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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:	<p>Premise. 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.</p> <p>Methods. 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.</p> <p>Results. 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.</p> <p>Discussion. We encourage artificial grass traps for broad adoption of measuring seed rain in grasslands to increase links between theoretical and empirical community ecology.</p>
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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

² **Premise.** Seed dispersal is a critical process for plant community assembly, however nat-
³ ural rates of seed arrival are rarely quantified when compared to other assembly mecha-
⁴ nisms, especially in herbaceous communities. This discrepancy arises from the difficulty in
⁵ recovering small seeds.

⁶ **Methods.** Here we compare the utility of artificial grass carpet squares ('artificial grass')
⁷ for capturing seed rain to classic 'sticky trap' methods. While artificial grass has been
⁸ used in Arctic systems, we examine its efficacy in temperate grasslands. We placed paired
⁹ sticky traps and artificial grass squares in two grassland ecosystems. We added known
¹⁰ numbers of seeds of multiple species to each trap, and recovered seeds at one week, one
¹¹ month and two month intervals.

¹² **Results.** We found that while both trap types lost seeds through time at similar rates,
¹³ sticky traps recovered more small seeds while artificial grass recovered more large seeds.
¹⁴ Overall sticky traps retained more seeds, but recovering seeds was difficult, and recovery
¹⁵ was hindered by debris stuck to the traps. Alternatively, seeds recovered from artificial
¹⁶ grass could be handled easily and retained for long-term storage.

¹⁷ **Discussion.** We encourage artificial grass traps for broad adoption of measuring seed rain
¹⁸ in grasslands to increase links between theoretical and empirical community ecology.

¹⁹ INTRODUCTION

²⁰ Dispersal is a critical process that structures populations and communities, linking local
²¹ patch-scale dynamics to regional landscape level processes (Amarasekare, 2003; Snyder &
²² Chesson, 2003; Leibold & Chase, 2017). Within vegetative communities, seed dispersal is
²³ one of the primary mechanisms of arrival to new habitats, allowing species to track chang-
²⁴ ing environmental conditions and promoting landscape connectivity (Cubíña & Aide, 2001;
²⁵ Simberloff, 2009; Beckman & Sullivan, 2023). Dispersal also plays a critical role in assem-
²⁶ bly and long-term diversity patterns, such as maintaining source-sink dynamics (Mou-
²⁷ quet & Loreau, 2003; Craig *et al.*, 2025), allowing long-term species co-existence (Snyder
²⁸ & Chesson, 2003; Berkley *et al.*, 2010), and maintaining genetic diversity in populations
²⁹ (Jordano, 2017). A species' dispersal ability also has direct management implications,
³⁰ often increasing native diversity after restoration, or alternatively, facilitating the inva-
³¹ sion of non-native species (Von Der Lippe & Kowarik, 2007; Sperry *et al.*, 2019; Brudvig
³² *et al.*, 2009). Despite its importance as a critical process for populations and communities
³³ (Vellend, 2010; Schupp & Fuentes, 1995; Levine & Murrell, 2003), dispersal is notoriously
³⁴ difficult to quantify empirically (Beckman & Sullivan, 2023; Bullock *et al.*, 2006). These
³⁵ methodological challenges have created a gap between our theoretical understanding of
³⁶ the importance of dispersal versus our empirical understanding and use in applied settings
³⁷ (Bolker *et al.*, 2003), making dispersal arguably the least empirically understood mecha-
³⁸ nism of community assembly (HilleRisLambers *et al.*, 2012; Vellend, 2016).

³⁹ One way to measure seed dispersal is by estimating seed rain, or the seeds that fall into a
⁴⁰ given area (Arruda *et al.*, 2018a). While this method captures only a single point in the
⁴¹ dispersal trajectory of a seed (the settlement phase - Travis *et al.* 2012), it is arguably
⁴² the most important phase to understand for plant community ecology, as it provides in-
⁴³ formation on the number and type of seeds that arrive to a specific location. If seeds are

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

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

70 seed dispersal in temperate grasslands (Rabinowitz & Rapp, 1980). Lastly, using recovered
71 seeds from sticky traps for additional work, such as germination trials or trait measure-
72 ment, is rarely possible as seeds become coated with the sticky residue.

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

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

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

103 METHODS

104 Study sites and seed mixes

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

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

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

115 Experimental design and tests of trap performance

116 We tested the effectiveness of sticky traps versus artificial grass carpets for seed reten-
117 tion through time. Following standard protocol (Rabinowitz & Rapp, 1980; Kollmann &

¹¹⁸ Goetze, 1998; Chabrierie & Alard, 2005), sticky traps consisted of 10 cm x 10 cm Plexiglass
¹¹⁹ plates coated with Tangle-Trap® sticky coating. To compare this standard method to seed
¹²⁰ carpets, we used 10 cm x 10 cm synthetic lawn turf squares (TrafficMASTER® TruGrass
¹²¹ Emerald Artificial Turf) with blade heights between 1.5 to 2.5 cm tall.

¹²² At the two sites, we replicated 10 blocks of paired sticky traps and carpets that we col-
¹²³ lected 1 week, 1 month, and 2 months after deployment to examine seed recovery through
¹²⁴ time. We initially deployed all traps on July 10, 2019 in Colorado and July 17, 2019 in
¹²⁵ Missouri. Each block consisted of three sticky traps and three carpets for a total of 10
¹²⁶ replicates of the two methods for each each time point and each site. When deploying
¹²⁷ traps, we removed any litter or vegetation directly under the traps so that they were placed
¹²⁸ directly on the soil surrounded by natural vegetation (Fig. 1E). We used two ground sta-
¹²⁹ ples to secure opposite sides of each trap. On each trap, we then placed 20 seeds of 8 lo-
¹³⁰ cally occurring species, where seed mixes were chosen such that they encompassed a range
¹³¹ of functional groups and seed mass (see Table 1 for species and associated seed mass, Fig.
¹³² 1C, D). At the Colorado site, we used only 10 seeds for the species at the highest end our
¹³³ seed mass range, *Yucca glauca*, due to their large size, resulting in a total of 150 (CO) and
¹³⁴ 160 (MO) seeds per trap.

¹³⁵ We collected paired sticky traps and carpets 1 week, 1 month, and 2 months after deploy-
¹³⁶ ment. All traps were taken back to the lab for processing. We recorded the total number
¹³⁷ of seeds of each focal species that were recaptured on each trap, and noted if seed frag-
¹³⁸ ments were evident to suggest seed herbivory or animal activity.

¹³⁹ At the Missouri site, we also wanted to test the efficacy of the sticky traps after they had
¹⁴⁰ been in the field for some time and accumulated leaves and other debris. Therefore, at the
¹⁴¹ initial trap deployment date, we placed an additional sticky trap at each block that was
¹⁴² coated in Tangle-Trap®, but did not have the seed mix added initially. After one month of
¹⁴³ sitting in the grassland and accumulating leaves and other debris naturally, we added the

¹⁴⁴ same seed mix as above to these traps, and then collected these traps along with the two-
¹⁴⁵ month traps. We termed this treatment, the ‘post-sticky’ treatment. We recovered and
¹⁴⁶ identified seeds from these traps in the same manner as mentioned above. This allowed us
¹⁴⁷ to more closely examine how well sticky traps recovered seeds after longer periods of time
¹⁴⁸ in the field.

¹⁴⁹ Statistical analysis

¹⁵⁰ To visualize how relative seed recovery varied across species and trap type, we calculated
¹⁵¹ log response ratios of seed recovery of sticky traps relative to artificial grass carpet traps
¹⁵² for each species at each site (i.e. the log of % recovery on sticky traps divided by % recov-
¹⁵³ ery on artificial grass traps). For this formulation, values greater than zero indicate seeds
¹⁵⁴ are more likely to be recovered on sticky traps, values of less than zero are more likely to
¹⁵⁵ be recovered on carpets, and values of zero indicate seeds are equally likely to be recovered
¹⁵⁶ on both traps. This allows for ease of visualization of which trap type tends to recover rel-
¹⁵⁷ atively more seeds of a given species at a given time.

¹⁵⁸ To determine how absolute seed recovery depended on the trap type, seed mass and the
¹⁵⁹ amount of time the traps remained in the field, we used generalized linear mixed effects
¹⁶⁰ models using the ‘glmmTMB’ package (Brooks *et al.*, 2017) in R v4.3.3. (R Core Team,
¹⁶¹ 2024). The percent of recovered seeds was our response variable, and accordingly we used
¹⁶² a binomial model with weights specified as the number of seeds placed on the traps to
¹⁶³ account for differing numbers of seeds per species used in the experiment. Our predictor
¹⁶⁴ variables included the interaction of trap type, seed mass and time in the field. We also in-
¹⁶⁵ cluded an additive random intercept for block nested within site (MO or CO). We used a
¹⁶⁶ backward selection approach to determine which interactions we kept in the model, and re-
¹⁶⁷ moved non-significant interactions when they arose. We calculated contrasts between trap
¹⁶⁸ type predictions for given seed masses using ‘emmeans’ (Lenth, 2023).

¹⁶⁹ To determine how well the sticky traps recovered seeds once the traps had been in the field
¹⁷⁰ for some time and acquired debris, we explored how recovery differed between the post-
¹⁷¹ sticky treatment and the other trap types that contained seeds for one month. At the Mis-
¹⁷² souri site only, we subset our data to all traps that had seeds on them for one month (arti-
¹⁷³ ficial grass, sticky and post-sticky). We then ran a similar generalized linear mixed effects
¹⁷⁴ model as above, with our response variable as the proportion of seeds recovered (modeled
¹⁷⁵ as a binomial distribution), our predictor variable as trap type, and two additive random
¹⁷⁶ intercepts, one for block and one for species. We then calculated contrasts with ‘emmeans’
¹⁷⁷ between trap type.

¹⁷⁸ We wrangled and visualized data with the ‘tidyverse’ package (Wickham *et al.*, 2019), and
¹⁷⁹ ran all code in R Studio v2024.12.0+467 (Posit team, 2024).

¹⁸⁰ RESULTS

¹⁸¹ Relative seed recovery varied by species and time (Fig. 2). We observed that some species
¹⁸² were more likely to be recovered on sticky traps (positive log response ratio, e.g. *C. tinc-*
¹⁸³ *toria*, *D. purpurea*), others were more likely to be recovered on artificial grass traps (neg-
¹⁸⁴ ative log response ratio, e.g. *H. annuus*, *S. heterolepis*), and many were equally likely to
¹⁸⁵ be recovered on either trap type (e.g. *S. scoparium*, *B. dactyloides*). These trends often
¹⁸⁶ varied with time.

¹⁸⁷ We next explored how trap type, seed mass, and the time the traps spent in the field al-
¹⁸⁸ tered the absolute proportion of seeds recovered. We found a significant interaction be-
¹⁸⁹ tween seed mass and trap type, and a significant additive effect of time (Table 2). On av-
¹⁹⁰ erage, sticky traps recovered more seeds than artificial grass traps, with sticky traps re-
¹⁹¹ covering $\sim 74\% \pm 13\%$ of seeds, and artificial grass traps recovering $\sim 52\% \pm 18\%$ of
¹⁹² seeds. However, this relationship depended on seed mass (Fig. 3). As seed mass increased,

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

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

206 DISCUSSION

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

217 based methods; Kollmann & Goetze, 1998). While both methods are successful for recov-
218 ering seeds, our experimental comparison has led us to encourage the use of artificial grass
219 traps for capturing seed rain in grasslands, especially for seeds that are larger in mass, for
220 the reasons we describe below. Obtaining estimates of local dispersal across a range of
221 grassland communities will help bridge the gap between dispersal theory and empiricism
222 (Bolker *et al.*, 2003; Amarasekare, 2003; Myers & Harms, 2009).

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

preference experiments 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

269 continue to effectively collect and store seeds regardless of time or temperature. Our work
270 strongly supports the use of artificial grass traps as a primary method to measure seed
271 rain in grasslands because these traps improve the ease of identifying unknown seeds, and
272 can successfully recover seeds under many different site conditions and time-scales.

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

295 considering all possible concerns listed above). However if the goal is to understand ‘effec-
296 tive dispersal’, which focuses more on which seeds remain in an area and are available to
297 germinate and establish into the vegetative community, we encourage the use of artificial
298 grass traps because they allow natural processes such as secondary dispersal and granivory
299 to occur.

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

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³¹⁸ **Author Contributions**

³¹⁹ LLS and LGS designed and implemented experiment, conducted statistical analysis, and
³²⁰ wrote the manuscript, all authors helped with data collection and manuscript editing.

³²¹ **Data Availability**

³²² 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
³²³ upon 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.

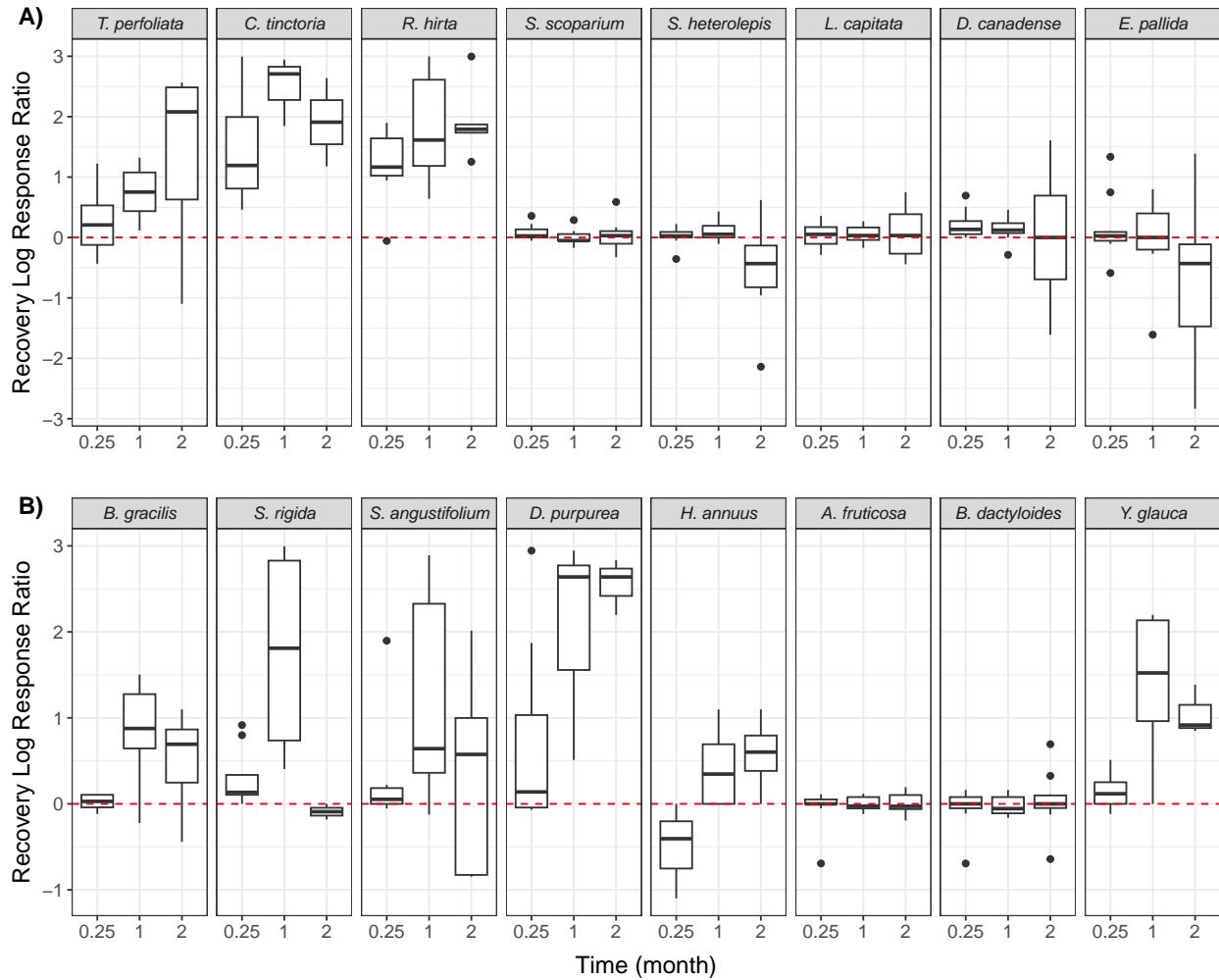


Figure 2: Log response ratio of proportion of seeds recovered in sticky traps relative to proportion of seeds recovered on artificial grass traps from the A) Missouri site, and B) Colorado site. For each state, panels are in seed size ordered from smallest (left) to largest (right). Values of zero (red 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.

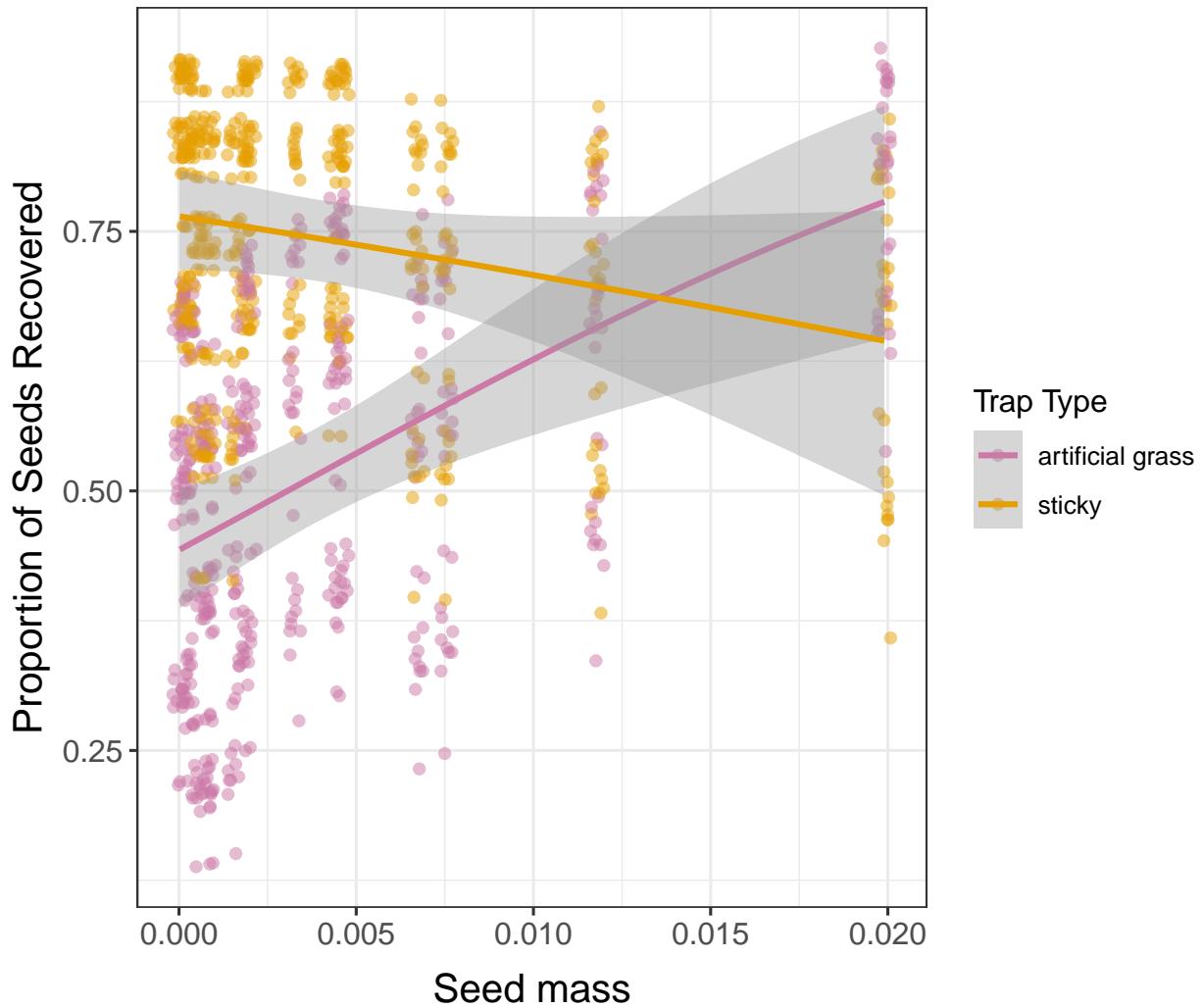


Figure 3: Proportion of seeds recovered in relationship to seed mass with respect to trap type (pink points are artificial grass traps, orange points are sticky traps). As seed mass increases, we find a decrease in the proportion of seeds recovered from sticky traps, and an increase in proportion of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

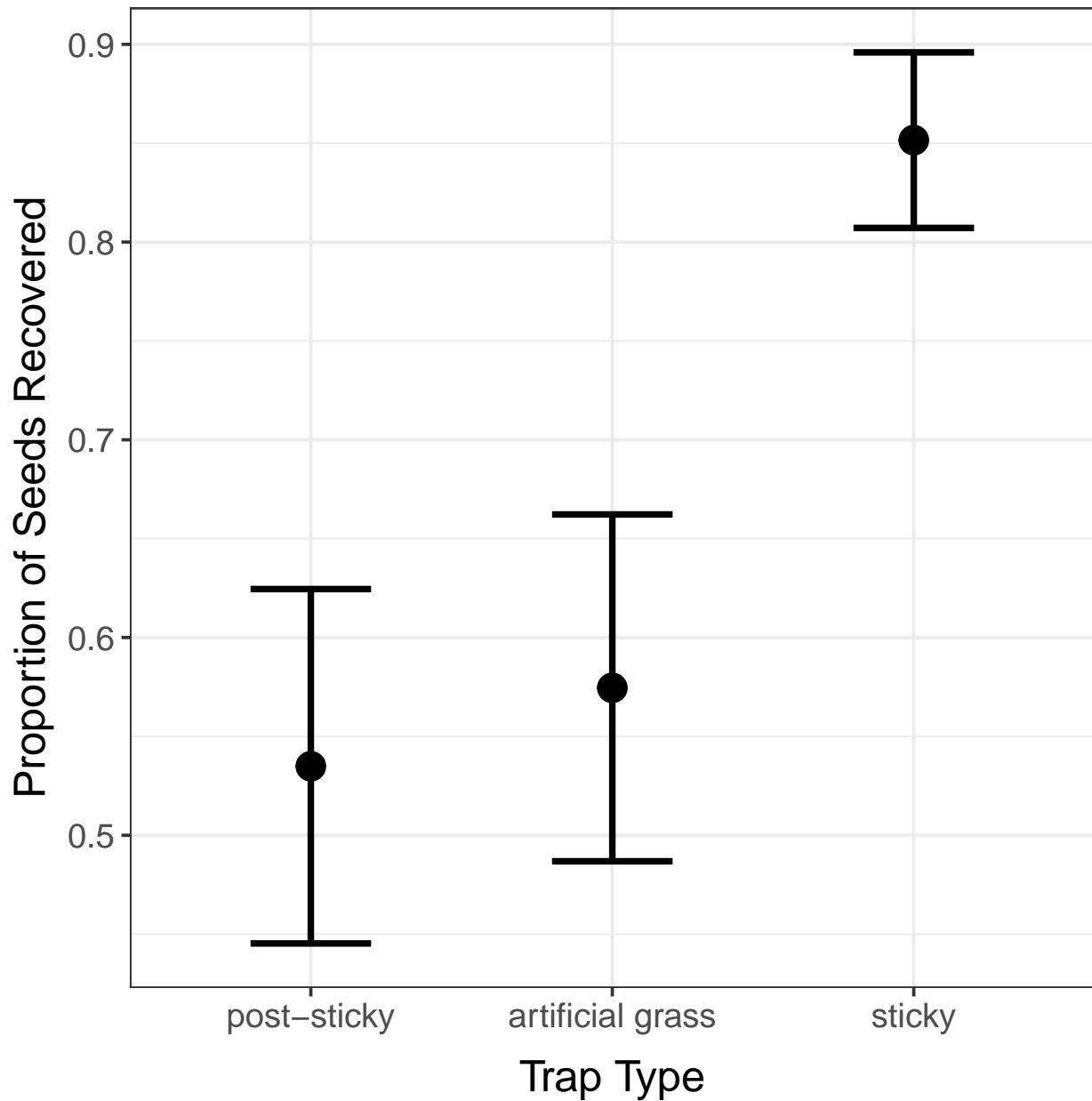
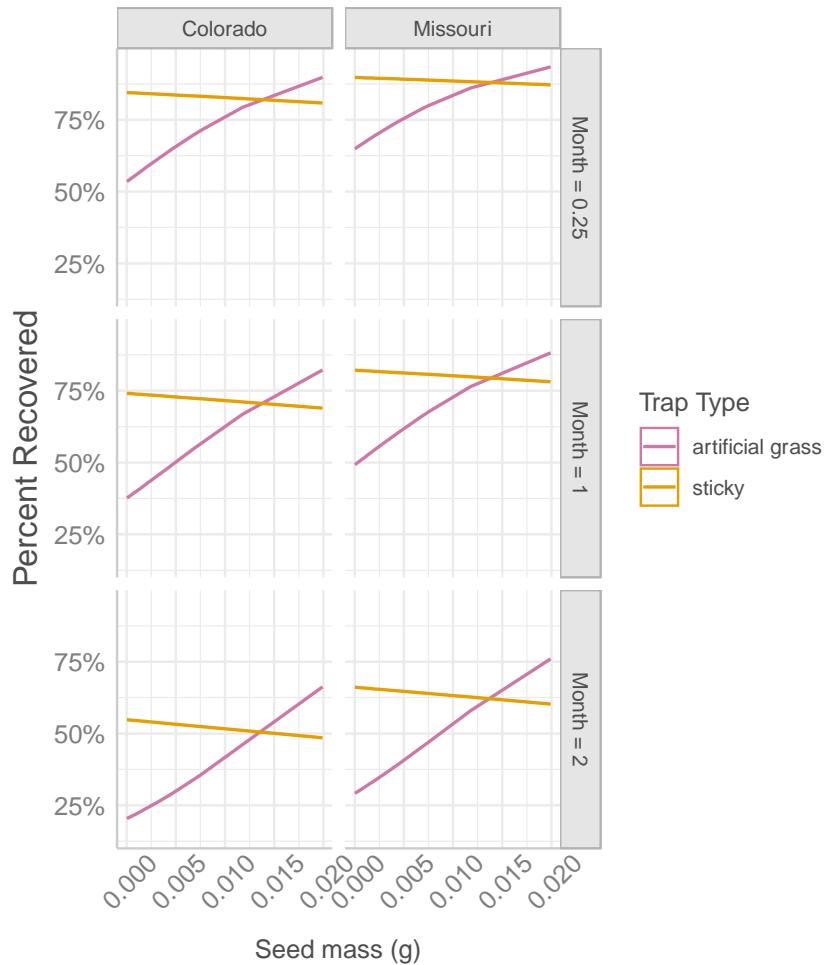


Figure 4: Proportion of seeds recovered with respect to trap type for the traps that had been out in the field for one month in Missouri (i.e. sticky, artificial grass and post-sticky traps). Data are mean model predicted values, and error bars represent standard deviation.



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).