Centaurea and Cirsium)- - due to their stem-iness, prickles, and repulsive compounds].
Third, reports from many grasslands show and discuss, as undesirable, exotic-induced reductions in species diversity (e.g. Chapin et al 2000). We find no reports documenting species-by-species effects needed, for example, to evaluate changes in forage quality or habitat for specific invertebrates or birds.

Our objectives are **first**, to determine the effects of projected extensive exotic invasion of a mesic grassland by comparing native meadow vegetation (*Festuca idahoensis*=FEID) and imbedded clonal communities dominated by exotics, either *Poa pratensis*=Poa or *Bromus inermis*= Brome. Our null hypotheses are that Feid community phases (Feid/Cafi and Feid/Brci, Mueggler and Stewart 1980) are like each other (to be accepted) and that they are like the exotic Poa and Brome communities (to be rejected). Our comparisons include production, forage quality, and community composition. And, **second** to consider the management implications of such changes on our meadow, similar fescue meadows (Muggler and Stewart 1980) and mesic grasslands of other regions.

METHODS

Our study site is a windswept mountain meadow with vegetation dominated by the *Festuca idahoensis/Carex filifolia* type in its drier segments and the *Festuca idahoensis/Agropyron caninum* type on slightly moister segments (Mueggler and Stewart 1980, Weaver 1974). The *Festuca idahoensis* grassland types range widely in foothills and higher meadows of the northern Rocky Mountains i.e. Wyoming Idaho, Montana, and Alberta. The actual study site (4.2 Ha) lies in the Bangtail SIA (Special interest area, USFS), includes the Bangtail USFS Ranger Station, which is located 19 km NE of Bozeman MT (45˚46'59" N, 110˚46'40" W). The area, originally fenced for occasional short-term use of horses of rangers working the remote area (~ 1930-1960) and fully devoted to research since 1969, is effectively a long term exclosure since it has excluded domestic cattle/sheep grazing, (though not wild game) occurring on the surrounding hundreds of acres. Average annual precipitation of about 960 mm provides adequate soil water except from mid-July through mid-September (Weaver and Collins 1977, Brookshire and Weaver 2015). Average maximum/minimum temperatures were 22/8C in July and -5/-10 in January (Weaver and Collins 1977). Soils of the site are loamy typic cryoboralls (Buchanan 1971, Weaver and Collins 1977). Intense monitoring of the site began in 1969 through the auspices of NSF and the International Biological Program (Weaver and Haglund 1974, Weaver and Collins 1998) and at least skeletal measurements have been conducted annually ever since (Brookshire and Weaver 2015)

The meadow is dotted with clonal patches of exotic Poa or Brome, first noticed by me in the early 1970's (Weaver, pc). Individuals of both species are assumed to have established randomly at low rates (possibly1-5 per acre), probably through the light horse use of the 1930-1970 period. Since then their presence has increased both by vegetative expansion of the clones laterally and, to a lesser extent, by initiation of new clones through seeding from the already established circular colonies. Current clone diameters are 2-4m for Poa and 5-10m for Brome. Poa clones are most common in the more general Feid/Cafi phase, Brome clones are most common in the apparently moister Feid/Agca phase, and both phases support clones of both types.

To compare the behavior/nature of native vs exotic communities/ecosystems we compared the vegetation of paired native-exotic samples, that is, one sample from the center of a randomly chosen Poa or Brome clone and another from a quadrat randomly placed 2-5 meters outside of it in the native vegetation matrix. In both native and exotic treatments we excluded micro-sites which were disturbed - - for example, by gophers which rarely used Poa vegetation and still more rarely used Brome vegetation (Weaver pc). Ten paired sites (replications) were studied for Poa and six were used for Brome. Our examination of nature's experiment compares favorably with three other invasive strategies considered (Appendix text I).

To compare production and quality of forage in the natural vegetation (outside of clones) and the invading exotic vegetation (inside the clones), we harvested plant material from 0.5 x 1.0 m quadrats inside and outside each clone studied. To index yields we clipped material above 1cm height near maximum standing crop (30-31 August 2014), separated grasses and forbs, dried the samples to constant weight (43-49C) and recorded the weights. To determine forage quality we ground the entire samples (< 1mm), subsampled, and analyzed for carbon and nitrogen content [*C/N*]. The C and N measurements were made with a Leco TruSpec CN analyzer (Leco Corp, St Joseph, MI), that is, with flash combustion and gas chromatography. Thanks to Engle/Wallander lab, MSU. To calculate the aboveground N standing crop we multiplied standing crop by N concentration.

To compare community composition we used **five** measures. 1) Species richness of each community was determined (30 July 2014) by listing the species found in 1.5 x 0.75 m (1.125m2) quadrats placed inside and outside of each clone studied. Richness was measured again (8-9 September) by listing species found in 0.5x1 m quadrats immediately adjacent to the harvested quadrats. 2) 'Geographic' ubiquity (= frequency, Daubenmire 1968) of each species in each community, was determined (30 July) by gridding each 1.1 m2 richness frame into fifteen 25x25 cm subplots and expressing the frequency of each species therein as number of subplots occupied divided by the fifteen possible, *ie* the percentage of the subplots occupied. 3) Cover was estimated in a 0.5 x 1.0m plot immediately adjacent to each harvested frame on 8-9 Sept 2014; two individuals (TW and SB) visually estimated the cover of each species and the similar values were averaged. 4) Species evenness (Simpson 1949) was calculated from frequency data (July) and cover data (September). 5) Finally, to demonstrate compositional differences at a

functional level (Weaver 2016= this paper), we define and calculate a novel life form (= guild) evenness index [forb biomass/total (=grass &forb) biomass measured in August.

We compared the vegetation of our four 'communities', character-by-character, by use of ANOVA and Tukey's hsd contrasts (Tukey 1949). The four (candidate) communities were native fescue vegetation outside the Poa (FeidP) patches, adjacent exotic Poa vegetation, native fescue vegetation outside the Brome patches (FeidB) and adjacent Brome vegetation. We hypothesized great similarity in the native matrix, i.e. between the native paired plots outside of the exotic Poa and Brome clones and, after showing it, we combined the Feid communities (FeidP & FeidB) and compare the composite type with the Poa and Brome communities. Thus our statistical analysis treats the two native 'types' separately to demonstrate their similarity- - and thus to provide a basis for pooling them in our more general comparison (see below) of Feid overall (i.e. ave of Feid P and Feid B), Poa [*P. pratensis*], and Brome [*B. inermis*] vegetation types. We hypothesize increasing yields and declining community complexity on the gradient from the native vegetation (combined Feid) through Poa to Brome.

RESULTS

Our attack. In the following, we compare the production and composition of native (FeidP &FeidB), exotic Poa and exotic Brome community types. First, we sampled the four 'types' separately and statistically compared them with ANOVA (Table 1, Fig 1, Fig 2, and Fig 3). And second, for the following results and discussion sections, we simplify to the desired three types by comparing 'non-statistically', for each quality/character, the average of FeidP&FeidB with averages from the exotic Poa and Brome communities. We justify the averaging/combination of FeidP and FeidB by noting, via statistical contrasts, the, usual, 'identity' (Table 1) of the Feid types and the consistent trends in production (upward) and richness and evenness (downward) from native Feid (combined) through exotic Poa to exotic Brome. Direct summary data are reported in Table 1. In contrast, to facilitate discussion in the following results and discussion sections, data for each parameter are reported in the text as a percentage of the un-invaded 'control'; in addition, the direct quantitative measure (e.g. mean gm/m2) for that control is presented to calibrate the series. The significance of each ANOVA is reported in Table 1 and the

results of comparisons are indicated by letters indicating differences measured with Tukey's LSD; values followed by the same letter are statistically indistinguishable. We note also that, despite FeidP and FeidB similarities, species composition suggests that the FeidB site may be slightly moister than the FeidP site, cf. Appendix Table 1).

Forage. Maximum standing crop, as an in index of productivity, was average Feid (i.e. FeidP and FeidB) 100% ('**cc**' contrasts', 97 gm/m2 base), increasing to 164% for Poa ('**b**' contrast) and 267%, for Brome ('**a**' contrast') (Tab 1, Fig 1). The increase in the grass component was stronger, from average Feid 100% ('**cc**'contrasts, 64 gm/m2 base) doubling (195% '**b'**) to Poa and quadrupling (384%, **'a**') to Brome. The complementary forb component shrank from average Feid 100% ('**aa**', 36 gm/m2 base) though Poa 94% ('**a**') to Brome 33% ('**b'**) The pooling of FeidP and FeidB data is justified by their statistical 'identity' and the trend across types; the comparisons reported in Table 1 are indicated/repeated by lower-case letters following the percentage comparisons and the Feid mass is repeated as the base.

Late summer N composition, as an index of total forage quality, fell significantly from average Feid (FeidP and FeidB) (100%, **ab/a**, 1.13 %) through Poa (92%, **b**) to Brome (0.82%, **c**) (Fig1, Table 1). The decline resulted from a slight decline in grass N (100%,**aa** / 0.91%, **ab**/ 0.87%,**b**] complemented by an increase in the N content of the sparser forb component [100,**c/ab** / 102, **b** / 110%, **a**). The pooling of FeidP and FeidB is justified by their statistical identity (except in forbs) and trend across types. Protein content is often approximated as the product of N concentration x 6.25 (FAO 2003).

Despite slightly opposing trends, the aboveground N stock, excluding litter, rose from average Feid (100%, **cc**, 1.10 gm/m2) to Poa (145%, **b**) to Brome (222%, **a**) (Fig 1, Tale 1). The grass component increased from averaged Feid (100%, **cc**, 63 gm/m2), to Poa (180%, **b**) and to Brome (356%, **a**). And, while the forb stock of average Feid 100%, aa,46 gm/m2) and Poa(**a**) were equal, that of the Bromus community was much less (39%, **b**) than either. The pooling of FeidP and FeidB is justified by their statistical identity and consistent trend across types.

Composition. The presence of individual species is compared, across the communities, with respect to cover (dominance) and frequency (=ubiquity, Daubenmire 1968) with a releve table (Appendix table 1).

Richness, measured at mid-season (30 July) as the average number of spp/1.125m2 declined from average Feid (FeidP& FeidB) (100%, **a/b**=14) through Poa (76% **b**) to Brome (30% **c**) (Table 1.). While the decline in richness is consistent and significant, FeidP and FeidB are not statistically identical. Late in the season (8 September), a parallel non-significant trend was measured while making the cover estimates in a 0.50m2 frame: Feid (100% **aa**,8.6), Poa (85% **a**) and Brome (85% **a**).

Evenness was measured both at the species and life form/guild levels. **First**, traditional Simpson evenness, the deviation from equal species representation (Simpson 1949), measured using frequency data (July), was similar in the combined Feid (FeidP & Feid B) (100% **aa**, 0.86) and, Poa (94% **a**) matrices but much lower in Brome (0.49% **b**) (Table 1). Again, the combination of FeidP and FeidB is justified and the decline is consistent. Calculations based on cover data measured later (September) showed a parallel statistically significant trend (Table 1.): Feid (100% **ab/a**, 0.68), Poa 78%, **b**) and Brome (40%, **c**). **Second**, we novel-ly indexed evenness at the life form level as forb/total biomass. Forb dominance decreases from average Feid (100%, **a/ab** 0.41), Poa (56%, **b**) to Brin (12% **c**) Complimentarily, grass dominance increases from average Feid (100%,**b/bc**. 0.62) through Poa (124%, **b**) to Brin (153% **c**).

DISCUSSION

Presentation. We report large changes (+/-) in production and composition between the average native/fescue matrix community (FeidP and FeidB) and the embedded exotic clones of Poa and, even more-so from the embedded Brome clones (Fig 1, Fig 2, Fig 3, Tab 1). Because comparisons between either exotic Poa or Brome clones and their matrices are parallel, combining- - as outlined in the results section- - simplifies and facilitates discussion. In the following we compare the three types and consider application of our observations.

Forage. We indexed production (gm/m2/yr) with measures of maximum standing crop (gm/m2). Overall, maximum standing crops (production) increased 'exponentially' from the native community though Poa to Brome vegetation. Grasses, the primary vegetative component, accounted for the increase. In contrast, forb standing crops fell from Feid to Poa and still more to Bromus, the decline being overridden in the total by the strong increases in the dominant grasses. We note that while our 'maximum standing crop' measure is conventionally used as a proxy for production in grasslands, it underestimates to an unknown degree the potential productivity of all grasslands in two ways, neither significantly affecting our primary conclusions. First, a single harvest misses both material produced and dropped from the canopy before the measure and material yet to be produced (Singh, et al 1975). Our measure may especially underestimate forb production- - because the harvest was post-MSC- - and in proportion to the importance of forbs, ie the under-estimate decreases from Feid through Poa to Brome. And second, to the extent that production of continuously grazed vegetation exceeds that of ungrazed vegetation (McNaughton 1985 and Frank and McNaughton1993) we underestimated the 'potential' production possibly achievable under *domestic* gazing.

The apparent benefit of the exotics to the grazier is reinforced by considering three nutritional factors. **First**, quality is often associated with the content of nitrogen and protein (estimated as 6.25 x N content, FAO 2003). The nitrogen concentration of grasses declined slightly with exotic invasion. Contrary-wise, the N concentration content of forbs increased slightly with invasion. Because the forb component is so small, forage quality for generalist feeders like cattle may have declined, but only slightly. On the other hand, the small increase in forb quality might conceivably have a slight positive impact on herb/forb feeders like sheep, deer, and elk. **Second**, palatability is high for all three grass species, possibly declining from Brome to Feid to Poa (Meuggler and Stewart1980). In all three palatability certainly varies with season, for example, Brome may be most palatable in spring but, due to its stem-iness, least palatable in late summer/fall. **Third**, if such a meadow were to be cut for hay, the manager wants the product of biomass and N content, i.e. an index of forage N per square meter. With respect to both total forage and grass this desirably increases significantly from Feid through Poa to Brome. On the other hand, while the nitrogen concentration of forbs increases, the decline in forb mass results in a significant decline in forb nitrogen per square meter.

Community composition. We consider four measures of community composition. A **releve** table, richness (spp number measured at two seasons), Simpson (1949) evenness (measured at two seasons), and, our novel life-form index, forb/total biomass.

The releve' table (Appendix Table 1) demonstrates vegetation differences largely irrelevant to our theme. It documents species composition differences between FeidP and FeidB vegetation, and identifies species lost/not lost with increasing exotic competition. Such a table should be useful to individuals wanting/needing to know the effect of invasion on particular species, groups of species, or organisms which are dependent on particular plant taxa (eg insects or birds, Cook-Patton and Agrawal 2014). In our case, casual examination shows that, relative to the native community, there is exotics related reduction in some species: some competition related (Feid vs Poa/Brome) and some seemingly related to change in plant height (ie to short Feid/Poa vs taller Brome).

Richness, the number of species observed in our sample, declined both with season and across vegetation types from Feid to Poa and Brome. First, we attribute the decline in diversity between the July and September measures, both to the disappearance (drying) of Feid's rich spring flora and to the use of a smaller sample area. Second, and more relevant to our question. July data showed a significant Feid/Poa/Brome decline. While this was paralleled in September data, the trend there was not significant- - surely due to disappearance of ephemeral species present in the Feid's rich spring flora. We suggest the following mechanism for the cross-community trend. The high richness in Feid vegetation is likely due to its high lateral heterogeneity; the bunch-grass physiognomy presents a gradient (~ 10 cm) between near-bunch high (water-nutrient) competition to between-plant lower-competition sites. [Competition on this gradient may be seasonal, ie greatest in late spring when water/nutrients vary most along the gradient and less both in earlier moist spring and later dry summer.] In contrast, richness is less in Poa and Brome vegetation because clonal communities have little lateral differentiation. It declines still further in the Brome community because taller more productive brome vegetation further impact Feid and its short meadow associates both by so out-producing (RGR) them (i.e. via water/nutrient capture) and by its overtopping them (i.e. via by shading (Gioria and Osborne 2014)

The decline in species evenness (Simpson 1949) demonstrates/emphasizes the dominance of the invading grasses. July data demonstrate the early dominance of Brome: combined Feid 86, Poa 81, and Brome 42 (significant). By late August the capacity of both exotics to dominate is seen, Feid 67, Poa 53, Brome 27 (significant). The cross season decline in evenness is surely due to the disappearance of Feid's rich spring flora.

Our life-form evenness index, forb/total biomass (30 August), rigorously compares the separate capacities of Feid, Poa and Brome to dominate the forb community. First, in the drier FeidP (Poa matrix) the dominance of grasses is less than that in the moister FeidB (Brome matrix), perhaps because summer drought thins FeidP most and thus provides more spring inter-clump resource for the forbs. Second, and of greater interest to us, is the fact that grass dominance increases from average Feid through Poa to Brome. Again, we attribute the decline in forb success across the series to their decreasing capacity to compete with the exotics both laterally (Poa and Brome) and vertically (Brome) (Gioria and Osborne 2014).

Management. Following Daubenmire (pers. comm.), we reason that invasion of our rangeland Feid habitat type by either/or Poa and Brome will gradually eliminate the vegetation type as we know it (Mueggler and Stewart 1980). The argument involves four steps: 1) The exotic grasses colonize at densities varying with seed availability and the availability of 'soft sites' e.g. sites with disturbance [eg gopher] or moist soils. 2) Even if established at low density, the exotic grasses spread inexorably by rhizomes. 3) The resultant intimate intermixture of exotic and native plants makes exotic dominance likely, as demonstrated. 4) And it makes control unlikely, for the following three reasons. a. Chemical or biocontrol agents sufficiently specific to remove only Poa/Brome do not exist and are not likely to be developed. b. While in a warm season grassland one can select against cool season **exotic** grasses by burning or heavy grazing in the spring (when warm season grasses are inactive, Slather 2013), this strategy can't work in cool season grasslands (ranging from the mixed grass prairie to our mountain meadows**)**, because both native and exotic plants are favored by the same cool-season conditions. c. Due to its high palatability, there is undoubtedly selection against Brome growing in cool season grassland but, while normal grazing inhibits Brome, it doesn't control it. This selection might be intensified by oft repeated bursts of high intensity grazing, i.e. by selecting against the most palatable grass without pressuring the less palatable grasses- - this method has, however, not been certified

(Slather 2013, 2014, Toledo et al 2014). 5) Our measures have demonstrated that invasion of Poa/Brome increases total production, reduces Feid, and reduces diversity locally.

We assert that our results are widely applicable in mountain meadows as well as other cool season grasslands. **First**, our results clearly apply directly to the meadow studied (the statistician's 'sphere of inference'). The sphere of application is, however, much wider. **Second**, because our fescue meadow is representative of the widespread Feid/Dain and Feid/Aghi communities identified by Mueggler and Stewart (1980), we expect our results to apply where Poa and Brome invade other sites in these vegetation types, i.e. in mountains and foothills of the northern Rocky Mountains. **Third**, both grasses invade and dominate other cool-season mesic grasslands of the northern states. Daubenmire (pc 1974) observed invasion in fescue grasslands of Idaho and Washington and predicted that Poa will dominate them. In mixed grass prairie to the east, Poa dominates extensively (Toledo et al 2014) and Brome invades even more vigorously than in our fescue meadows (Weaver and Plaggemeyer 2004, Hartz-Rubin et al 2005). And **fourth**, though they are naturally widespread in Eurasia, for similar reasons, both plants are expected to invade cool mesic grasslands of the southern hemisphere where they are not native.

IMPLICATIONS.

Due to the inexorable spread of exotic Poa and Brome (and other rhizomatous exotics) we expect them to slowly replace much of the native grassland in mesic cool-season regions. One may deduce from our data that, with such invasion, yields will generally increase and community diversity will decrease. We suggest, then, that - - as with other anthropogenic factors (n-pollution, organic pollution, and even climate change (Vitousek et al.1997) developing management adaptations to the inexorable change is more useful than resisting or lamenting such change (cf. Toledo et al 2014). Possibly more important, beside production and diversity, we should consider changes in other ecosystem processes- - e.g. water movement, erosion, leaching, nutrient and water cycles, fire, insect and wildlife habitat- - and how can we best contain or use the resultant changes?

ACKNOWLEDGMENTS

The problem and study site were chosen by T Weaver and he did much of the field work. S Bao helped with the field work, did the lab processing, and did the statistical analyses. L Rew provided encouragement, consultation and minor editing. We expect Lisa to contribute giant-ly to final publication of the work.

LITERATURE CITED

J Brookshire and T Weaver. 2015. Long-term decline in grassland productivity driven by increasing dryness. *Nature Communications.* doi: 10.1038/ncomms8148 http://www.nature.com/ncomms/2015/150514/ncomms8148/full/ncomms8148.html

B Buchanan 1971. Ecological effects of weather modification, Bridger Range area, Montana: Relationship of soil, vegetation and microclimate. PhD dissertation Montana State University, Bozeman. 135 pgs

WF Chapin, E Zavaleta, V Eviner, R Naylor, P Vitousek, H Reynolds, D Hooper, L Savorl, O Sala, S Hobbie, M Mack, and S Diaz 2000. Consequences of changing biodiversity. Nature 405: 234-242

S Cook-Patton and A Agrawal 2014 Exotic plants contribute positively to biodiversity functions but reduce native seed production and arthropod richness. Ecology 95:1642-1650.

R Daubenmire 1968. Plant communities. Harper and Row, NY. 300 pgs.

FAO 2003. Food energy - - methods of analysis and conversion factors. FAW food and nutrition paper 77. Analytical methods for proteins in foods. . Association of official analytical agricultural chemists (AOAC). Food and agriculture organization of the United Nations ISSN 0254-4725

D Frank and S McNaughton 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96: 157-161

M Gioria and R Osborne 2014. Resource competition in plant invasions: emerging patterns and research needs. Frontiers in Plant Science 5: 501.. 10.3389/fpls.2014.00501

J Hartz-Rubin, T Weaver. C Rubin, and J Plaggemeyer ~2005. Effect of fire and grazing on invasive species in northern mixed grass prairie. Final Report (draft): Joint Fire Science Program [USFS, BIA, BLM, NPS, USFWS, USGS) (Contract 01B-3-3-03)] 65 pgs. https://www.firescience.gov/projects/01B-3-3-03/project/01B-3-3-03_final_report.pdf

J Maron, H Auge, D Pearson, L Korell, I Hensen, K Suding, C Stein 2014. Staged invasions across disparate grasslands: effects of consumers, disturbance and seed provenance on productivity and species richness. Ecology letters 17: 499-507

S McNaughton 1985. Ecology of a grazing ecosystem: the Serengeti. Ecological Monogaphs 55: 259-294

W Mueggler and W Stewart. 1980. Grassland and shrubland habitat types of western Montana. USDA Forest Service Gen Tech Rept INT-66. 154 pgs.

N Sather2013. Bromus inermis, TNC element stewartship abstract. http://wiki.bugwood.org/Bromus_inermis

N Sather 2014/1996. P. pratensis pratensis, TNC element stewartship abstract. http://wiki.bugwood.org/P. pratensis

J Singh, W Lauenroth, and R Steinhorst 1975. Review and assessment of various methods for estimating net aerial primary production in grasslands from harvest data. Bot Review 41: 181-232

E Simpson, 1949. Measurement of diversity. Nature 163: 688.

D Toledo, M Sanderson, K Spaeth , J Hendrickson, and J Printz 2014. Extent of kentucky bluegass and its effect on native plant species diversity and ecosystem services in the northern great plains of the United States. Invasive plant science and management 7: 543-552

Tukey, John (1949). "Comparing Individual Means in the Analysis of Variance". Biometrics. 5 (2): 99–114

Vitousek P. M., D'Antonio C. M., Loope L. L., Westbrooks R. 1996. Biological invasions as global environmental change. Am. Sci. 84, 468–478

P Vitousek, H Mooney, J Lubchenco, and J Melillo. 1997. Human domination of earth's ecosystems. Science 277: 494-499

T Weaver and D Collins 1977. Possible effects of weather modification (increased snow pack) on *Festuca idahoensis* meadows. J. Range Management 30: 451-456.

T Weaver and B Haglund 1974. An overview of Bridger Biomass data: 1969-1973. US IBP Grassland Biome Technical Report 304. Colorado State University, Fort Collins. 109 pp.

T Weaver 1974. Ecological effects of weather modification: effect of late snow melt on Festuca idahoensis meadows. American Midland Naturalist 92: 346-356.

T. Weaver, and D. D. Collins. 1998. NPP Grassland: Bridger, U.S.A., 1970-1973. Data set. Available on-line [http://www.daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.

T Weaver. J Plaggemeyer, et al 2004. Fire and adaptive management of northern prairies: the prairies, fuel, and weeds. Final report on USDI Fire Coordination Committee Research Initiative 1422-R220A8-0011: Applications of satellite imagery in adaptive resource management. 118 pgs. https://www.firescience.gov/projects/01B-3-3-03/.../01B-3-3-03_final_report.pdf

Table 1. PRODUCTIVITY AND COMPOSITION OF FEID/POA/BROME COMMUNITIES.

Shading links statistically similar values, and thus simultaneously distinguishes dissimilar ones, across communities.

		FOUR COMMUNITIES: FEID (p & b), POA, AND BROME					
		FEID p	FEID	**FEID b**	**POA**	**BROME**	ANOVA
		Poa out *TMR*	**ave p&b**	Brom out *TMR*	Poa in *TMR*	Brom in TMR	Prob.
PRODUCTION							
BIOMASS (gm/m2)	*(Fig 1)*						
GrassForb	*	97.12 c	*96.68*	96.24 c	158.9 b	258.54 a	8.34E-10
Grass	*	57.02 c	*63.67*	70.31 c	124.82 b	246.06 a	9.38E-11
Forb	*	40.11 a	*36.03*	31.94 a	34.08 a	12.46 b	0.00098
forb/grass&forb		0.42 a	*0.38*	0.34 ab	0.23 b	0.05 c	1.03E-05
grass/grass&forb		0.58 c	*0.62*	0.66 bc	0.77 b	0.95 a	1.03E-05
Litter		18.46 c	*23.32*	28.16 bc	42.78 b	98.21 a	2.75E-07
N %	*(Fig 1)*						
GrassForb	*	1.11 ab	*1.13*	1.15 a	1.04 b	0.93 c	0.0029
Grass		1.04 a	*1.04*	1.03 a	0.95 ab	0.9 b	0.0464
Forb		1.22 c	*1.31*	1.39 ab	1.34 b	1.44 a	0.0002
Litter		1.2 a	*1.21*	1.23 a	1.36 a	0.87 b	0.0001
N/m2 (g/m2)	*(Fig 1)*						
grass + forb	*	1.08 c	*1.1*	1.11 c	1.59 b	2.42 a	2.54E-07
grass	*	0.61 c	*0.63*	0.65 c	1.14 b	2.24 a	1.98E-08
forb	*	0.48 a	*0.46*	0.44 a	0.45 a	0.18 b	0.0021
litter		0.22 b	*0.29*	0.35 b	0.65 a	0.78 a	6.71E-05
gr+ fb+ lit		1.31 c	*1.38*	1.45 c	2.24 b	3.2 a	3.18E-08
C/N by biomass							
grass + forb		41.28 b	40.49	39.69 b	44.22 b	49.56 a	0.00259
grass		43.65 b	43.84	44.03 b	48.46 ab	51.51 a	0.0327
forb		38.01 a	35.72	33.43 bc	34.76 b	31.9 c	0.00021
litter		37.45 b	36.89	36.33 b	33.23 b	55.9 a	0.00023
COMPOSITION							
RICHNESS	*(Fig 2)*						
July/frequency	*	15.7 a	*13.94*	12.17 b	10.6 b	4.17 c	4.95E-10
Sept/cover		8 a	*8.59*	9.17 a	7.3 a	7.33 a	0.167
EVENNESS, Simpson	*(Fig 3)*						
July/frequency	*	0.88 a	*0.86*	0.84 a	0.81 a	0.42 b	3.01E-07
Sept/cover		0.63 ab	*0.68*	0.72 a	0.53 b	0.27 c	2.61E-05
EVENNESS, by biomass	*(Fig3)*						
forb/grass&forb	*	0.42 a	*0.41*	0.34 ab	0.23 b	0.05 c	1.03E-05
grass/grass&forb		0.58 c	*0.62*	0.66 bc	0.77 b	0.95 a	1.03E-05

Asterisks in colum four indicate material graphed in Figures 1-3.

Forb and grass biomass based biomass evenness both appear in Figure w, the first transparent (top) and the second blank.

Forb and grass 'biomass based' evenness both appear in Figure 3. Forb mass is transparent (top) and grass mass is black (bottom)

TMR indicates 'true multiple range' comparisons.

FROM d.AnovaD&PrdBEST

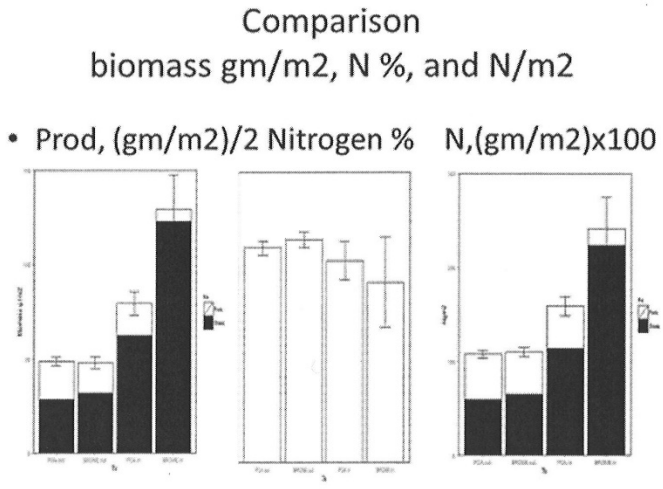

Fig 1. Comparison of Feid, Poa, and Bromus vegetation with respect to std crp (gm/m2), N composition (%) and N standing crop (gm/m2). The bar height indicates total standing crop; the shaded lower portion reports the portion which is grass. Elaborated in Table 1. *Fig 1, 2, and 3 are modified from d1stDraftTWvAbb FIGURES(002). Verify: to correct Std Crop multiply by 2, % N is OK, divide N std crop by ten.*

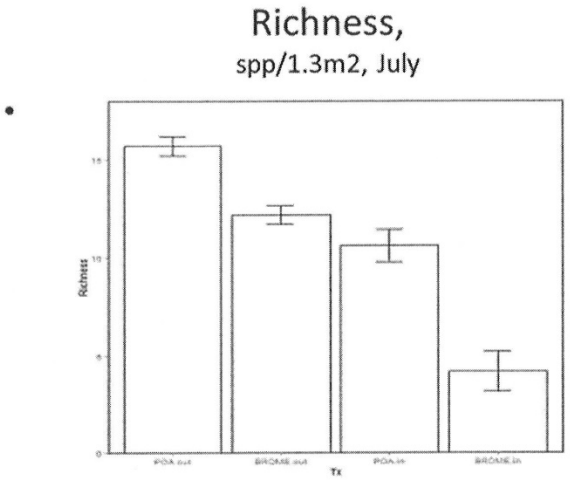

Fig 2. Richness (spp/1.3M2) in Feid 1(Feid of Poa) , Feid 2 (Feid of Brome), Poa, and Brome. .

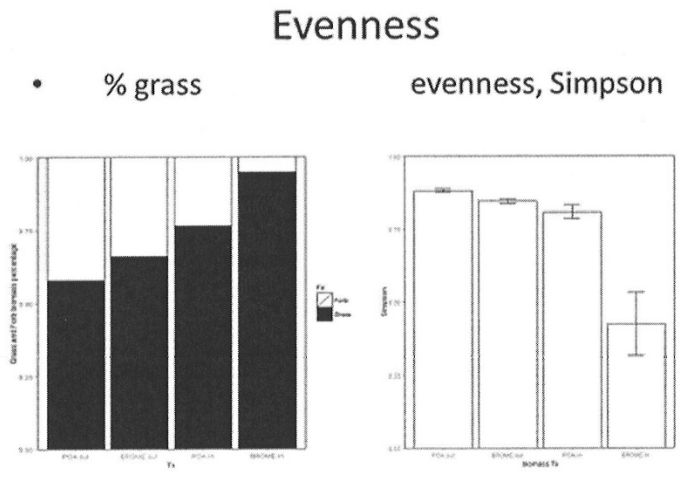

Fig 3. Evenness of composition. A) % grass increases from Feid 1 (Feid/Poa) through Feid 2 (Feid/brome) and Poa to Brome. *As % forb, its inverse (portion of the bars), it declines as do richness and Simpson evenness.* B) Evenness (Simpson, frequency) across the same four vegetation types. Elaborated in Table 1. *Source, see Fig 1.*

Appendix table 1. Summary releve table comparing species presence across four communities: Feid 1 (Poa matrix), Feid 2 (Brome matrix), Poa clone and Brome clone. The species are listed on the left and measures of their presence (constancy and cover) in each communiy appear in separate columns under each community heading. Shading empasizes species linking, distinguishing, and neutral across communities.

	FOUR COMMUNITIES							
	FEID I (dry)		FEID I (moist)		POA		BROM	
	cnst	cvr	cnst	cvr	cnst	cvr	cnst	cvr
BROMUS CORE								
Lactuca							0.2	
Geranium							0.2	
BROM	0.1		0.3		0.2		1.0	81
POA CORE								
POA					0.9	38	0.5	1
FESTUCA CORE								
FEID	1.0	33	1.0	24	0.6	3	0.7	3
Erigeron	0.7	2	0.7	6	0.7	1	0.3	
Arenaria	0.6	3	0.7	3	0.4		0.2	
Antenaria	0.3		0.3		0.2			
Agropyron	0.2		0.2		0.2			
Carex	0.3		0.3		0.2			
Timothy	0.1		0.2					
Erissimum	0.1		0.2					
DRY VS MOIST FESCUE								
Eriogonum	0.4							
Silene	0.2							
Besseya	0.1							
Collomia	0.1						0.3	
Thalaspi/Arabis			0.2				0.2	
Solidago			0.3				0.2	
Polygonum bistort			0.2					
Frasera			0.3					
Dodecatheon			0.3					
Gallarida			0.3					
Koeleria			0.2					
INDIFFERENT								
Achillea	0.8	1	1.0	2	0.7	1	0.8	1
Cerastium	0.8	3	1.0	3	0.5	1	0.7	1
Campanula	0.5	1	0.5	1	0.7	1	0.3	
Galium	0.7	1	0.7	2	0.8	3	0.8	1
Senecio	0.1		0.2		0.1		0.3	
Agoseris	0.3				0.6	2	0.2	
Lupinus	0.3				0.2		0.3	
Delphinium			0.2		0.2		0.2	

The communities, named for the dominant grass are Feid 1, Feid 2, Poa, and Brome. This table compares the distribution of all recorded species among the four communities. Constancy (cnst) is the percent of sites in a community type which contain the spp, Yellow > 50%. Cover is the median cover of the species in community types containing it. Shading: gray > 2%, blue > 1%.

APPENDIX text 1

alternative field experiments considered.

` Our 'experimental' strategy is suitable and is the most practical of four complementary methods (discussed below) for determining the effect of an invading plant on a vegetation type. , ***First*** we compare the productivity and species richness of clonal invasive communities and the broader community in which they are imbedded. In-out clone differences could be due either to differences in the plant species involved (obvious) or from undetected micro-environmental differences. For the following three reasons, we doubt significant micro-environmental causes. The overall site is nearly level and unbroken by identifiable geomorphological features like [vegetation modifying] drainage ways. The clones are randomly distributed in the matrix, like fungal/bacterial colonies on an agar plate, rather than following any (identifiable) environmental pattern. And the clones are large relative to any micro-environmental variation expected in the matrix community. Analysis of this natural experiment compares favorably with three more experimental methods discussed below.

Second**,** one might experimentally plant adjacent (paired) examples of the native and the mixed community and compare their performance (cf **Cook-Patton and Agrawal 2014, *J Maron, et al 2014 or Gloria and Osborne*= Callaway?). While this approach seems conceptually ideal, we note that early-on one is comparing the invading community to an early-seral example of the native community and that the relevant end-point comparison only becomes valid when the vegetation of the native plots reaches climax. In a separate succession experiment on this site, the native vegetation of experimental disturbances/gardens is only approaching equilibrium after twenty years of development/succession- - far longer than most weed scientists wish to wait. We note also that, in such an experiment, underlying micro-environmental variation would be similar to that found in our 'natural experiment.'

Third, to reduce the likelihood that the exotic outperformed the native vegetation by occupying especially rich micro-sites one might experimentally institute paired plots, as in method one, by randomly locating native plots and introducing embedded exotic communities for comparison. While this method may be most intellectually satisfying, development of comparable imbedded exotic communities would be 'unacceptably slow', i.e. decades long.

Fourth, a variant of method three (B Maxwell PC), would be to compare the native community to plots of the exotic community established, not by planting, but by expansion/advance of an exotic clone into surrounding native vegetation. This method is both subject to two criticism. First, if the exotic clone occupies especially rich sites (cf method 1), the experimental pair occupies especially rich sites and is therefore not representative of the most general case. And second, the method is also 'unacceptably' slow because one must await the exotic clone's spread. The first criticism might be refuted by demonstrating that, while the exotic clone established in a rich site, it had spread into the normal environment/vegetation beyond the rich site. The same refutation applies to large clones studied in our method #1.

S Cook-Patton and A Agrawal 2014 Exotic plants contribute positively to biodiversity functions but reduce native seed production and arthropod richness. Ecology 95:1642-1650.

M Gioria and R Osborne 2014 Resource competition in plant invasions: emerging patterns and research needs. Frontiers in Plant Science 5: 501.. 10.3389/fpls.2014.00501

M Gioria and R Osborne 2014 Resource competition in plant invasions: emerging patterns and research needs. Frontiers in Plant Science 5: 501.. 10.3389/fpls.2014.00501