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RESEARCH ARTICLE

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Grassland woody plant management rapidly changes woody vegetation persistence and abiotic habitat conditions but not herbaceous community composition

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Abstract

1. Grasslands are among the most imperilled ecosystems worldwide, and many have experienced degradation due to the loss of historical disturbance regimes and subsequent woody encroachment. Management practitioners often use physical and chemical management interventions in combination with fire to counter encroachment, altering aboveground structure and belowground function, respectively. This may disrupt the feedbacks that perpetuate encroachment and restore the herbaceous community.
2. We use a large-scale field experiment to assess the initial effects of different management interventions on woody vegetation persistence, abiotic habitat conditions, and herbaceous community composition. We evaluate these effects across seven sites spanning a natural soil moisture gradient to capture one aspect of environmental heterogeneity with which managers regularly contend.
3. We found that chemical intervention, both with and without the addition of physical intervention, was most effective at reducing woody plant cover and abundance, and a second application reduced woody plant abundance by more than one application alone. We also found that any management intervention increased light availability and air temperature and decreased soil moisture, with the combination of physical and chemical interventions having the greatest effects. Finally, none of the management interventions affected herbaceous richness and functional group cover within the study period, indicating delayed or nonexistent effects on herbaceous community composition.
4. *Synthesis and application*. Our findings suggest that management should focus on chemical intervention for the greatest effects on woody plant persistence and abiotic habitat conditions. Changes to herbaceous community composition may occur in the long term and seem likely since short-term effects of management were successful in altering processes related to encroachment feedbacks.

KEYWORDS
ecological restoration, ecosystem structure, microclimate, microhabitat, restoration outcomes, tallgrass prairie, vegetation dynamics, woody encroachment

1 | INTRODUCTION

Grasslands are among the most imperilled ecosystems worldwide. In many regions, more than half of the original grassland land area has been lost in the last century (Overbeck et al., 2015; Sohl et al., 2012). Conversion to agriculture is one of the greatest threats to grasslands (Hoekstra et al., 2005), however, those areas that remain intact, old-growth grassland (sensu Veldman et al., 2015) have still experienced degradation due to changing climate, species invasion, and lack of disturbance (Stevens et al., 2022). Grasslands often have sufficient soil moisture and nutrients for woody plant growth but are maintained as open-canopied, grass- and forb-dominated ecosystems by disturbances such as frequent, low-intensity fire (Bond et al., 2005; Bond & Keeley, 2005). Loss of disturbance allows woody plants to establish and spread (Ratajczak et al., 2014). This phenomenon, known as woody encroachment, decreases grassland biodiversity (Ratajczak et al., 2012; Wieczorkowski & Lehmann, 2022) and alters ecosystem services (Archer et al., 2017; Jackson et al., 2022). Preventing and reducing encroachment is a priority for old-growth grasslands worldwide, yet doing so is notoriously difficult.

One reason why preventing and reducing woody encroachment is so difficult is because altered disturbance regimes, such as the loss of fire, can generate positive feedbacks that favour woody species over the long term (D'Odorico et al., 2012). Without frequent fire, senesced herbaceous plant tissue continues to accumulate, slowly creating thermoregulated and moist conditions that may favour the germination and establishment of woody species (Hassan et al., 2021; Loydi et al., 2013). These individuals would otherwise be unable to establish if the highly flammable herbaceous litter instead served as fuel for fire that kills young woody plants (Bond, 2008; Engber et al., 2011). Continued litter accumulation can also lead to nutrient-enriched soil as organic matter decomposes rather than becomes volatilized by fire, further benefitting woody plant growth (Xiong & Nilsson, 1999). Once established, woody plants change plant community structure and increase canopy shading, further inducing cool and moist conditions and reducing soil evaporation (Breshears et al., 1998; D'Odorico et al., 2007), thereby dampening the intensity and spread of fire (Ratajczak et al., 2011; Trauernicht et al., 2012). Additionally, woody plants can combat moisture limitation by accessing deep soil water typically unused by drought-tolerant grassland species (Nippert et al., 2013; Ratajczak et al., 2011). Established woody plants may also uplift water and limit soil nutrients (Bleby et al., 2010; Boutton & Liao, 2010; Zhou et al., 2018), aiding in the establishment of more woody individuals that would otherwise be outcompeted by herbaceous species that rapidly uptake water and nutrients at the soil surface (Ratajczak et al., 2011). Thus, even after the reintroduction of fire, woody vegetation can persist and spread (Miller et al., 2017; Robertson & Hmielowski, 2014).

To address the challenges posed by these feedbacks, grassland management practitioners often use additional management interventions in combination with fire to counter woody encroachment. Management can be physical (e.g., cutting), chemical (e.g., foliar herbicide), or some combination thereof (e.g., cut-stem herbicide; Midwest Invasive Plant Network, 2023). Physical intervention involves cutting off the connection between the photosynthesizing parts of the plant and its roots, removing the aboveground structure with minimal effect on belowground function. While fire is physical, this term typically refers to mechanical removal. Physical intervention is often applied multiple times, as many woody plants can regrow from energy stored belowground (Bellingham & Sparrow, 2000; Bond & Midgley, 2001). Chemical intervention targets plant tissue and can harm belowground stores crucial for regrowth in woody plants (depending on the mode of action; Sherwani et al., 2015) but has minimal effects on the aboveground structure on its own. Standing dead aboveground woody material is typically left in place to naturally decompose (Midwest Invasive Plant Network, 2023), so while chemical intervention can halt aboveground resource acquisition, aboveground abiotic habitat conditions may remain the same. The combination of both physical and chemical interventions affects both the aboveground structure and the belowground function of woody plants. When interventions are repeated in short frequency, such as is the case when fire occurs in the same growing season as another intervention or when interventions are repeated across growing seasons, they may prevent woody plant recovery, ultimately leading to declines in woody vegetation (Ratajczak et al., 2018).

While feedbacks operate over long, multi-decadal timescales, management interventions operate on much shorter timescales (e.g., a single fire, mowing, or herbicide application), and it is unclear if these short-term effects can alter longer-term feedbacks. A key to understanding the timescales over which feedbacks play out is deciphering the independent effects of different types of management interventions and the repetition of their application not only on the persistence of woody vegetation but also on abiotic habitat conditions (e.g., temperature and moisture) and, ultimately, the herbaceous community. For example, physical intervention may alter the maintenance of cool and moist conditions, and chemical intervention may alter the uplift of water and nutrients, which favour woody plant establishment and spread. These abiotic habitat conditions are also determinants of herbaceous community composition (Boonman et al., 2021), thus management-induced feedbacks are likely to benefit herbaceous species in the long term, helping to restore herbaceous species losses following encroachment (Ratajczak et al., 2012; Wieczorkowski & Lehmann, 2022).

Environmental heterogeneity and stochasticity also play important roles in our understanding of management outcomes (Brudvig & Catano, 2021; Perring et al., 2015). The same type of management intervention may produce different results across space and time as managers contend with variable environmental conditions such as resource availability (e.g., Bakker et al., 2003; Grman et al., 2013) and climate variability (e.g., MacDougall et al., 2007; Vaughn & Young, 2010). It is imperative to perform studies that explicitly control and evaluate the effect of environmental heterogeneity on woody plant management, especially when management is standardized across large regions.

Here, we use a large-scale field experiment to assess the initial effects of different management interventions (physical, chemical, or both) and repetition (one or two applications) across two growing seasons on woody vegetation persistence, abiotic habitat conditions, and herbaceous community composition in tallgrass prairie. We evaluate these effects across seven different remnant tallgrass prairies spanning a natural soil moisture gradient to capture one aspect of environmental heterogeneity that managers frequently encounter (Hoffmann et al., 2012; Moeslund et al., 2013). Specifically, we ask: (1) which management interventions are most effective at reducing woody plant cover and abundance, (2) does management alter light, temperature, and moisture, and (3) does management increase herbaceous richness and functional group cover? We tested our hypotheses that: (1) chemical (i.e., herbicide) intervention is most effective at reducing woody plant cover and abundance because of its effect on belowground function, (2) physical (i.e., cut-stem) intervention most increases light availability and air temperature and decreases soil moisture because of its effect on aboveground structure, and (3) any intervention will increase herbaceous richness and functional group cover because of changes to woody plant structure and function.

2 | MATERIALS AND METHODS

2.1 | Experimental setup

We established a field experiment to quantify the effects of woody plant management on woody vegetation persistence, abiotic habitat conditions, and herbaceous community composition at seven tallgrass prairies (Table 1; Figure 1). We selected sites from all publicly accessible remnant (i.e., unplowed or old-growth) prairie within 100 miles of Madison, Wisconsin, United States. Those selected met our study criteria of having lost their historical fire regime following European colonization but have since had fire management reintroduced. At the start of the study (i.e., 2020), all sites had not been burned since at least 2018 (Table S1). American bison (*Bison bison* L.) were once common in the region and played a role in maintaining grasslands through grazing but have been locally extirpated for centuries (Axelrod, 1985). While grazing cattle have since been introduced to Wisconsin, they are not currently found at our study sites. We selected sites along a soil moisture gradient, where dry sites have a higher percentage of sand content in the soil than mesic sites (Table S2; Figures S1 and S2). Sites also varied in their topography and vegetation communities (Appendix S1). Sites were accessed with permission from the Prairie Enthusiasts Empire-Sauk Chapter, the Southern Wisconsin Bird Alliance, the University of Wisconsin-Madison Arboretum (2020–2011), and the Wisconsin Department of Natural Resources State Natural Areas Program (SNA20-18).

At each site, we identified areas with similar amounts of a single focal species, allowing us to directly compare the effects of management without the confounding effects of species identity. We chose the common native shrub *Cornus racemosa* Lam. as our focal species because it was present in high abundance at all sites, spreads rapidly via clonal vegetative reproduction, and is a species of management concern. We mapped areas with approximately 20%–60% *C. racemosa* canopy cover ranging from 0.5–1.5 m tall using Avenza Maps v3.9 (Avenza Systems, Toronto, Canada), then randomly selected locations for eight 32-m^2 plots within these areas using a random point generator in ArcMap 10.6 (Esri, Redlands, United States). We established a total of 56 plots, with each of the eight plots at the seven sites separated by at least 2 m. Nested within each plot were two 10-m^2 and two 1-m^2 subplots for a total of 112 subplots of each size across the study (Figure 1).

2.2 | Experimental treatments

Following setup, we applied management interventions at the beginning of each growing season (i.e., 2021–2022; Table S1). We randomly assigned two plots at each site to one of four treatment groups

TABLE 1 Study sites fall along a natural moisture gradient, primarily characterized by soil sand content.

Site	Ownership	Coordinates	Size (ha)	Sand content (%)
Black Earth Rettenmund State Natural Area (BE)	The Prairie Enthusiasts[a]	43.139107 N, 89.773512 W	6.88	65.2
Oliver Prairie State Natural Area (OP)	University of Wisconsin-Madison Arboretum[b]	42.684028 N, 89.500793 W	1.62	32.0
Empire Prairies State Natural Area Hauser Road Unit (HR)	The Prairie Enthusiasts[a]	43.259394 N, 89.437066 W	18.21	30.5
Faville Prairie State Natural Area (FP)	University of Wisconsin-Madison Arboretum[b]	43.148796 N, 88.877923 W	35.21	27.5
Curtis Prairie (CP)	University of Wisconsin-Madison Arboretum[b]	43.038499 N, 89.430762 W	29.54	25.0
Snapper Prairie State Natural Area (SP)	Southern Wisconsin Bird Alliance[c]	43.162540 N, 88.889233 W	12.14	22.8
York Prairie State Natural Area (YP)	Wisconsin Department of Natural Resources[d]	42.850566 N, 89.790356 W	31.16	18.2

[a]https://www.theprairieenthusiasts.org/.
[b]https://arboretum.wisc.edu/.
[c]https://swibirds.org/.
[d]https://dnr.wi.gov/.

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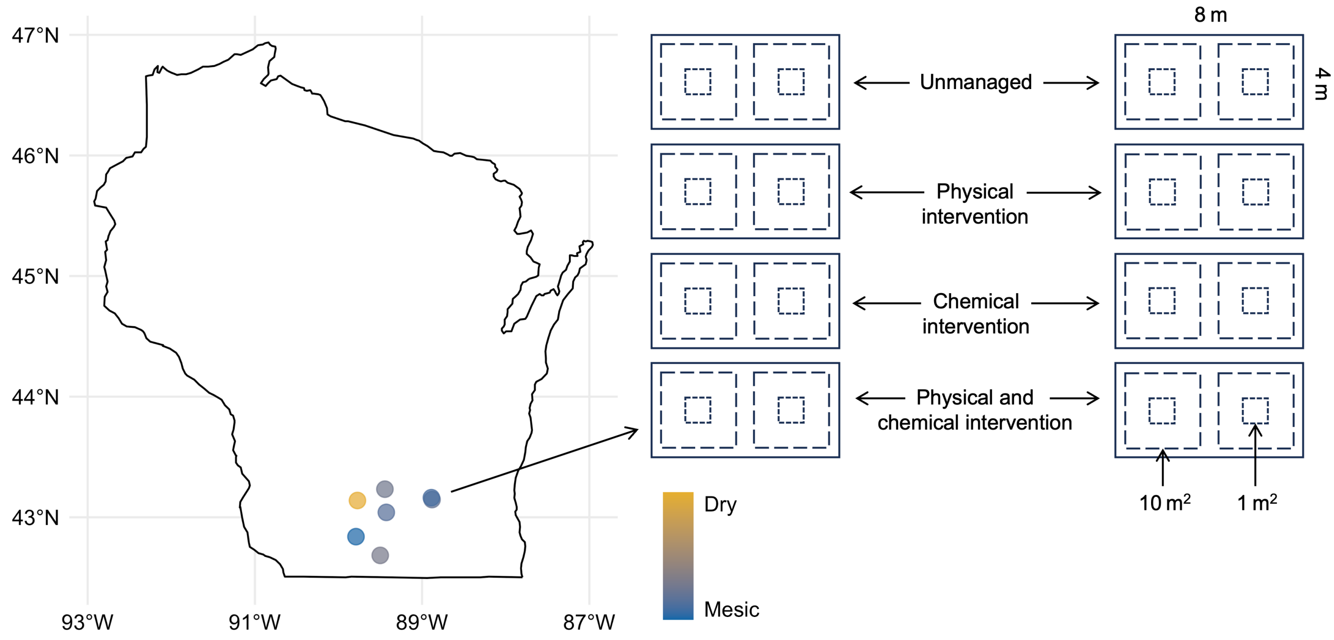

FIGURE 1 Map of study sites in southern Wisconsin (left). Sites fall along a natural moisture gradient, where yellows represent higher soil sand content and blues lower. Experimental design was fully replicated at each study site (right). We established eight 32-m^2 experimental plots (solid lines) randomly placed within patches of *Cornus racemosa*. Each plot contained two nested 10-m^2 (large dashes) and 1-m^2 (small dashes) subplots. We randomly applied one of four woody management interventions to each plot.

(i.e., unmanaged, physical intervention, chemical intervention, and both physical and chemical intervention; Figure 1) and ensured there were no statistically significant differences between treatments in the starting conditions of interest (Figure S3). Unmanaged plots received no management intervention for the duration of the study, other than fire. For physical interventions (both with and without chemical intervention, i.e., cut-stem herbicide and cut stems), all aboveground woody plant biomass (including woody species other than *C. racemosa*, if present; Table S4) was cut to approximately 2 cm using hand clippers. For the combined physical and chemical interventions (i.e., cut-stem herbicide), exposed cut stems were immediately treated after clipping with a 20% Triclopyr 4 (Alligare, Opelika, United States) in oil surfactant penetrant and basal bark oil (Helena Agri-Enterprises, Collierville, United States) solution using a spot applicator. For the chemical (only) interventions (i.e., foliar herbicide), leaves were sprayed with a 5% Triclopyr 3 (Alligare) in water solution using a carefully aimed hand-held fine-mist sprayer.

All sites were burned in the dormant season (November–April) before both the first and second treatment applications (Tables S1 and S3). Our goal was to ensure fire top-killed the woody species within our plots before management interventions, so in the few instances where this did not naturally occur, we revisited plots after fire with a modified blowtorch and heat-treated stems to ensure the meristematic tissue was damaged (following Meunier et al., 2021). This was necessary at two of our sites in four total plots spread across three of the four treatment groups (two unmanaged, one physical intervention, and one combined physical and chemical intervention). We also added seeds to a randomly assigned subplot in each plot in the spring following the first fire (i.e., 2021; Appendix S2). Thus far, we have observed no seedling establishment from this overseeding treatment, so reported changes to the herbaceous community are presumably from vegetative spread.

2.3 | Data collection

To assess the effectiveness of our experimental treatments, we collected woody plant cover data annually (i.e., 2020–2022; once pretreatment, once following one management application, and once following two management applications in two successive years) in mid-August by visually estimating percent cover to the nearest whole percent of all woody species in both the 1- and 10-m^2 subplots. For all cover estimates, we counted vegetation that intersected with any part of the plot and allowed species to overlap, so total cover could exceed 100%. We also collected abundance data of *C. racemosa* twice annually by recording the number and height of ramets in the 10-m^2 subplots. We took measurements in late May, capturing abundance after fire but before that season's management intervention, and again in mid-August, capturing abundance near the end of the growing season and following management. Clustering of stems within a ramet was usually clearly defined, but if it was not, densely packed stems within 10 cm of one another were counted as one.

We measured percent openness of the total vegetation canopy as a proxy for light availability using hemispherical photos taken at ground level. We levelled the camera and took all photos in diffuse light conditions annually in mid-August, then quantified canopy openness using Gap Light Analyser (Frazer et al., 1999). We also installed 56 TMS-4 dataloggers (Wild et al., 2019) in the center of one of the two subplots to measure temperature 15 cm above the soil surface and soil moisture 6 cm below the soil surface at 15-min intervals year-round. Dataloggers were installed after setup and remained in the field for the duration of the study (i.e., 2021–2022). From these data, we calculated average daily June, July, and August (JJA) means and 1st and 99th percentiles of temperature and soil moisture in each year.

Finally, we counted the number of herbaceous species in the 1-m^2 subplot to measure richness annually in late August. We also visually estimated the percent cover of the graminoid and forb functional groups in the 1-m^2 subplots to the nearest whole percent. We sampled the herbaceous community during peak flowering for most of the species in this ecosystem, which allows species to be confidently distinguished from one another but may lead to under-representation of ephemeral early-season species (~13% of species, estimated from Cochrane et al., 2006).

2.4 | Data analyses

To test the effects of management on woody plant persistence, abiotic habitat conditions, and herbaceous community composition, we built linear mixed effect models (LMMs) and generalized linear mixed effect models (GLMMs) using the fixed effects of management type (i.e., chemical intervention, physical intervention, or their combination), management repetition (i.e., one or two applications), and soil sand content. We chose the percentage of sand content in the soil as a meaningful measure of plot-level soil characteristics following a principal components analysis of five soil characteristics known to affect soil moisture (i.e., percent sand, silt, and clay, percent organic matter, and bulk density; Gupta & Larson, 1979; Figure S1). We investigated the possibility of an interaction between management type and soil sand content, but given the interaction was a significant predictor only for soil moisture and increased model complexity without adding much explanatory power (Table S5), we chose to interpret only the main effects of management type and soil sand content (Table 2). We also did not include a term for pre-treatment starting conditions as these were not significantly different among management types (Figure S3) and some were correlated with sand content (Figure S4). Each model included random intercepts for site and plot to account for the nested design of our experiment.

We fit separate models for *C. racemosa* cover, *C. racemosa* ramet count, canopy openness, air temperature, soil moisture, herbaceous species richness, graminoid cover, and forb cover. Percent cover of *C. racemosa* was highly correlated with percent cover for all woody species across years and scales (Figure S5), so we did not run separate mixed models for these. Similarly, the number of *C. racemosa* ramets was correlated with average ramet height across years and seasons (Figure S6), so we again did not run separate mixed models for these. While *C. racemosa* cover, *C. racemosa* ramet count, and canopy openness are correlated (Figure S7), we still chose to run these as separate models because their correlation weakened with repeated management interventions (Figure S7) and they represent different aspects of woody vegetation persistence and abiotic habitat conditions (i.e., dominance, abundance, and light availability, respectively). To account for non-normal, zero-inflated, and over-dispersed *C. racemosa* cover and ramet count data, we used GLMMs with a negative binomial distribution. The canopy openness, air temperature, soil moisture, and herbaceous functional group cover models were run as LMMs with Gaussian distributions, and the herbaceous community richness model was run as a GLMM with a Poisson distribution. We ran all models using the lme4 package 1.1.35.1 (Bates et al., 2015) in R 4.3.1 (R Core Team, 2023) and used the lmerTest package 3.1.3 (Kuznetsova et al., 2017) to calculate test statistics and *p*-values based on Satterthwaite (LMMs) and Laplace (GLMMs) approximations. We used the emmeans package 1.8.9 (Lenth, 2022) to calculate estimated marginal means for each management type and repetition grouping and the rsq package 2.6 (Zhang, 2022) to calculate the proportion of variation explained by the fixed effects in each model. Finally, to test for indirect effects of management inventions on abiotic habitat conditions mediated by woody vegetation persistence and on herbaceous community composition mediated by abiotic habitat conditions and woody vegetation persistence, we built a piecewise structural equation model from eight linear mixed-effects models using the piecewiseSEM package 2.3.0 (Lefcheck, 2016) and the nlme package 3.1-164 (Pinheiro et al., 2023; Appendix S3). The significance for all analyses was determined at an alpha of 0.05.

3 | RESULTS

Percent cover of *C. racemosa* was reduced by chemical intervention (Table 2), which led, on average, to 16% less *C. racemosa* cover than physical intervention or no management (Figure 2). The number of *C. racemosa* ramets was also reduced by chemical intervention, however, we additionally found a main effect of management repetition (Table 2). On average, chemical intervention led to 58 fewer ramets than physical intervention or no management, and a second application of chemical intervention led to three fewer ramets than a single application (Figure 2).

Canopy openness was raised by chemical intervention (Table 2). Combined chemical and physical intervention led to 24% greater openness on average than unmanaged canopies after the first application but did not differ from other management treatment groups (Figure 3). Across growing seasons, daily air temperature and soil moisture varied greatly (Figures S8 and S9). Average JJA air temperature was raised by physical and chemical intervention and their combination, as well as management repetition (Table 2). All interventions were 1.6°C warmer on average after the first application than air temperatures in unmanaged plots following the second application (Figure 3). Average JJA volumetric soil moisture was not affected by management type but was by management repetition (Table 2). The greatest difference in soil moisture was between the combined chemical and physical interventions after one application and unmanaged plots following the second application, the latter being 15% wetter than the former on average (Figure 3). Average daily 1st and 99th percentiles of temperature and moisture responded similarly to management type and repetition as the averages (Table S6; Figure S10).

TABLE 2 Summary of mixed model results testing the effects of management type, management repetition, and soil sand content on woody plant persistence, abiotic habitat conditions, and herbaceous community composition. Results show the estimated coefficient (β), test statistic (z or t), and significance (p) for each fixed effect, along with the overall variance explained by the fixed effects (r^2) for each model.

Model and fixed effects	β	z or t	p	r^2
Cornus racemosa cover				0.278
Chemical intervention	−2.977	−10.516	<0.001***	
Physical intervention	0.006	0.027	0.978	
Chemical + physical intervention	0.002	0.004	0.997	
Second application	0.118	1.501	0.133	
Soil sand content	−0.001	−0.117	0.907	
Number of *C. racemosa* ramets				0.414
Chemical intervention	−2.311	−9.309	<0.001***	
Physical intervention	0.074	0.314	0.754	
Chemical + physical intervention	0.088	0.254	0.800	
Second application	−0.602	−6.062	<0.001***	
Soil sand content	0.009	1.505	0.132	
Canopy openness				0.239
Chemical intervention	15.914	3.556	<0.001***	
Physical intervention	5.405	1.199	0.236	
Chemical + physical intervention	1.294	0.204	0.839	
Second application	−3.164	−1.358	0.177	
Soil sand content	0.256	1.338	0.193	
Average JJA air temperature				0.427
Chemical intervention	0.562	4.744	<0.001***	
Physical intervention	0.390	3.130	0.003**	
Chemical + physical intervention	−0.433	−2.495	0.016*	
Second application	−1.077	−20.916	<0.001***	
Soil sand content	−0.002	−0.268	0.790	
Average JJA soil moisture				0.338
Chemical intervention	−2.052	−1.094	0.277	
Physical intervention	−2.304	−1.173	0.244	
Chemical + physical intervention	0.935	0.342	0.733	
Second application	11.967	8.729	<0.001***	
Soil sand content	0.002	0.025	0.980	
Herbaceous species richness				0.298
Chemical intervention	−0.070	−0.944	0.345	
Physical intervention	0.020	0.282	0.778	
Chemical + physical intervention	0.125	1.220	0.222	
Second application	0.044	1.027	0.304	
Soil sand content	0.013	3.969	<0.001***	
Graminoid cover				0.045
Chemical intervention	4.440	0.863	0.393	
Physical intervention	−8.495	−1.643	0.107	
Chemical + physical intervention	9.215	1.266	0.212	
Second application	−2.269	−0.987	0.325	
Soil sand content	−0.141	−0.605	0.549	

(Continues)

TABLE 2 (Continued)

Model and fixed effects	β	z or t	p	r^2
Forb cover				0.070
Chemical intervention	−9.878	−1.637	0.109	
Physical intervention	−0.761	−0.126	0.901	
Chemical + physical intervention	9.960	1.167	0.249	
Second application	−5.067	−2.324	0.021*	
Soil sand content	0.465	1.900	0.072	

Note: Significant predictors are indicated by asterisks where: *$p<0.05$, **$p<0.01$, and ***$p<0.001$.

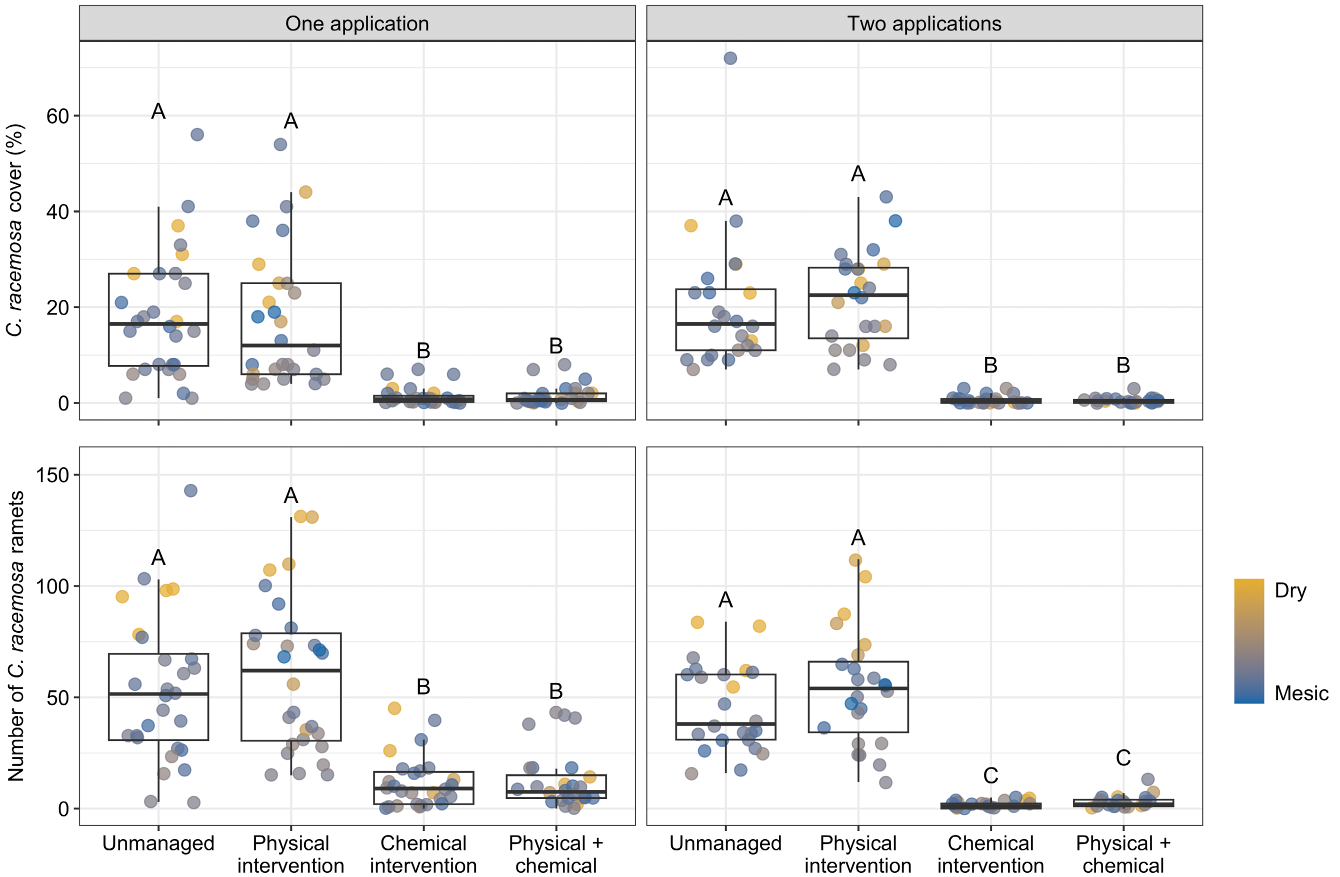

FIGURE 2 Percent cover (above) and number of ramets (below) of *Cornus racemosa* across management interventions after one (left) and two (right) applications. Each point represents a subplot, where yellows represent higher soil sand content and blues lower. Box plots show the median (middle line), interquartile range (box), and one and half times the interquartile range (whiskers). Letters indicate significantly different management type and repetition group means.

Herbaceous species richness was affected only by sand content (Table 2; Figure 4). However, the magnitude of effect sand content is predicted to have on richness is small; for every 77% increase in sand content, richness grows by just one. Graminoid cover was not significantly affected by any of the modelled predictors (Table 2; Figure 4). Forb cover was affected only by management repetition (Table 2), but this did not lead to differences in estimated marginal means (Figure 4).

The piecewise SEM indicated that there were indirect effects of management interventions on abiotic habitat conditions mediated by woody vegetation persistence and other abiotic habitat conditions and on herbaceous community composition mediated by abiotic habitat conditions (Table S7; Figure S11). Both canopy openness and average JJA air temperature were positively affected by number of *C. racemosa* ramets and negatively affected by *C. racemosa* cover, while average JJA soil moisture was negatively affected by canopy openness and average JJA air temperature. Graminoid cover was positively affected by average JJA air temperature, while forb cover was negatively affected by canopy openness. However, the variances explained by the fixed effects of each component model were relatively low (Figure S11), and the overall fit of the SEM was poor (Fisher's $C=35.023$, $p=0.068$).

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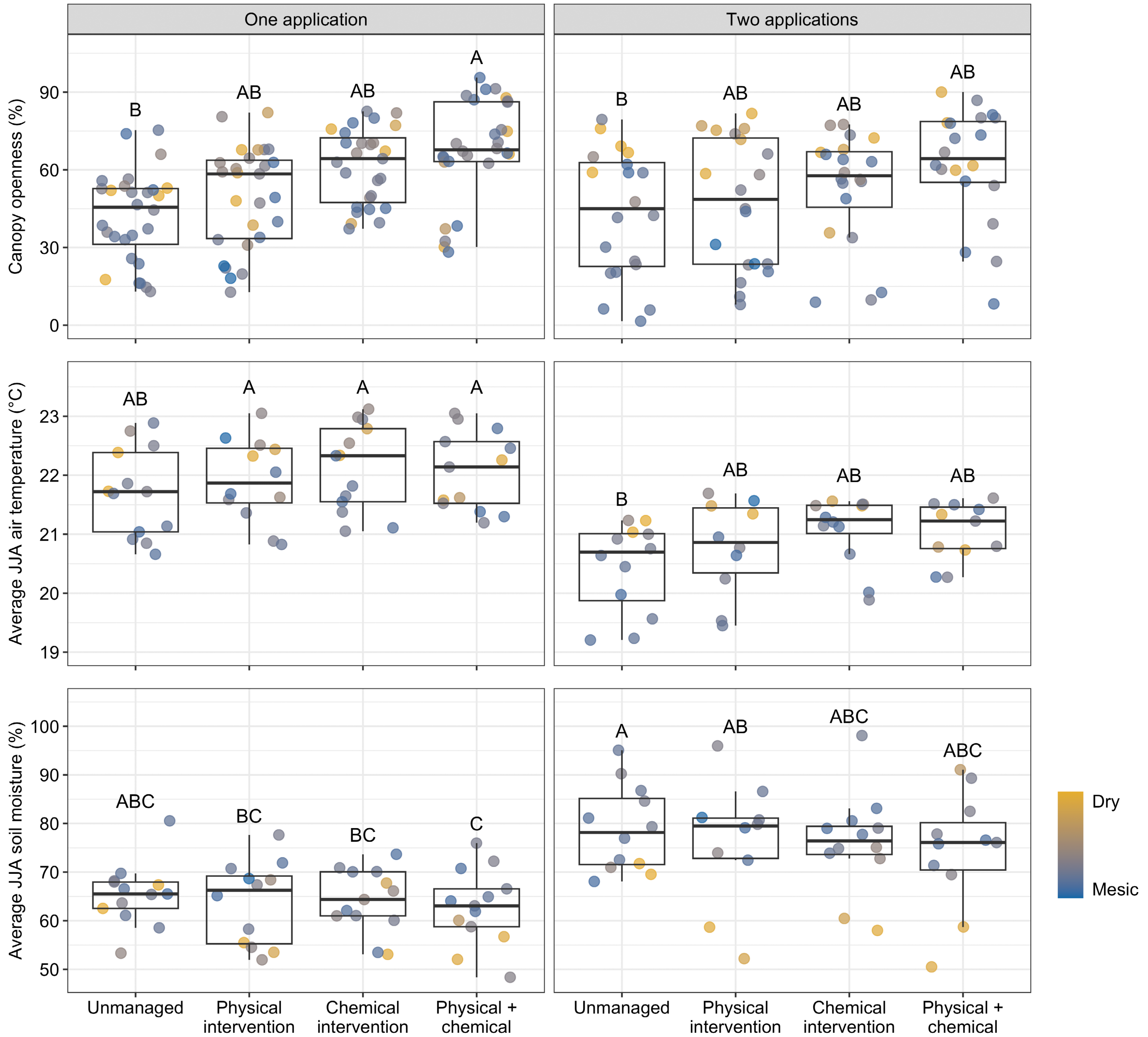

FIGURE 3 Canopy openness (above) and average June, July, and August temperature (middle) and soil moisture (below) across management interventions after one (left) and two (right) applications. Each point represents a subplot, where yellows represent higher soil sand content and blues lower. Box plots show the median (middle line), interquartile range (box), and one and half times the interquartile range (whiskers). Letters indicate significantly different management type and repetition group means.

4 | DISCUSSION

Our experiment demonstrates that: (1) chemical intervention is most effective at reducing woody plant persistence, and a second application reduces abundance more than one application alone (Figure 2), (2) any intervention can alter abiotic habitat conditions, matching expected historical conditions, with the combination of physical and chemical interventions having the greatest effects (Figure 3), and (3) management interventions do not affect herbaceous community composition in the short term (Figure 4). This matched our first and, partially, our second hypothesis, but not our third.

The support we found for our first two hypotheses can be attributed to the expected effects of physical versus chemical management on aboveground structure versus belowground function. Reduction in *C. racemosa* cover and abundance was likely linked to increased mortality with chemical intervention. This is a particularly important mechanism of control for resprouting woody species such as *C. racemosa*, as without mortality, ramets may repeatedly continue to regrow (Bellingham & Sparrow, 2000; Bond & Midgley, 2001). Anecdotally, physical intervention appeared to increase the resprouting vigour of *C. racemosa*, consistent with findings that mowing, burning, and other management practices that alter only aboveground structure without affecting belowground function may

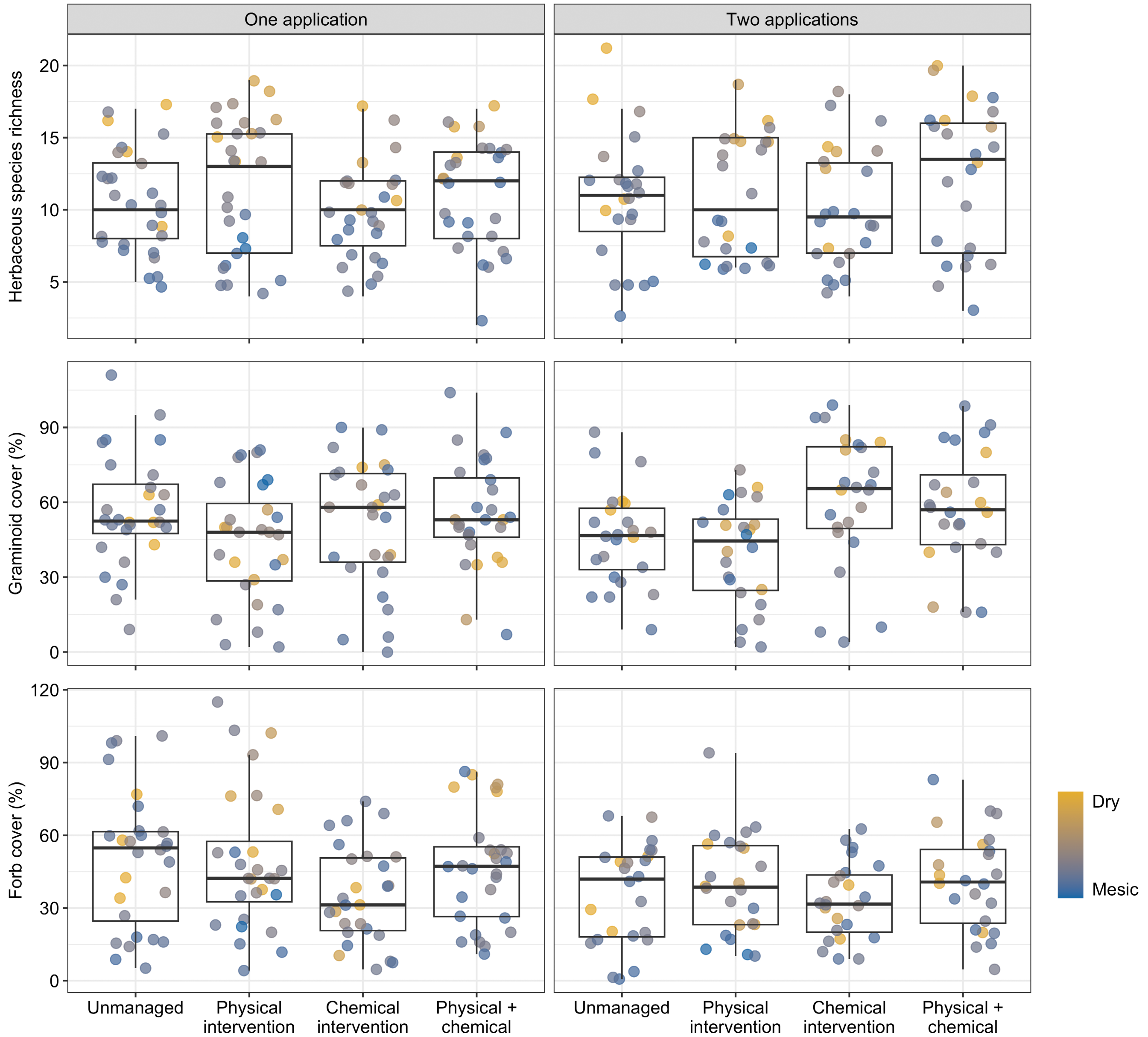

FIGURE 4 Herbaceous species richness (above) and graminoid (middle) and forb (below) cover across management interventions after one (left) and two (right) applications. Each point represents a subplot, where yellows represent higher soil sand content and blues lower. Box plots show the median (middle line), interquartile range (box), and one and half times the interquartile range (whiskers). There were no significantly different management type and repetition group means.

promote persistence or even further encroachment of resprouting woody species (Clark & Wilson, 2001; Eldridge & Ding, 2021; Miller et al., 2017). This may be partially attributed to clonal integration allowing ramets outside the study plots to continue aboveground resource acquisition (e.g., photosynthesis) and transfer resources (e.g., carbon) to resprouting ramets within plots (Liu et al., 2016). Thus, physical intervention may be more effective at controlling species that are non-clonal and invest less in belowground versus aboveground biomass (e.g., non-resprouters; Pausas et al., 2015).

Chemical intervention was also necessary to increase overall canopy openness and thus light availability. However, air temperature increased with physical intervention, both with and without chemical intervention, consistent with intact woody vegetation inducing cooler mid-summer conditions (Breshears et al., 1998). In this case, altering aboveground structure was enough to temporarily return abiotic habitat conditions to those expected of intact grasslands, but with only physical intervention, these effects waned later in the season due to regrowth of the aboveground structure (Figure S8).

We did not find support for our third hypothesis in the short term, despite evidence of changes to woody vegetation persistence and abiotic habitat conditions that would be expected to benefit the herbaceous community. This is consistent with a recent global meta-analysis by Ding and Eldridge (2023) that suggests that woody plant management only reverses about half of the observed changes to herbaceous community composition that follow encroachment. This same study also suggests that management outcomes change through time, as feedbacks result in different short- and long-term effects. Without changes to the feedbacks that maintain woody plant persistence in the short term, it is unlikely that compositional changes will be revealed in the long term. Since we did observe short-term effects of management on some of the conditions involved in woody encroachment feedbacks, compositional effects may occur in the long term. Additionally, richness and functional group cover are fairly coarse estimates of herbaceous community composition. More nuanced measures, such as species cover, species turnover, and diversity metrics, might respond to management on shorter timescales.

Surprisingly, soil moisture did not affect management outcomes. Globally across many different grassland ecosystems, there is evidence that management is more effective and leads to greater structural changes at mesic sites (Ding & Eldridge, 2019). This may be due to the common observation that woody plants have higher cover and abundance at mesic sites (e.g., Ratajczak et al., 2014), however, this observation was only partially supported by our pre-treatment data (Figure S4). In ecosystems where the range of variation in soil moisture is low, moisture may not effect encroachment or management. Regardless, management outcomes are highly site- and system-specific, so more research is needed to understand what aspects of environmental heterogeneity drive variation in outcomes within and between regions.

To better manage encroached grasslands, there remains a need to better understand how management alters feedbacks, however, we often assess only woody plant persistence and herbaceous community composition without considering abiotic habitat conditions that may link the two. Research can help guide the effectiveness of the work orchestrated globally to conserve and restore grasslands, especially when managers are resource-limited (Cortina-Segarra et al., 2021; Peters et al., 2018).

4.1 | Management recommendations

Given limited resources, our findings suggest that management should focus on chemical intervention for the greatest effects on woody plant persistence and abiotic habitat conditions. We observed an added effect of a second chemical intervention, which may be a mechanism to promote longer-lasting effects. However, chemical intervention may impact non-target organisms, such as the herbaceous community, and, moreover, may not always be a feasible solution due to ecological, safety, and legal concerns (e.g., herbicide bans, *as per* the European Union Habitats Directive). Alternative approaches include reintroduction of disturbance (e.g., fire, grazing), which can prevent continued encroachment but typically does little to reduce woody vegetation (Judge, 2020; Miller et al., 2017), or belowground physical intervention (e.g., trenching and uprooting; Smith et al., 2013; Utaile et al., 2023), which can be time-consuming and disturb herbaceous species. Though we did not observe promising effects of aboveground physical intervention on its own, and anecdotally observed it increase resprouting vigour, it may be more effective if used both mid-summer (rather than at the onset of the growing season) and across many years (R. Hoffman, personal communication, 25 May 2023), which needs to be tested. Finally, managers in our region can anticipate similar management outcomes at sites with different moisture availability.

AUTHOR CONTRIBUTIONS

Both authors contributed to project conceptualization. Katherine T. Charton led investigation, data collection and curation, formal analysis, visualization, and writing of the initial manuscript draft. Ellen I. Damschen contributed to manuscript editing and review and provided lab infrastructure and supervision. Both authors are researchers at a U.S.-based university and have interests in the conservation, restoration, and management of fire-adapted grasslands. The authorship team represents the region of study, as we live, work, and recreate in the area, contributing to appropriate interpretation of results. Our research was discussed with local managers to seek feedback on questions, methods, and interpretation.

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This research took place on ancestral Ho-Chunk land. The Ho-Chunk were forced to cede their territory in 1832, including their rights to hunt, fish, and gather on their lands, and decades of ethnic cleansing followed. The history of colonization informs our work and is integral to our understanding of grassland ecology in North America, as Indigenous burning practices maintained and stewarded these ecosystems for millennia. The relationships we investigate here are held as Traditional Ecological Knowledge, and we are not the first to discover them. We recognize our collective responsibility to acknowledge the continuing presence and importance of Indigenous peoples and knowledge in this region. We thank our collaborators at the Prairie Enthusiasts Empire-Sauk Chapter, the Southern Wisconsin Bird Alliance, the University of Wisconsin-Madison Arboretum, and the Wisconsin Department of Natural Resources State Natural Areas Program. We are particularly grateful to Katherine and Thomas Brock, Nathan Fayram, Michael Hansen, Drew Harry, Richard Henderson, Bradley Herrick, Randy Hoffman, Christy Lowney, Thomas Meyer, and Karen Oberhauser. We also thank field technicians Sam Ahler, Hannah Davidson, Cailee Peterson, Rosalie Powell, Eliza Soczka, and Abigail Widell. Thanks to the prescribed fire crews that burned our study sites in alignment with our research needs and to Tim Kuhman who helped complete top-kill blowtorch treatments. The final version of this manuscript was greatly improved by thoughtful peer review from Pieter De Frenne, Norbert Hölzel, and an additional anonymous reviewer. This research was supported by the National Science Foundation (DEB-1754764), the University of Wisconsin-Madison Arboretum, and the University of Wisconsin-Madison Department of Integrative Biology.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data are available via the Environmental Data Initiative: https://doi.org/10.6073/pasta/ed2ee3aa27fa90aebde48a83b571a1c4 (Charton & Damschen, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Principle components analysis of plot-level soil characteristics known to affect soil moisture.

Figure S2. Study sites within a soil texture triangle representing the percentage of sand, silt, and clay in the soil.

Figure S3. Differences in pre-treatment starting conditions among treatments of *Cornus racemosa* Lam. cover (upper left), *C. racemosa* ramets (middle left), canopy openness (lower left), herbaceous species richness (upper right), graminoid cover (middle right), and forb cover (lower right).

Figure S4. Correlation between soil sand content and pre-treatment starting conditions of plots *Cornus racemosa* Lam. cover (upper left), *C. racemosa* ramets (middle left), canopy openness (lower left), herbaceous species richness (upper right), graminoid cover (middle right), and forb cover (lower right).

Figure S5. Correlation between *Cornus racemosa* Lam. and all woody species covers across years (pre-treatment, 2020, left; post-one treatment application, 2021, middle; and post-two treatment applications, 2022, right) and scales (1-m^2 subplot, above; and 10-m^2 subplot, below).

Figure S6. Correlation between *Cornus racemosa* Lam. ramets and average ramet height across years (post-one treatment application, 2021, left; and post-two treatment applications, 2022, right) and seasons (early-, above; and late-season, below).

Figure S7. Correlation between *Cornus racemosa* Lam. cover, *C. racemosa* ramets, and canopy openness across years (pre-treatment, 2020, top left; post-one treatment application, 2021, top right; and post-two treatment applications, 2022, bottom left).

Figure S8. Time series of June, July, and August average daily air temperature across four experimental management interventions after one (2021; left) and two (2022; right) management applications.

Figure S9. Time series of June, July, and August average daily soil moisture across four experimental management interventions after one (2021; left) and two (2022; right) management applications.

Figure S10. Average daily June, July, and August 1st (top) and 99th (second from top) percentiles of temperature and 1st (third from top) and 99th (bottom) percentiles of soil moisture across management interventions after one (left) and two (right) applications.

Figure S11. Piecewise structural equation model depicting the direct effects of management interventions on woody vegetation persistence (*Cornus racemosa* Lam. cover, number of *C. racemosa* ramets), woody vegetation persistence on abiotic habitat conditions (canopy openness, average July, July, and August [JJA] air temperature, average JJA soil moisture), and both woody vegetation persistence and abiotic habitat conditions on herbaceous community composition (herbaceous species richness, graminoid cover, forb cover).

Table S1. Study site management and experimental treatment history.

Table S2. Average study site soil characteristics.

Table S3. Average study site post-fire percent of vegetation consumed, litter depth, and visible bare soil.

Table S4. Full list of woody plant species treated within management plots.

Table S5. Summary of mixed model results testing the effects of management type, management repetition, soil sand content on woody plant persistence, abiotic habitat conditions, and herbaceous community composition, including an interaction term between management types and soil sand content.

Table S6. Summary of mixed model results testing the effects of management type, management repetition, and soil sand content on the 1st and 99th percentiles of June, July, and August air temperature and soil moisture.

Table S7. Summary of piecewise structural equation model results.

Appendix S1. Detailed descriptions of study site topography and vegetation communities.

Appendix S2. Detailed information about overseeding treatment.

Appendix S3. Detailed piecewise structural equation model methodology.

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