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Are they two seeds in a pod? Comparing seed rain recovery using artificial grass carpets versus sticky traps in grasslands.

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Abstract:	Seed dispersal is a critical process for plant community assembly, however natural rates of seed arrival are rarely quantified when compared to other assembly mechanisms, especially in herbaceous communities. This discrepancy arises from the difficulty in recovering small seeds. Here we compare the utility of artificial grass carpet squares ('artificial grass') for capturing seed rain to classic 'sticky trap' methods. While artificial grass has been used in Arctic systems, we examine its efficacy in temperate grasslands. We placed paired sticky traps and artificial grass squares in two grassland ecosystems. We added known numbers of seeds of multiple species to each trap, and recovered seeds at one week, one month and two month intervals. We found that while both trap types lost seeds through time at similar rates, sticky traps recovered more small seeds while artificial grass recovered more large seeds. Overall sticky traps retained more seeds, but recovering seeds was difficult, and recovery was hindered by debris stuck to the traps. Alternatively, seeds recovered from artificial grass could be handled easily and retained for long-term storage. We encourage artificial grass traps for broad adoption of measuring seed rain in grasslands to increase links between theoretical and empirical community ecology.
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To the Editorial Board,

It is my pleasure to submit our manuscript titled “Are they two seeds in a pod? Comparing seed rain recovery using artificial grass carpets versus sticky traps in grasslands” on behalf of my coauthors to Applications in Plant Sciences as an Application Article. We were thrilled that our inquiry about our manuscript to the special issue on “Quantifying plant and fungal dispersal: New methods from multiple discipline” was met with enthusiasm.

Plant community assembly is a critical concept for community ecologists, and the role that competition, resource availability, and herbivory play in structuring communities have been the foci of empirical research for many years. However, the process of seed dispersal still remains vastly understudied as an assembly mechanism compared to these other processes. Much of the difficulty in understanding the role dispersal plays for plant communities, especially in grassland ecosystems where seeds are very small, is the difficulty in capturing and identifying seeds. Here we tested the viability of two methods for measuring seed rain in grasslands, the standard sticky trap method vs the artificial grass carpet method. The artificial grass method is borrowed from the Arctic, where it has been successful at recovering seed rain, but has yet to be implemented broadly in grasslands. We placed known numbers of seeds that varied in mass on both sticky and artificial grass traps at two temperate grassland sites and recovered seeds one week, one month and two months after initial deployment. We found that overall both methods successfully recovered seeds. While we recovered a lower proportion seeds on artificial grass as compared to sticky traps, the artificial grass traps captured seeds over a longer time period, and seeds recovered from the grass traps could be saved for later identification via germination trials. In addition, the artificial grass traps represent effective dispersal, in that seeds recovered from this method are those that have survived consumption and secondary dispersal and are thus likely to germinate in that given area. Therefore, we encourage the use of artificial grass traps as a successful method of measuring seed rain in grasslands broadly.



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Thank you for your consideration.

A handwritten signature in black ink, appearing to read "Lauren Sullivan".

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Running head: Sullivan et al. Grassland seed rain methods comparison

Are they two seeds in a pod? Comparing seed rain recovery using artificial grass carpets versus sticky traps in grasslands.

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1 ABSTRACT

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3 seed arrival are rarely quantified when compared to other assembly mechanisms, especially
4 in herbaceous communities. This discrepancy arises from the difficulty in recovering small
5 seeds. Here we compare the utility of artificial grass carpet squares ('artificial grass') for
6 capturing seed rain to classic 'sticky trap' methods. While artificial grass has been used in
7 Arctic systems, we examine its efficacy in temperate grasslands. We placed paired sticky
8 traps and artificial grass squares in two grassland ecosystems. We added known numbers of
9 seeds of multiple species to each trap, and recovered seeds at one week, one month and two
10 month intervals. We found that while both trap types lost seeds through time at similar
11 rates, sticky traps recovered more small seeds while artificial grass recovered more large seeds.
12 Overall sticky traps retained more seeds, but recovering seeds was difficult, and recovery was
13 hindered by debris stuck to the traps. Alternatively, seeds recovered from artificial grass
14 could be handled easily and retained for long-term storage. We encourage artificial grass
15 traps for broad adoption of measuring seed rain in grasslands to increase links between
16 theoretical and empirical community ecology.

¹⁷ INTRODUCTION

¹⁸ Dispersal is a critical process that structures populations and communities, linking local
¹⁹ patch-scale dynamics to regional landscape level processes (Amarasekare, 2003; Snyder &
²⁰ Chesson, 2003; Leibold & Chase, 2017). Within vegetative communities, seed dispersal is
²¹ one of the primary mechanisms of arrival to new habitats, allowing species to track changing
²² environmental conditions and promoting landscape connectivity (Cubína & Aide, 2001; Sim-
²³ berloff, 2009; Beckman & Sullivan, 2023). Dispersal also plays a critical role in assembly and
²⁴ long-term diversity patterns, such as maintaining source-sink dynamics (Mouquet & Loreau,
²⁵ 2003; Craig *et al.*, 2025), allowing long-term species co-existence (Snyder & Chesson, 2003;
²⁶ Berkley *et al.*, 2010), and maintaining genetic diversity in populations (Jordano, 2017). A
²⁷ species' dispersal ability also has direct management implications, often increasing native
²⁸ diversity after restoration, or alternatively, facilitating the invasion of non-native species
²⁹ (Von Der Lippe & Kowarik, 2007; Sperry *et al.*, 2019; Brudvig *et al.*, 2009). Despite its
³⁰ importance as a critical process for populations and communities (Vellend, 2010; Schupp &
³¹ Fuentes, 1995; Levine & Murrell, 2003), dispersal is notoriously difficult to quantify empir-
³² ically (Beckman & Sullivan, 2023; Bullock *et al.*, 2006). These methodological challenges
³³ have created a gap between our theoretical understanding of the importance of dispersal
³⁴ versus our empirical understanding and use in applied settings (Bolker *et al.*, 2003), mak-
³⁵ ing dispersal arguably the least empirically understood mechanism of community assembly
³⁶ (HilleRisLambers *et al.*, 2012; Vellend, 2016).

³⁷ One way to measure seed dispersal is by estimating seed rain, or the seeds that fall into
³⁸ a given area (Arruda *et al.*, 2018a). While this method captures only a single point in the
³⁹ dispersal trajectory of a seed (the settlement phase - Travis *et al.* 2012), it is arguably the
⁴⁰ most important phase to understand for plant community ecology, as it provides information
⁴¹ on the number and type of seeds that arrive to a specific location. If seeds are recovered

42 before post-dispersal seed predation or secondary dispersal occurs, then this is considered
43 a measure of *primary dispersal*. However, if seeds that fall to a given area are then lost
44 to these processes this measure of seed arrival is considered to be *effective dispersal* as it
45 constitutes the seeds that have a chance to germinate and establish in a given area (Nathan
46 & Muller-Landau, 2000). Quantifying seed rain as a measure of seed arrival across many
47 different natural environments is critical for building strong links between plant community
48 ecology experiments and theory (Myers & Harms, 2009).

49 Seed rain is typically measured through the use of seed traps placed on or near the
50 ground in an ecosystem of interest (Cottrell, 2004; Kollmann & Goetze, 1998). Seed traps
51 are commonly used in forest systems to measure seed rain (Cottrell, 2004; Rogers *et al.*, 2017;
52 Huanca Nuñez *et al.*, 2021; Piotto *et al.*, 2019), and when there are known parents, dispersal
53 trajectories can be calculated using inverse modeling (Wälder *et al.*, 2009; Nathan & Muller-
54 Landau, 2000). Seed rain measurements, however, are much less common in ecosystems
55 with predominantly herbaceous communities (e.g. grasslands, tundra), with only a handful
56 of studies estimating seed rain in grasslands specifically (Rabinowitz & Rapp, 1980; West &
57 Durham, 1991; Schott & Hamburg, 1997; Kettenring & Galatowitsch, 2011; Willand *et al.*,
58 2015; Wynne *et al.*, 2024). This dearth of knowledge on herbaceous seed rain likely occurs
59 because recovering small herbaceous seeds is challenging (Myers & Harms, 2009) and seed
60 identification resources for even common species' can be scarce (Wynne *et al.*, 2024). The
61 main method for capturing seed rain in grasslands is via sticky traps, where a flat surface
62 (often a petri dish) is sprayed with a sticky substance, and seeds that falls onto the surface
63 are captured and later recorded (Rabinowitz & Rapp, 1980). Sticky traps present multiple
64 practical problems, including that they have to be replaced frequently because the sticky
65 surface can become completely covered in leaves and debris, thereby blocking newly fallen
66 seeds from capture. Furthermore, sticky traps are no longer sticky once temperatures fall
67 below freezing, despite this being a critical time for seed dispersal in temperate grasslands

68 (Rabinowitz & Rapp, 1980). Lastly, using recovered seeds from sticky traps for additional
69 work, such as germination trials or trait measurement, is rarely possible as seeds become
70 coated with the sticky residue.

71 An alternative method for measuring seed rain is to use artificial grass carpets. With
72 this method, artificial grass patches are fixed to the ground, seeds are dispersed into traps,
73 and they are caught in artificial grass strands. This method is used to sample seed rain
74 in the Arctic (Molau, 1996; Molau & Larsson, 2000), and provides a potential solution to
75 the many issues that arise with collecting seed rain via sticky traps in grasslands more
76 generally. Artificial grass can remain in the field for long periods of time and still capture
77 seeds, withstand large temperature and hydrologic fluctuations, and collected seeds can be
78 germinated after capture should visual identification not be possible due to lack of seed
79 identification resources (Wolters *et al.*, 2004; Molau, 1996). These features make artificial
80 grass carpets a viable option for seed rain studies in grasslands. For example, recently
81 Wynne et al. 2024 used artificial grass carpets for capturing seed rain in a successional
82 chronosequence of temperate tallgrass prairies and were able to recover ~27,000-124,000
83 seeds per square meter depending on the age of the grassland. Although the artificial grass
84 carpet method appears promising for widespread use for collecting seed rain in grasslands,
85 we currently lack a comparison between this and the sticky trap method to compare their
86 ability to recover seeds and to consider potential biases across methods.

87 Here, we investigate the effectiveness of traditional sticky traps (Tangle-Trap® resin
88 on Plexiglass® Petri plates) as compared to artificial grass traps for measuring seed rain
89 in grasslands. We examined the seed retention efficacy of both methods through time,
90 comparing the proportion of seeds recovered across two temperate grassland ecosystems, a
91 diversity of species, and a range of seed sizes. While traditional sticky traps had a higher
92 recovery rate of smaller seeds, both methods recovered a high proportion of seeds overall,
93 and seeds from artificial turf traps were in better condition for counting, identification,

94 and post-processing measurements. As such, we suggest that artificial turf traps be used
95 for measuring seed rain in grassland communities, especially when it may be beneficial to
96 germinate collected seeds or in remote locations where it is difficult to replace traps frequently
97 (Rabinowitz & Rapp, 1980; Cottrell, 2004). By having robust comparisons of different seed
98 rain capture methods, we can better advance our empirical understanding of dispersal, thus
99 narrowing the current gap between theory and data, and advancing our understanding of
100 the role of dispersal in grassland restoration and conservation.

101 METHODS

102 Study sites and seed mixes

103 We replicated experimental tests of seed capture methods for detecting seed rain in two
104 distinct grassland communities: a shortgrass prairie in northern Colorado, and a tallgrass
105 prairie in central Missouri (Fig. 1A, B).

106 The Colorado (CO) study occurred on private land bordering the Cathy Fromme Prairie
107 Open Space, a 267 ha remnant of native shortgrass prairie. The site is relatively flat, sur-
108 rounded by mature cottonwood trees, and receives approximately 38 cm of precipitation
109 annually (Balok *et al.*, 1995).

110 The Missouri (MO) study occurred on a restored tallgrass prairie owned by the University
111 of Missouri. The prairie was located on campus, and is surrounded by buildings and foot-
112 traffic, and receives approximately 108 cm of annual precipitation (Gu *et al.*, 2015).

113 Experimental design and tests of trap performance

114 We tested the effectiveness of sticky traps versus artificial grass carpets for seed retention
115 through time. Following standard protocol (Rabinowitz & Rapp, 1980; Kollmann & Goetze,

¹¹⁶ 1998; Chabrerie & Alard, 2005), sticky traps consisted of 10 cm x 10 cm Plexiglass plates
¹¹⁷ coated with Tangle-Trap® sticky coating. To compare this standard method to seed carpets,
¹¹⁸ we used 10 cm x 10 cm synthetic lawn turf squares (TrafficMASTER® TruGrass Emerald
¹¹⁹ Artificial Turf) with blade heights between 1.5 to 2.5 cm tall.

¹²⁰ At the two sites, we replicated 10 blocks of paired sticky traps and carpets that we
¹²¹ collected 1 week, 1 month, and 2 months after deployment to examine seed recovery through
¹²² time. We initially deployed all traps on July 10, 2019 in Colorado and July 17, 2019 in
¹²³ Missouri. Each block consisted of three sticky traps and three carpets for a total of 10
¹²⁴ replicates of the two methods for each each time point and each site. When deploying traps,
¹²⁵ we removed any litter or vegetation directly under the traps so that they were placed directly
¹²⁶ on the soil surrounded by natural vegetation (Fig. 1E). We used two ground staples to secure
¹²⁷ opposite sides of each trap. On each trap, we then placed 20 seeds of 8 locally occurring
¹²⁸ species, where seed mixes were chosen such that they encompassed a range of functional
¹²⁹ groups and seed mass (see Table 1 for species and associated seed mass, Fig. 1C, D). At the
¹³⁰ Colorado site, we used only 10 seeds for the species at the highest end our seed mass range,
¹³¹ *Yucca glauca*, due to their large size, resulting in a total of 150 (CO) and 160 (MO) seeds
¹³² per trap.

¹³³ We collected paired sticky traps and carpets 1 week, 1 month, and 2 months after deploy-
¹³⁴ ment. All traps were taken back to the lab for processing. We recorded the total number of
¹³⁵ seeds of each focal species that were recaptured on each trap, and noted if seed fragments
¹³⁶ were evident to suggest seed herbivory or animal activity.

¹³⁷ At the Missouri site, we also wanted to test the efficacy of the sticky traps after they
¹³⁸ had been in the field for some time and accumulated leaves and other debris. Therefore, at
¹³⁹ the initial trap deployment date, we placed an additional sticky trap at each block that was
¹⁴⁰ coated in Tangle-Trap®, but did not have the seed mix added initially. After one month
¹⁴¹ of sitting in the grassland and accumulating leaves and other debris naturally, we added

¹⁴² the same seed mix as above to these traps, and then collected these traps along with the
¹⁴³ two-month traps. We termed this treatment, the ‘post-sticky’ treatment. We recovered and
¹⁴⁴ identified seeds from these traps in the same manner as mentioned above. This allowed us
¹⁴⁵ to more closely examine how well sticky traps recovered seeds after longer periods of time
¹⁴⁶ in the field.

¹⁴⁷ Statistical analysis

¹⁴⁸ To visualize how relative seed recovery varied across species and trap type, we calculated
¹⁴⁹ log response ratios of seed recovery of sticky traps relative to artificial grass carpet traps for
¹⁵⁰ each species at each site (i.e. the log of % recovery on sticky traps divided by % recovery on
¹⁵¹ artificial grass traps). For this formulation, values greater than zero indicate seeds are more
¹⁵² likely to be recovered on sticky traps, values of less than zero are more likely to be recovered
¹⁵³ on carpets, and values of zero indicate seeds are equally likely to be recovered on both traps.
¹⁵⁴ This allows for ease of visualization of which trap type tends to recover relatively more seeds
¹⁵⁵ of a given species at a given time.

¹⁵⁶ To determine how absolute seed recovery depended on the trap type, seed mass and the
¹⁵⁷ amount of time the traps remained in the field, we used generalized linear mixed effects
¹⁵⁸ models using the ‘glmmTMB’ package (Brooks *et al.*, 2017) in R v4.3.3. (R Core Team,
¹⁵⁹ 2024). The percent of recovered seeds was our response variable, and accordingly we used
¹⁶⁰ a binomial model with weights specified as the number of seeds placed on the traps to
¹⁶¹ account for differing numbers of seeds per species used in the experiment. Our predictor
¹⁶² variables included the interaction of trap type, seed mass and time in the field. We also
¹⁶³ included an additive random intercept for block nested within site (MO or CO). We used
¹⁶⁴ a backward selection approach to determine which interactions we kept in the model, and
¹⁶⁵ removed non-significant interactions when they arose. We calculated contrasts between trap
¹⁶⁶ type predictions for given seed masses using ‘emmeans’ (Lenth, 2023).

¹⁶⁷ To determine how well the sticky traps recovered seeds once the traps had been in the field
¹⁶⁸ for some time and acquired debris, we explored how recovery differed between the post-sticky
¹⁶⁹ treatment and the other trap types that contained seeds for one month. At the Missouri
¹⁷⁰ site only, we subset our data to all traps that had seeds on them for one month (artificial
¹⁷¹ grass, sticky and post-sticky). We then ran a similar generalized linear mixed effects model as
¹⁷² above, with our response variable as the proportion of seeds recovered (modeled as a binomial
¹⁷³ distribution), our predictor variable as trap type, and two additive random intercepts, one
¹⁷⁴ for block and one for species. We then calculated contrasts with ‘emmeans’ between trap
¹⁷⁵ type.

¹⁷⁶ We wrangled and visualized data with the ‘tidyverse’ package (Wickham *et al.*, 2019),
¹⁷⁷ and ran all code in R Studio v2024.12.0+467 (Posit team, 2024).

¹⁷⁸ RESULTS

¹⁷⁹ Relative seed recovery varied by species and time (Fig. 2). We observed that some species
¹⁸⁰ were more likely to be recovered on sticky traps (positive log response ratio, e.g. *C. tinctoria*,
¹⁸¹ *D. purpurea*), others were more likely to be recovered on artificial grass traps (negative log
¹⁸² response ratio, e.g. *H. annuus*, *S. heterolepis*), and many were equally likely to be recovered
¹⁸³ on either trap type (e.g. *S. scorarium*, *B. dactyloides*). These trends often varied with time.

¹⁸⁴ We next explored how trap type, seed mass, and the time the traps spent in the field
¹⁸⁵ altered the absolute proportion of seeds recovered. We found a significant interaction between
¹⁸⁶ seed mass and trap type, and a significant additive effect of time (Table 2). On average,
¹⁸⁷ sticky traps recovered more seeds than artificial grass traps, with sticky traps recovering
¹⁸⁸ $\sim 74\% \pm 13\%$ of seeds, and artificial grass traps recovering $\sim 52\% \pm 18\%$ of seeds. However,
¹⁸⁹ this relationship depended on seed mass (Fig. 3). As seed mass increased, the proportion
¹⁹⁰ of seeds recovered increased on artificial grass carpets, but decreased on sticky traps. For

191 small seed masses, artificial grass traps caught significantly fewer seeds (log odds estimate
192 at seed mass of 0, estimate= -1.56 ± 0.04 SE, $p < 0.001$). However, at large seed sizes,
193 artificial grass traps caught significantly more seeds (log odds estimate at seed mass of 0.02,
194 estimate= 0.75 ± 0.13 SE, $p < 0.001$). Additionally, the longer the traps were in the field,
195 the more seeds were lost (Supplemental Information). Across both trap types, $\sim 30\%$ seeds
196 were lost for each month the traps spent in the field.

197 Finally, to determine how well the sticky traps continue to capture seeds after some time
198 in the field, we conducted the ‘post-sticky’ trial at the Missouri site. We found that sticky
199 traps caught a significantly larger proportion of seeds than the post-sticky treatment, but
200 there was no difference found between the seeds captured with the aritifical grass and the
201 post-sticky treatments (Fig. 4, Table 3). The post-sticky traps captured $\sim 30\%$ less seeds
202 than the sticky traps.

203 DISCUSSION

204 A broader understanding of the natural rates of seed rain in grasslands is necessary to
205 understand the role of seed arrival for the assembly and reassembly of plant communities
206 under global change (Myers & Harms, 2009; Arruda *et al.*, 2018b). Standardized methods for
207 estimating seed arrival and dispersal dynamics that are flexible and can adequately recover
208 seeds under a myriad of conditions is critical, given that grasslands span $\sim 40\%$ of the Earth’s
209 surface, and occur on all continents across a wide range of precipitation and temperature
210 regimes (Buisson *et al.*, 2022). Here we provide a test of the seed recovery efficacy of two
211 methods for measuring seed rain in grassland communities: artificial grass traps and sticky
212 traps. These methods are both easy to deploy because of their size and minimal impact
213 on the local community (as compared to other funnel or pitfall-based methods; Kollmann
214 & Goetze, 1998). While both methods are successful for recovering seeds, our experimental

215 comparison has led us to encourage the use of artificial grass traps for capturing seed rain
216 in grasslands, especially for seeds that are larger in mass, for the reasons we describe below.
217 Obtaining estimates of local dispersal across a range of grassland communities will help
218 bridge the gap between dispersal theory and empiricism (Bolker *et al.*, 2003; Amarasekare,
219 2003; Myers & Harms, 2009).

220 We find that both the artificial grass and sticky trap methods have high rates of seed
221 recovery (72% for sticky traps on average, compared to 52% for artificial grass traps), with
222 decreasing recovery through time. Seed loss from both trap types was due to both abiotic
223 and biotic reasons, such as strong rainfall events washing seeds off carpets or herbivory of
224 seeds. In our study, we found evidence for both scenarios; for example a large, single-day
225 rainfall event decreased seed recovery at the Colorado site between time point 1 (1 week
226 after deployment) and time point 2 (1 month after deployment). Evidence of both insect
227 and small mammal herbivory occurred across both sites, with hundreds of ants on some
228 sticky traps (Fig. 1G), cottontail rabbit (*Sylvilagus sp.*) feces on seed carpets (Fig. 1F),
229 and husks of seeds post-consumption were found on both trap types, especially after longer
230 periods of time. These findings indicate that no trap type is a perfect representation of
231 primary dispersal, but instead represents a measure of *effective dispersal* (Nathan & Muller-
232 Landau, 2000), where recovered seeds are those that have escaped herbivory or secondary
233 dispersal and could germinate and join the aboveground community. Therefore, the artificial
234 grass trap method arguably represents more “ecologically relevant dispersal” for the local
235 community, because the traps allow for seed loss that would occur naturally on the soil
236 surface - leading to recovered seeds being those that have the potential to germinate. We
237 suggest future studies examine herbivory rates on seed carpets, deploying paired carpets
238 in herbivory removal and control plots. Seed carpet methods could be extended from our
239 current focus on seed rain to examine herbivory rates or even conduct preference experiments
240 in grasslands (Edwards & Crawley, 1999; Bakker & Olff, 2003).

While sticky traps are more commonly used in field studies (e.g. Rabinowitz & Rapp, 1980) and retain more seeds on average, they also have many drawbacks for accurately measuring seed rain. Sticky traps capture everything that comes in contact with the surface of the Petri dish (Fig. 1G), and thus sorting seeds from plant and soil debris as well as insect bodies can be difficult. Recovery is especially difficult for small seeds that have the potential to stick to debris in the trap and be easily missed. In our work we were focused on finding a known set of species. However, once the identity of seeds are unknown (as in classic seed rain studies, compared to our comparative methods-focused approach), the ability to lose seeds due to accidentally sticking to other material will decrease seed recovery. We also noticed that some species with thinner seed coats changed color after being in contact with Tangle-Trap® for long periods of time, which can hinder identification if seeds are not removed and identified quickly. Given how time-consuming seed removal and identification can be (Wynne *et al.*, 2024), it is critical to have a method that allows samples to be stored for long periods and remain unaffected. In addition, it is nearly impossible to recover seeds from sticky traps and then germinate them to determine viability or identity, whereas this is quite simple with artificial grass carpets. The potential to germinate ‘unknowns’ is, in our view, a key advantage of artificial grass traps, given unknowns are extremely likely in seed rain studies (Wynne *et al.*, 2024). Finally, the timing of sticky traps is extremely important for their effectiveness. Sticky traps no longer capture seeds effectively once they have been frozen (Molau, 1996), which makes post-frost seed rain collection impossible despite many temperate seeds dispersing late in the growing season or under snowy conditions (Rabinowitz & Rapp, 1980; Molau & Larsson, 2000). In addition, our results from the Missouri site clearly show that sticky traps work best when they are in the field for short periods of time, or else debris collects on the trap and hinders seed capture and recovery (Fig. 4). This is in comparison to artificial grass traps that continue to effectively collect and store seeds regardless of time or temperature. Our work strongly supports the use of artificial grass traps

as a primary method to measure seed rain in grasslands because these traps improve the ease of identifying unknown seeds, and can successfully recover seeds under many different site conditions and time-scales.

Our results demonstrated that the relationship between seed mass and seed recovery changes with trap type (Fig. 3). As seed size increases, we see a small decrease in the proportion of seeds recovered on sticky traps, but a large increase in the proportion of seeds recovered on artificial grass traps. This result likely arises from differences in the body size of the granivores consuming seeds from the traps. Broadly, there is a positive relationship between granivore body size and the size of seeds they consume (Muñoz & Bonal, 2008), with smaller-bodied insect granivores tending to favor smaller seeds than larger-bodied small mammal granivores (Radtke, 2011; Maron *et al.*, 2012; Rey *et al.*, 2002; Vaz Ferreira *et al.*, 2011). The loss of smaller seeds from the artificial grass traps likely reflects how well the Tangle-Trap® captures insects like ants that attempt to remove seeds from these traps, but instead become stuck to the surface of the sticky trap (Fig. 1G). Therefore, more smaller seeds remain to be recaptured on the sticky traps because insect granivores are not removing them. Conversely, larger seeds are more likely to be recovered on the artificial grass traps. Here, larger seeds are likely consumed by small mammals, and are likely easier to consume from sticky traps because they are fixed on the soil surface and not hidden among the strands of grass as they are in the artificial grass traps. This decrease in handling time could increase consumption rates of larger seeds from sticky traps. While the exact reason for why we find this interaction between trap type and seed mass should be further explored, this result underscores the importance of considering the difference in the results provided by the different trap methods. If the goal is to understand primary seed dispersal and to quantify the number and type of seeds that fall regardless of their fate, we encourage the use of sticky traps that are replaced very frequently (and of course considering all possible concerns listed above). However if the goal is to understand ‘effective dispersal’, which

293 focuses more on which seeds remain in an area and are available to germinate and establish
294 into the vegetative community, we encourage the use of artificial grass traps because they
295 allow natural processes such as secondary dispersal and granivory to occur.

296 Here we present a methodological comparison between the seed recovery ability of arti-
297 ficial grass traps and sticky traps for measuring seed rain in grasslands. While we find both
298 methods effectively recover seeds, overall this comparison underscored that artificial grass
299 traps are much simpler and less hassle to use. Artificial grass traps are effective at seed
300 recovery under a wider range of conditions, and allow for future, downstream use of seeds
301 once the traps have been removed from the field. This method will allow for coordinated
302 understanding of seed rain across grasslands (Arruda *et al.*, 2018b; Myers & Harms, 2009).
303 Future seed rain studies will do well to consider the time they leave the traps out in the field,
304 as seeds tend to be increasingly lost through time. This seed loss is inevitable, and represents
305 the fates of seeds on the soil surface (Forget *et al.*, 2005; Chambers & Macmahon, 1994), as
306 small mammals and insects consume many seeds in grasslands throughout the season (Howe
307 *et al.*, 2002; Peters, 2007; Kuli-Révész *et al.*, 2021).

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³¹⁴ **Author Contributions**

³¹⁵ LLS and LGS designed and implemented experiment, conducted statistical analysis, and
³¹⁶ wrote the manuscript, all authors helped with data collection and manuscript editing.

³¹⁷ **Data Availability**

³¹⁸ Code and data for analysis and figure generation can be found at Github ([https://github.com/Sullivan-Lab/project\\$_CarpetMethods](https://github.com/Sullivan-Lab/project$_CarpetMethods)), and will be made available at Dryad upon
³¹⁹ publication.

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Site	Family	Species	Seed Mass (mg)
Colorado	Fabaceae	<i>Amorpha fruticosa</i>	7.543 (\pm 0.243)
	Poaceae	<i>Bouteloua gracilis</i>	0.540 (\pm 0.073)
	Poaceae	<i>Buchloe dactyloides</i>	11.785 (\pm 0.555)
	Fabaceae	<i>Dalea purpurea</i>	1.545 (\pm 0.060)
	Asteraceae	<i>Helianthus annuus</i>	6.750 (\pm 0.330)
	Asteraceae	<i>Solidago rigida</i>	0.759 (\pm 0.025)
	Iridaceae	<i>Sisyrinchium angustifolium</i>	0.840 (\pm 0.044)
	Agavaceae	<i>Yucca glauca</i>	19.902 (\pm 0.518)
Missouri	Asteraceae	<i>Coreopsis tinctoria</i>	0.215 (\pm 0.014)
	Fabaceae	<i>Desmodium canadense</i>	4.420 (\pm 0.302)
	Asteraceae	<i>Echinacea pallida</i>	4.600 (\pm 0.183)
	Fabaceae	<i>Lespedeza capitata</i>	3.280 (\pm 0.099)
	Asteraceae	<i>Rudbeckia hirta</i>	0.250 (\pm 0.010)
	Poaceae	<i>Schizachyrium scoparium</i>	1.830 (\pm 0.114)
	Poaceae	<i>Sporobolus heterolepis</i>	2.000 (\pm 0.087)
	Campanulaceae	<i>Triodanis perfoliata</i>	0.025 (\pm 0.002)

Table 1: A list of all species used in the experiments in Colorado (CO) and Missouri (MO). Seed mass is measured in milligrams and reported as mean and standard deviation.

	Estimate	St. Error	z value	p value
Intercept(artificial grass)	0.589	0.185	3.18	0.001
trap type(sticky)	1.558	0.044	35.24	<0.0001
seed mass	102.518	5.683	18.04	<0.0001
time	-0.857	0.024	-36.24	<0.0001
trap type(sticky):seed mass	-115.204	7.667	-15.03	<0.0001

Table 2: Summary table of our statistical model results from our generalized linear mixed effects model exploring how trap type, seed mass and time since deployment alters the proportion of seeds recovered.

	Estimate	St. Error	z value	p value
Intercept(post-sticky)	0.152	0.286	0.53	0.596
artificial grass	0.166	0.33	0.507	0.612
sticky	1.647	0.394	4.18	<0.0001

Table 3: Summary table from our statistical model results from our ‘post-sticky’ analysis using a generalized linear mixed effects model exploring how trap type (post-sticky, vs artificial grass vs sticky) alters the proportion of seeds recovered.



Figure 1: Depiction of our experimental sites, seeds, and methods. A) The Colorado grassland site. B) The Missouri grassland site. C) Missouri seeds used in the experiment (from left to right: *Coreopsis tinctoria*, *Desmodium canadense*, *Echinacea pallida*, *Lespedeza capitata*, *Rudbeckia hirta*, *Schizachyrium scoparium*, *Sporobolus heterolepis*, *Triodanis perfoliata*). D) Colorado seeds used in the experiment (from left to right: *Amorpha fruticosa*, *Bouteloua gracilis*, *Buchloe dactyloides*, *Dalea purpurea*, *Helianthus annuus*, *Solidago rigida*, *Sisyrinchium angustifolium*, *Yucca glauca*). E) A comparison of the sticky and artificial grass traps after they were placed in the field. F) artificial grass traps with rabbit droppings. G) Sticky traps covered in ant bodies and leaves.

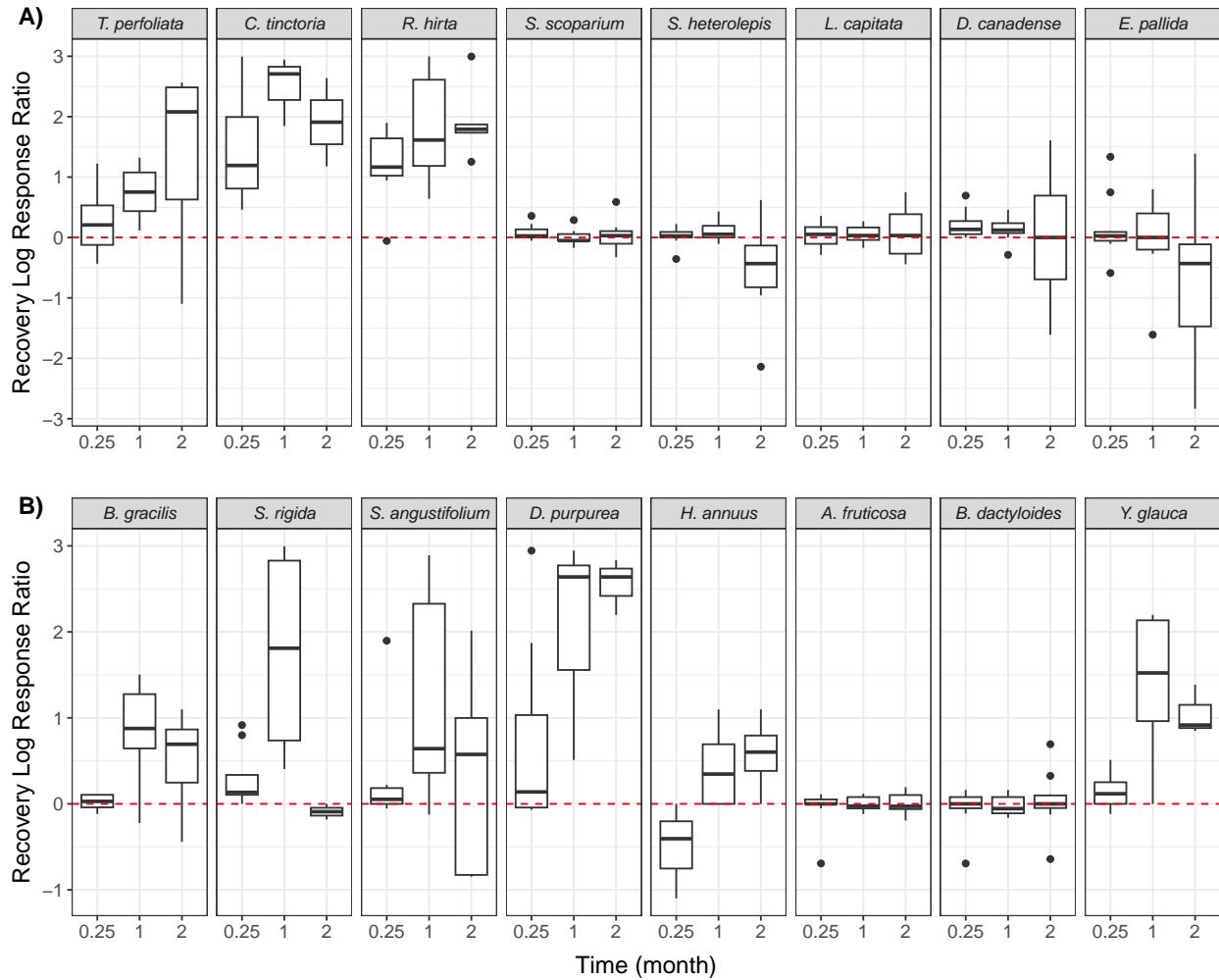


Figure 2: Log response ratio of proportion of seeds recovered in sticky traps relative to proportion of seeds recovered on artificial grass traps from the A) Missouri site, and B) Colorado site. For each state, panels are in seed size ordered from smallest (left) to largest (right). Values of zero (red dashed line) represent equal likelihood of recapture in sticky vs artificial grass traps. Values above zero indicate where seeds were more likely to be recovered on sticky traps. Values below zero represent where seeds more likely to be recovered on artificial grass traps.

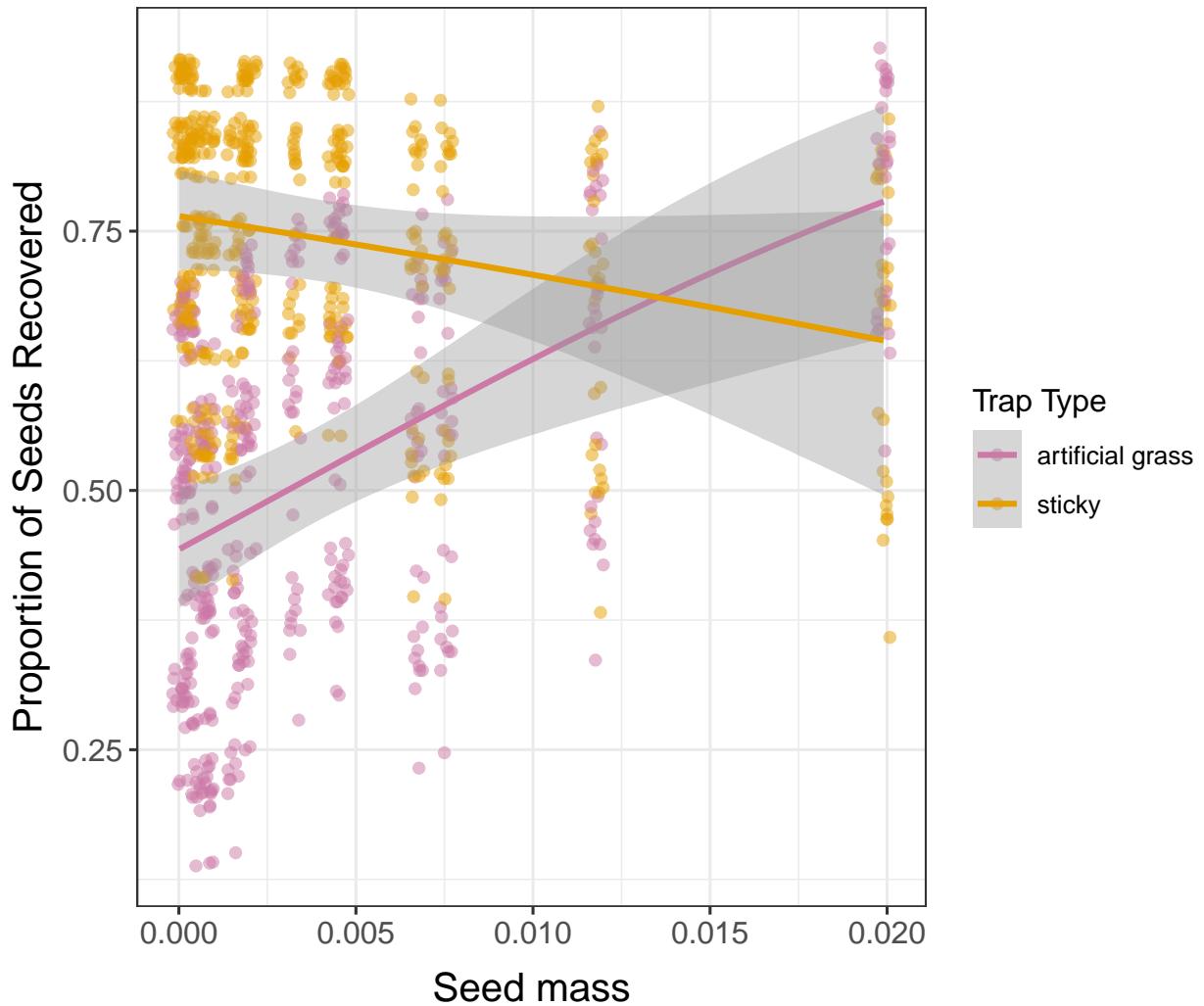


Figure 3: Proportion of seeds recovered in relationship to seed mass with respect to trap type (pink points are artificial grass traps, orange points are sticky traps). As seed mass increases, we find a decrease in the proportion of seeds recovered from sticky traps, and an increase in proportion of seeds recovered from artificial grass traps. Points and lines represent model predicted values.

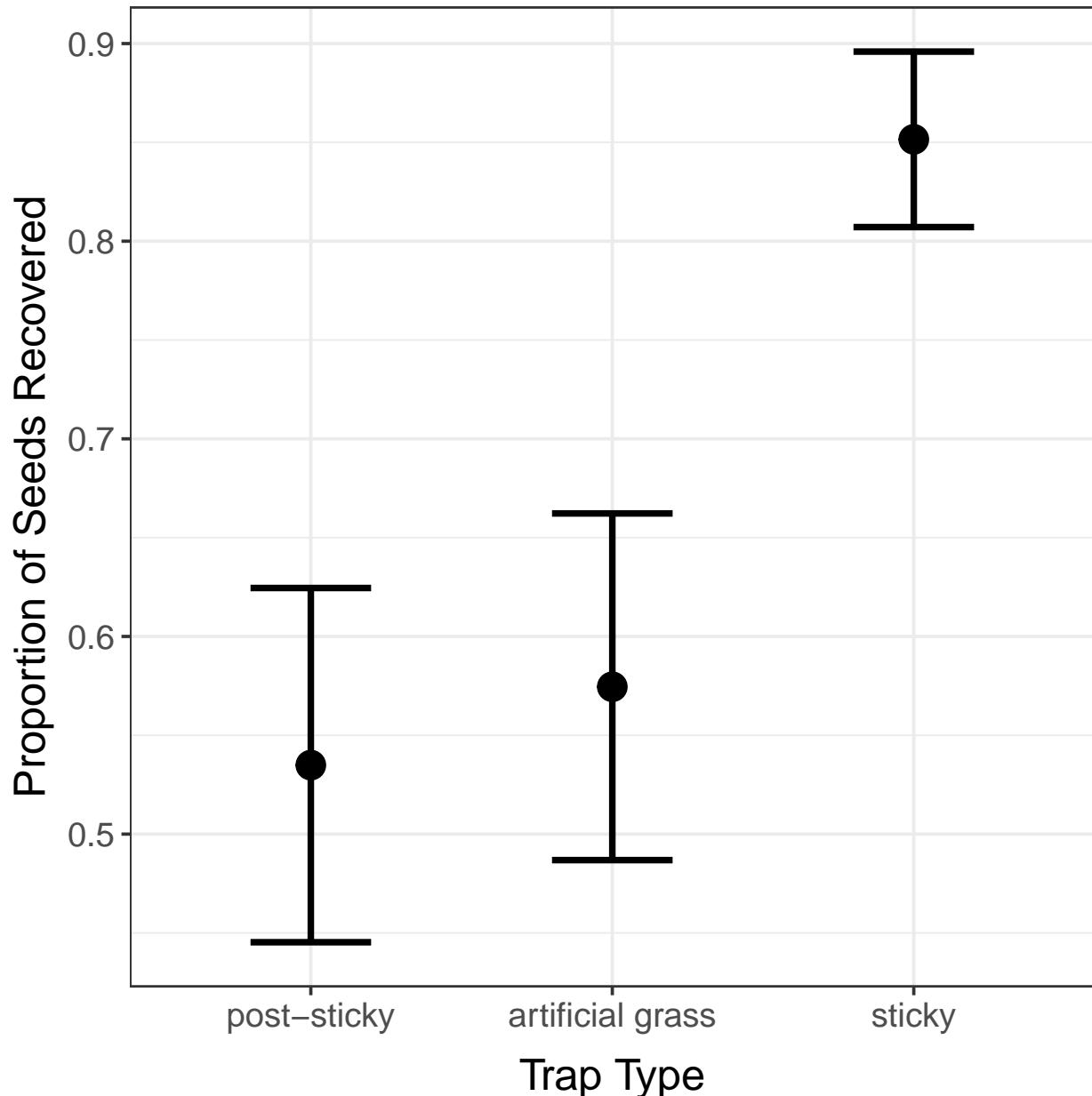
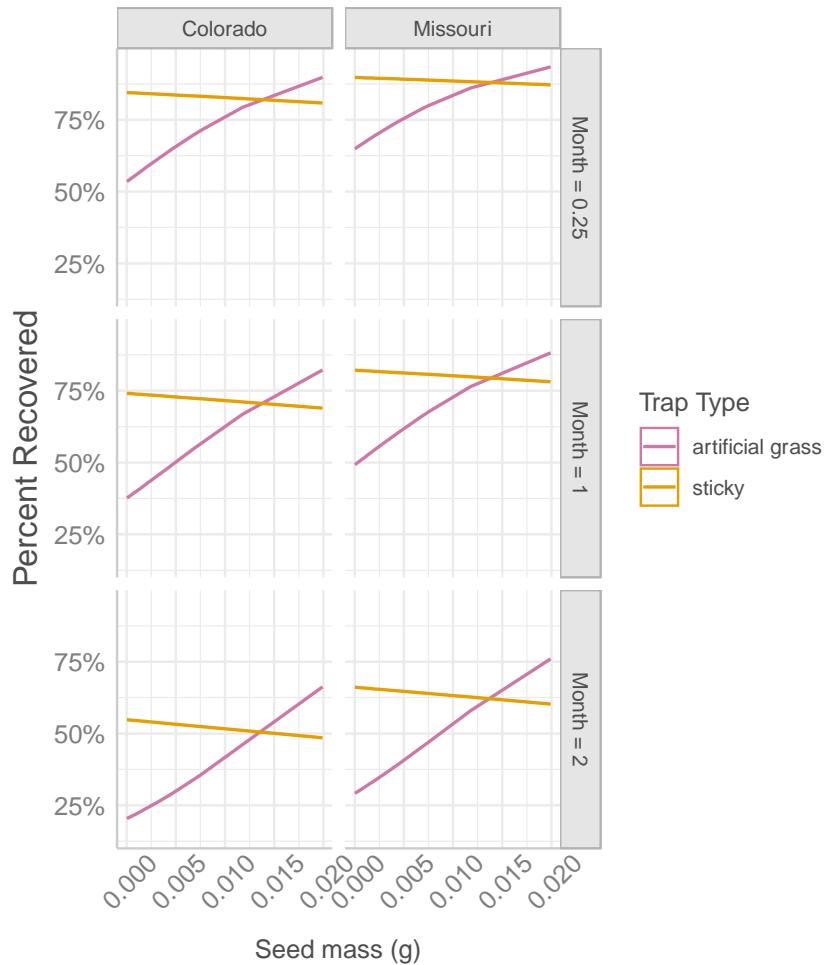


Figure 4: Proportion of seeds recovered with respect to trap type for the traps that had been out in the field for one month in Missouri (i.e. sticky, artificial grass and post-sticky traps). Data are mean model predicted values, and error bars represent standard deviation.



Supplemental Figure 1: Predicted values for all factors in the model – the relationship of percent of seeds recovered relative to seed mass across both sites and all three times.



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Potential cover image caption: Comparison of two methods for measuring seed rain in grassland ecosystems (traditional sticky trap method on the left, and artificial grass method on the right).