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**Ignite**

## Do plants respond to multi-year disturbance rhythms and are we missing the beat?

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Disturbance seasonality and return interval can create complex interactions of direct and indirect effects on species and ecosystems. Fire is a key grassland disturbance, yet long-term research examining seasonality and return intervals is limited. A 15-year experiment testing combinations of fire seasonality (summer, fall, spring) and return interval (2, 3, 6-year) plus non-burned controls was conducted in northern mixed prairie to evaluate effects on the plant community. *Hesperostipa comata* is a native C<sub>3</sub> bunchgrass and dominant species in northern mixed prairie and previously observed to be fire-sensitive. Current-year aboveground biomass results were generally counter to expectations based on short-term research. Fire increased *H. comata* biomass with a strong, rhythmic response pattern to a specific fire seasonality-return-interval combination (fall fire at 3-year return intervals) that periodically increased biomass to more than three times that with no fire. Through the first four post-fire growing seasons, biomass with summer, fall and spring fire across return intervals was 41, 89 and 93% of that with no fire. Afterward, no fire combination produced less biomass than no fire and recurring patterns emerged with large increases in biomass, particularly with fall fire at 3-year intervals. Peak biomass years were regularly two growing seasons after 3-year fall fire and occurred across wet, near-average and dry conditions. We hypothesize that productivity responses were driven by the combination of demographic processes of seedling recruitment and synchronization of multiple tiller age classes. Because short-term negative effects were reversed and regular patterns only emerged 5 years after study initiation, more long-term research evaluating fire regimes is recommended to expand upon tests of individual factors over short periods. This suggestion is based on fire research, but likely applies to multiple forms of disturbance and demonstrates how demographic processes can inform responses for individual species and larger ecosystem functions, such as productivity.

Keywords: disturbance regime, fire, rangeland, return interval, seasonality, semi-arid grassland



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## Introduction

Timing and frequency are among the most important disturbance properties affecting community responses (Garcia Molinos and Donohue 2011, Miller and Safford 2020, Turner and Seidl 2023). However, testing of disturbance effects is limited by the numerous potential timing-by-frequency combinations. Options can be narrowed somewhat by selecting within the range of historical disturbance regimes, if known, but long-term commitments are still required to apply them. With fire, seasonal timing can be important as it relates to plant phenology, resistance, and interactions with co-existing species, and fire frequency or return interval may variously promote or interrupt species recovery between disturbances (Whelan 1995). Fire is, or historically was, a recurring event. However, most tests of fire seasonality effects in rangelands assess short-term responses to single events and long-term fire frequency research is not only rare, but constrained with respect to seasonality of fire (Engle and Bidwell 2001, Knapp et al. 2009, Scheintaub et al. 2009).

We designed a long-term (15 years) experiment to evaluate fire seasonality and return interval effects in northern mixed prairie. Of particular interest was the response of  $C_3$  perennial bunchgrass, *Hesperostipa comata*, because it is one of the dominant species, an important forage source, and reported to decrease in biomass following fire (Wright and Klemmedson 1965, Vermeire et al. 2011). Results from the first two growing seasons after initial fires of what became the long-term study also indicated reductions in *H. comata* frequency with fire (Vermeire and Russell 2018). Evaluations of the bud bank revealed that direct bud mortality sometimes occurred with fire and that the number of active buds per tiller was reduced (Russell et al. 2015, 2019). Based on these negative short-term responses, we hypothesized that *H. comata* biomass would be reduced with repeated fires, to a greater extent with shorter fire return intervals and with spring fire.

## Material and methods

Data were collected as part of a 15-year experiment evaluating fire seasonality and return interval effects on soils, soil microbes, vegetation and grasshoppers (Reinhart et al. 2016, Vermeire and Russell 2018, Russell et al. 2019, Heimbuch et al. 2023) at Fort Keogh Livestock and Range Research Laboratory near Miles City, Montana, USA (46°24'N, 105°56'W). The site is northern mixed prairie on gently rolling loamy soils at an elevation of 815 m. The 15-year study period mean annual precipitation was 322 mm and average annual temperature was 8°C. Vegetation is dominated by perennial, native  $C_3$  graminoid species, *H. comata*, *Pascopyrum smithii*, *Poa secunda* and *Carex flifolia*, and the  $C_4$  species *Bouteloua gracilis*. Exotic annual grasses *Bromus japonicus* and *Bromus tectorum* are often prominent. Prior to study initiation, all plots shared a common history of moderate grazing by cattle and no record of fire for at least 12 years.

Experimental design was a thrice-replicated factorial arrangement of three fire seasonalities (summer, fall, spring)

with three fire return intervals (2, 3, 6 year) plus non-burned controls in 15 × 20-m plots. The 2-year interval was initially intended as annual fire with the expectation it would quickly stress the system. Due to interacting effects of fire and drought limiting fuel loads or fuel continuity, the treatment was redefined as a 2-year interval after burning the first two years consecutively. Summer fires were applied following summer quiescence of  $C_3$  grasses, fall fires followed the first killing frost (<−2°C), and spring fires were applied after *B. gracilis* had initiated growth (typically during April). Fires began during summer 2006 and followed a summer, fall, spring sequence to ensure post-fire growing seasons were synchronized among fire seasonality treatments. Prescribed fires were conducted with a ring-fire technique using drip torches and wet lines around mowed plot borders. Four thermocouples were randomly placed in crowns of four plants in each plot before ignition. Temperature was recorded at one-second intervals and heat dosage was calculated as the sum of the products of time and degrees > 60°C.

Plots were sampled at peak biomass during late July. Biomass was clipped to ground level by functional groups (*H. comata* was collected separately) from four randomly placed 0.25-m<sup>2</sup> circular quadrats in each plot. Biomass samples were dried to a constant weight at 60°C and weighed to the nearest 0.01 g before being separated into current and past years' growth and reweighed to determine current-year biomass as an estimate of productivity. Additionally, current-year biomass was estimated with a modified point intercept technique (Anderson et al. 2024) using 4, 5-m point-intercept transects in each plot, with points read at 20-cm intervals from 2017 through 2020. Point intercept data supplemented and were averaged with manual sorting data to increase coverage. Plot was the experimental unit and estimates were means of plot subsamples.

The full dataset was analyzed with a mixed model for repeated measures using SAS MIXED. The model included the main effects of fire treatment combination, year, and their interaction. Year was the repeated measure. The response variable was current-year *H. comata* biomass. Fires were initiated during summer 2006, but only data from 2008–2020 were analyzed because biomass was not separated by species or functional group during 2006 or 2007. Due to treatment combination-by-year interactions, additional analyses were conducted on year clusters based on observed patterns from initial analysis, with 1) 2008–2010 data before biomass amplification occurred, 2) data between biomass peak years and 3) peak biomass years (2011, 2014, 2017, 2020). Data for year clusters were converted to quotients of treatment/control. Models tested main effects of fire seasonality, fire return interval, year and all interactions, with year as a repeated measure. Heat dosage across years was tested for fire seasonality, fire return interval and their interaction (Supporting information). Significance of tests was declared when  $p < 0.05$  and interactions were followed by tests of simple effects. Key statistics are reported in text as discussed and full model statistical test results are provided in tables with Supporting information.

## Results

Fire seasonality-return interval combination effects on *H. comata* current-year biomass varied by year ( $p < 0.002$ ; Fig. 1). Although differences among treatments occurred during most of the study period, two results stand out for the magnitude of effects. During 2011, all seasonalities of fire at 3-year return intervals went from having only 24–66% of the biomass relative to plots with no fire, to exceeding them by 65–180%. Of greater interest is that 2011 was the beginning of a regular cycle through 2020 for which fall fire at 3-year return intervals more than tripled biomass compared to plots with no fire.

The cyclic relationship is clarified by simplifying to visual comparisons among fall fire at 3-year return intervals, the means of all other fire treatment combinations, and no fire

(Fig. 2). Biomass was not strictly synchronized with spring precipitation nor simply out of phase (Fig. 2). During 2010, biomass was much greater with no fire than with fire and increasing whereas biomass decreased or remained unchanged between years for burned plots. Afterward, oscillations in biomass followed the same general pattern across treatments, differing only in magnitude. Biomass peaks with fall fire at 3-year return intervals occurred two growing seasons following fire and this was repeated four times over 10 year across wet and dry conditions.

Although the response pattern was strong and consistent, it did not emerge until the fifth year after study initiation. Through 2010, data indicated no return interval effect ( $p = 0.200$ ) and that summer fire reduced *H. comata* biomass to 41% of that with no fire ( $p < 0.001$ ; Fig. 3). Between peak biomass years, fire seasonality and return interval had

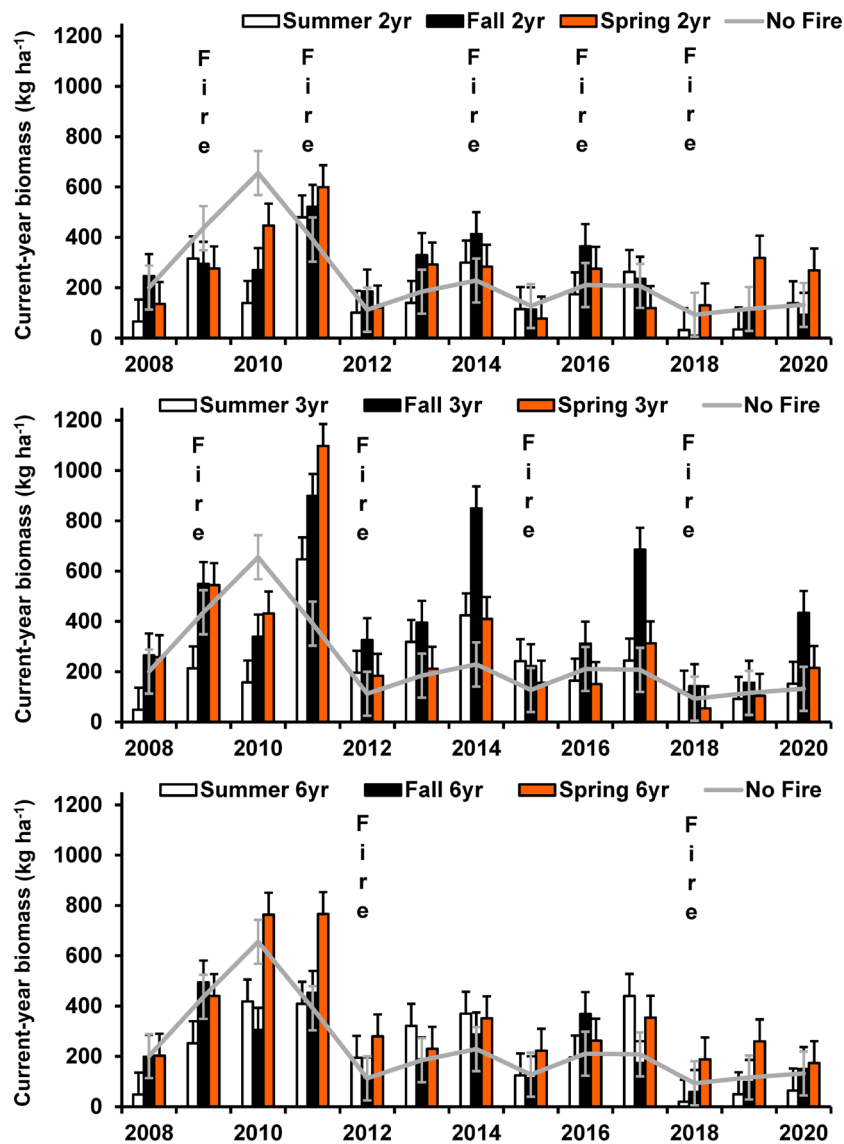


Figure 1. Mean current-year biomass for *Hesperostipa comata* by fire seasonality and return interval treatment combination and year with standard error bars and fire years indicated with text.

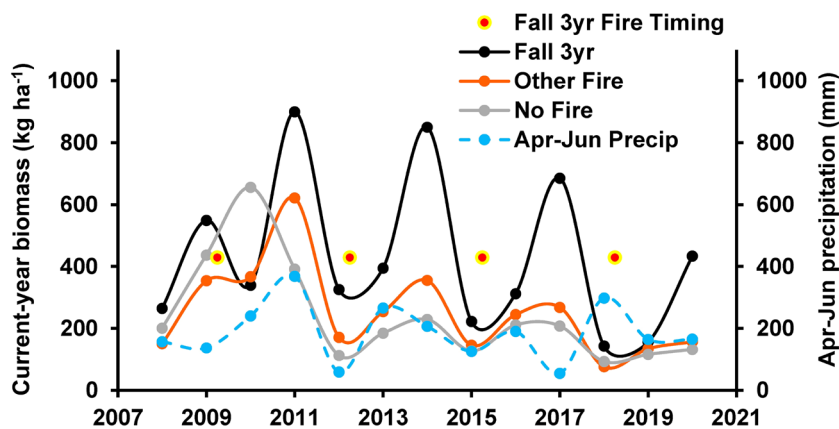


Figure 2. Current-year biomass of *Hesperostipa comata* for fall fire with 3-year return intervals, the mean of all other fire treatment combinations, no fire and yearly April–June precipitation (mm).

interacting effects ( $p < 0.002$ ) on biomass and only summer fire at 2-year intervals had less biomass than plots with no fire. During peak biomass years, a fire seasonality interaction with return interval ( $p < 0.007$ ) indicated fall fire at 3-year intervals more than tripled biomass, spring fire at 3-year intervals nearly doubled biomass and all other fire treatments increased biomass by an average of 33%.

## Discussion

The hypothesis that *H. comata* biomass would be reduced with repeated fires and to a greater extent with shorter fire return intervals was not only rejected, but initial negative fire effects became positive. We observed a strong, cyclic and lagged biomass response to fire that was specific to the seasonal timing of fire and fire return interval. The exact mechanisms were not identified, but previous research supports potential for both sexual and asexual production driving the response pattern. Acute soil heating increased *H. comata* seedling emergence and liquid smoke increased aboveground and belowground biomass, seedling length and leaf number (Blank and Young 1998, Abu et al. 2016). We observed small plants during some years of the study that may have originated from seed, but this was not quantified. If the biomass pulses were influenced by seedlings, fall fire would have been most conducive. Seeds would be exposed to combustion in the canopy and litter during summer fire and seedlings would be exposed during spring fire. In contrast, seeds were insulated by soil after self-drilling and many had not yet germinated during fall fires. Additionally, 2-year-old *H. comata* seed germinates better than younger seed, due to strong seed dormancy (Ogle et al. 2006). This would seem to match the lagged response, however, the increases in biomass would require an enormous number of seedlings and it is doubtful such regular and abundant germination and seedling survival occurred across the range of precipitation conditions. Although seedlings may have contributed to the responses, more broadly, perennial grass generation from seed is often limited, with the overwhelming majority of tillers

originating from belowground buds (Benson and Hartnett 2006, Ott et al. 2019).

*Hesperostipa comata* tillers are polycyclic, meaning they live multiple years, and were observed to follow 3-year cycles whereby buds transition to juvenile tillers that remain belowground the first year, then emerge aboveground as small tillers the second growing season, continue growth into large tillers the third growing season, and finally senesce or flower the fourth growing season (Ott and Hartnett 2015). A plant would typically be comprised of tillers from multiple generations and therefore stages. Based on Ott and Hartnett (2015), we hypothesize that the cycle of amplified biomass was driven by stimulation of the juvenile tillers or synchronization of two or more tiller cohorts to the juvenile tiller stage, such that two growing seasons after fire, a greater portion of the tillers were in the large tiller stage. In addition to explaining the lagged increases, our hypothesis would also account for initial biomass reductions because the large tiller cohort would be delayed. A 3-year fire return interval would allow tillers to reach the large tiller stage and prime another double cohort. The 2-year interval would reset tillers to juvenile or small tiller stages before they reached the large tiller stage. Limited responses to 6-year intervals may have been affected by fires occurring during or following dry years and the long intervals may have been insufficient to create multiple double cohorts, or the accumulation of litter could have negated the stimulus.

Specific combinations of disturbance may evoke very different responses and long-term research may be required to elicit or recognize responses. Studies incorporating demographic measurements could offer further explanation of the processes driving the observed response pattern. Although there is often a desire to identify effects that can be applied broadly across species and regions, species-specific responses can be very important (Koerner et al. 2018). It is possible that the response of *H. comata* to a specific combination of fire seasonality and return interval is unique. However, the facts that the response may never have been observed without inclusion of one specific treatment combination and could have been missed or misinterpreted with fewer observation years indicate high probability for such potential remaining

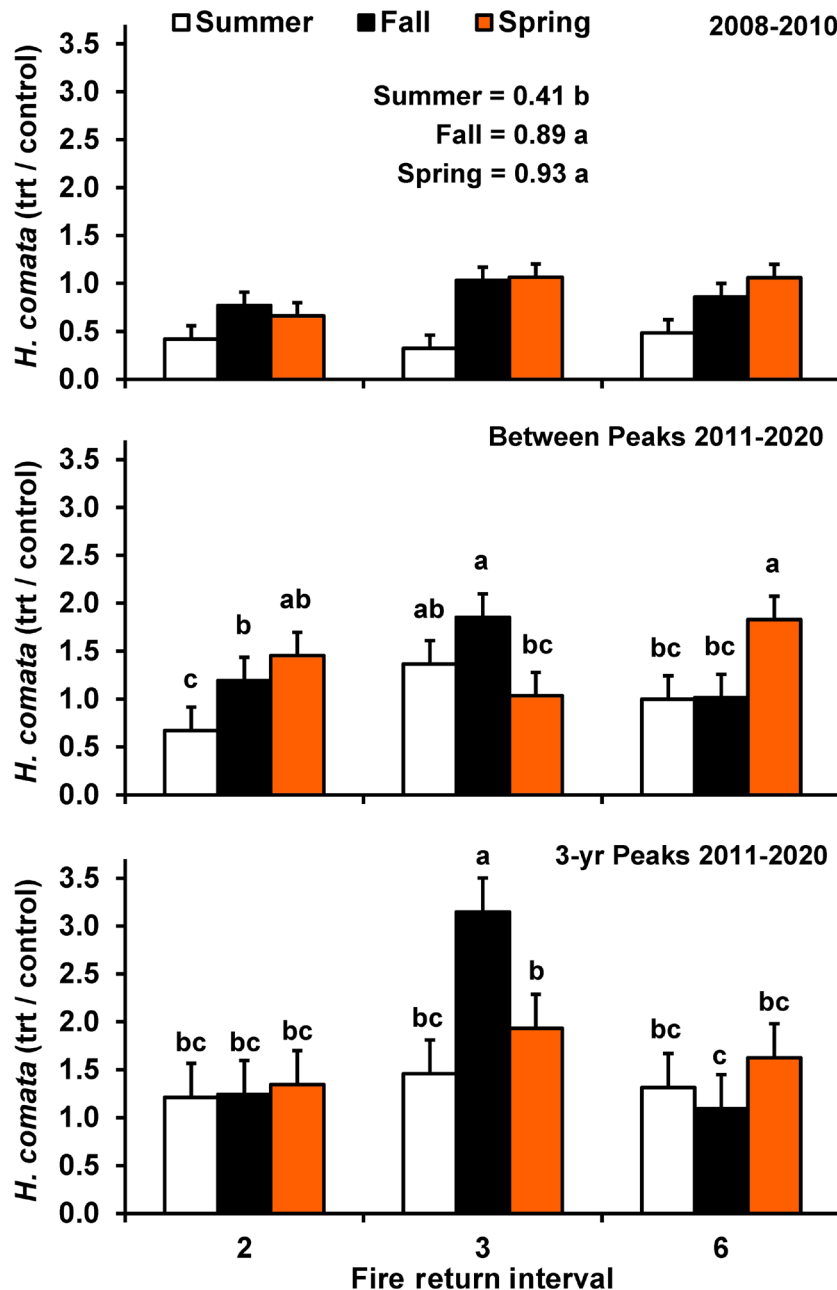


Figure 3. *Hesperostipa comata* current-year biomass expressed as the quotient of treatment and control by fire seasonality and return interval during the initial study period (2008–2010), between 3-year peaks, and during 3-year peaks. Fire treatment means within a panel with a common letter above standard error bars do not differ ( $p > 0.05$ ) based on pairwise comparisons.

undetected and a need for systematic, long-term experimentation with other disturbances and species. Disturbance ecologists are aware that factors such as disturbance timing, intensity and frequency are important and that the stimulation they provide may often be affected by the level and combinations of those factors (Pressler et al. 2019).

Had we not included the particular combination of fall fire every three years, we would not have had even a hint such a response was possible. Additionally, had we only measured plant responses for the first four years, we would have

concluded *H. comata* is reduced by summer fire. We were not specifically seeking the pattern we observed and were simply fortunate to have included fall fire at 3-year return intervals among our treatments. However, if *H. comata* had been the primary focus, the initial range of experimental treatments could have been narrowed by the same understanding of the species' biology we used to explain observations after the experiment. Long-term research and inclusion of multiple seasonal timings and disturbance return intervals are significant investments of time and other resources, but are

necessary to discover whether similar patterns may exist for other species and other disturbances.

### Author contributions

**Lance T. Vermeire:** Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Writing – original draft (lead); Writing – review and editing (lead). **Kurt O. Reinhart:** Writing – review and editing (equal). **Jacqueline Ott:** Writing – review and editing (equal).

### Data availability statement

Data are available from Ag Data Commons: <https://doi.org/10.15482/USDA.ADC/26349127.v1> (Vermeire 2024).

### Supporting information

The Supporting information associated with this article is available with the online version.

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