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ARTICLE

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Seed size of co-occurring forb species predicts rates of predispersal seed loss from insects

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Abstract

Plants often face chronic seed loss from predispersal seed predation by insects. Although many studies have documented the rates of seed loss for single species in different communities, it is unclear how rates of predispersal seed predation vary among co-occurring species within the same community. If interspecific asymmetries in seed loss are great, this common interaction could have important implications for coexistence. Species traits, such as seed size or seed nitrogen and carbon, might correlate with interspecific variation in predispersal seed predation among co-occurring grassland forb species. We collected infructescences from 13 co-occurring forb species from each of four western Montana grasslands over 2 years. We quantified the magnitude of seed loss due to predispersal seed predation by insects. The average level of seed loss was 15.8%. Larger seeded species suffered significantly higher levels of predispersal seed predation than smaller seeded species, and seed size predicted seed loss more than seed nitrogen or carbon. Although large-seeded species often have greater proportional recruitment and early survival than small-seeded species, our study suggests that these advantages are partially counterbalanced by greater predispersal seed loss for larger versus smaller seeded species. Asymmetries in predispersal seed predation may importantly affect coexistence among these species.

KEYWORDS
grassland forbs, herbivory, predispersal seed predation, safe sites, seed loss, seed size

INTRODUCTION

Plants are frequently attacked by insects that consume flower embryos and developing seeds. Though inconspicuous, predispersal seed loss imposed by insect herbivores is common and occurs in many ecosystems and species (Ehrlén et al., 2002; Janzen, 1971; Kolb et al., 2007; Kurkjian et al., 2016; Louda & Potvin, 1995; Stachurska-Swakoń et al., 2018). Interspecific variation in predispersal seed predation, however, can be substantial. Some species experience a low but chronic level of seed loss, where perhaps an average of 10% of seeds are destroyed per plant every year (Chen et al., 2017; Janzen, 1971; Kolb et al., 2007). In contrast, other species can suffer the almost complete elimination of all seeds produced (Combs et al., 2011; Janzen, 1971; Kolb et al., 2007; Szentesi & Jermy, 2003). More typical, however, are more moderate levels of seed loss (Kolb et al., 2007;

Leimu et al., 2002; Preisser & Bastow, 2005, but see Aguirrebengoa et al., 2021). Yet, even 20%–50% mortality of seeds can impose major reductions in recruitment (Weppler & Stöcklin, 2006), plant fitness (Herrera et al., 2002; Louda & Potvin, 1995; Root, 1996), target plant abundance (Katz, 2016; Maron & Crone, 2006), and even distribution (Baer & Maron, 2018; Louda, 1982; Stachurska-Swakoń et al., 2018).

Our understanding of interspecific variation in predispersal seed predation has come mainly from disparate studies of single species in different systems (Kolb et al., 2007; Preisser & Bastow, 2005). While informative, these studies do not enable us to determine how co-occurring species might differ in the extent of predispersal seed loss to insects. Plant traits have increasingly been used to predict the outcome of interactions between plants and insect herbivores (Carmona et al., 2010), but we know of few studies that have assayed how levels of predispersal seed predation vary among co-occurring species (but see Xi et al., 2020) and used traits of those species to predict variation in the magnitude of seed loss in grassland systems.

Community-wide studies are more common in the context of postdispersal seed predation by rodents. Measurements of seed loss from short-term seed offerings have shown that large-seeded species often suffer greater levels of seed predation than smaller seeded species (Donoso et al., 2004; Larios et al., 2017; Mittelbach & Gross, 1984; Pearson et al., 2011). Seed addition studies and longer term rodent exclusion experiments, particularly those performed in open habitats such as grasslands, have also shown that rodents impose greater negative impacts on the recruitment of large- versus small-seeded species (Brown & Heske, 1990; Maron et al., 2012, 2018; Reader, 1993). The propensity for rodents to focus on larger seeded species (where those large-seeded species are not so large as to preclude consumption, such as in forested communities) makes sense, given that larger seeds represent a greater caloric "bang for the foraging buck" than do smaller seeded species (Kerley & Erasmus, 1991; Pyke et al., 1977; Radtke, 2011). Other plant traits such as seed carbon and nitrogen content, which are correlated with protein and soluble carbohydrate content and therefore the nutritional value of the seed, can also be good predictors of the magnitude of postdispersal seed predation by rodents (Gong et al., 2014; Kelrick & MacMahon, 1985; Smith, 1987). Whether similar patterns hold true for predispersal seed predation by insects remains unclear.

Here, we quantify the magnitude of predispersal seed predation by insects among 13 co-occurring grassland forb species. We examined whether the magnitude of predispersal seed predation varied predictably across grassland forb species based on the size, nitrogen content, or carbon content of species' seeds. We know of no study that has addressed this question. Finally, we took advantage of the fact that the impacts of rodent postdispersal seed predation on the recruitment of our focal species have been previously measured (Maron et al., 2018). This allowed us to determine whether the same species that suffer decrements in recruitment due to postdispersal seed predation also experience high levels of predispersal seed predation. If these are correlated, it implies that there is likely a cumulative effect of pre- and postdispersal seed predation on the recruitment of forb species in our study system.

METHODS

Our study was conducted in Western Montana grasslands, with most sites located in the Blackfoot Valley (47°01′ N, 113°07′ W), which supports semiarid perennial grasslands dominated by rough fescue (*Festuca campestris*) and a diversity of perennial forb species. In the summers of 2019 and 2020, we collected inflorescences from 13 co-occurring perennial native forbs from four geographically separate sites (separated by approximately 2–81 km) within western Montana grasslands (Figure 1). Focal species were chosen because they are relatively common, consistently co-occur with each other in the grassland communities we sampled, and vary in seed size. Collections were made at the time when seeds were almost fully developed within infructescences, which varied by species depending on their phenology, ranging from July until mid-August. For each species, seeds of 20 individuals were collected at each site (Table 1), for a total of 80 individuals. At a subset of sites, only 19 individuals were collected for five species. At each site, we collected five infructescences from each individual with the exceptions of *Lupinus sericeus*, for which we collected 10 pods, and *Balsamorhiza sagittata*, *Gaillardia aristata*, *Geum triflorum*, and *Lomatium triternatum* for which we collected one infructescence per individual. We collected 10 pods from *L. sericeus* because individuals produced such a large number of pods that we had to collect 10 to achieve an accurate estimate of the magnitude of predispersal seed predation. For the species where only one infructescence was collected, this was the case because those species produce very few infructescences in total.

After collection, infructescences were carefully dissected in the laboratory and analyzed for seed damage/loss and the presence of insect herbivores. To calculate the level of seed loss due to herbivory on larger seeded species, we counted the number of damaged and undamaged seeds

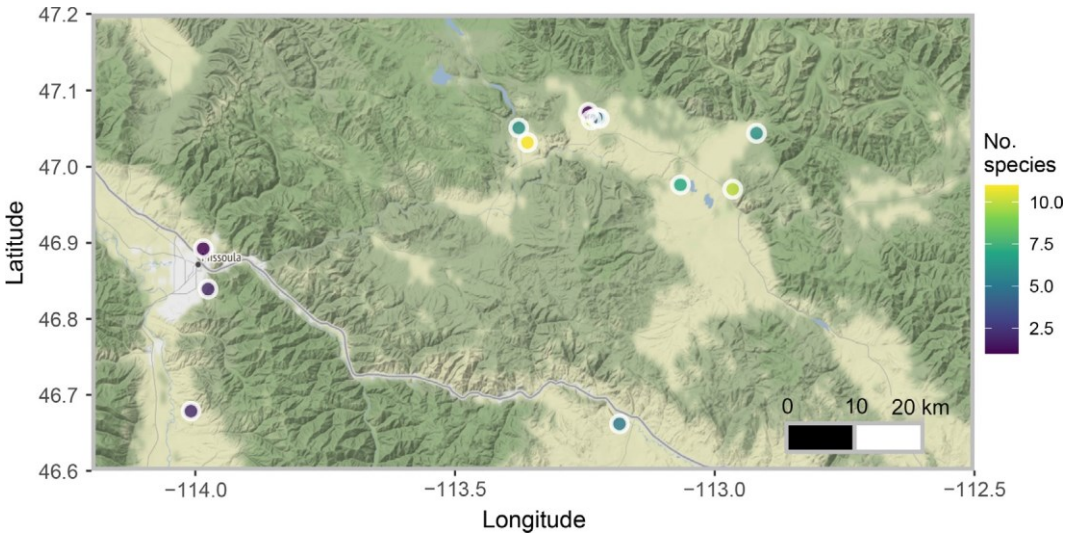

FIGURE 1 Map of study sites near Missoula, MT, USA. Points are colored by the number of species sampled at each site

TABLE 1 Genus and species of 13 focal plants, the number of sites where each plant was sampled in 2019 and 2020, mean seed loss due to predispersal seed predation for each species, seed nitrogen and carbon percentages, and the number of seed heads sampled per plant

Species	Family	No. sites 2019	No. sites 2020	Seed mass (mg)	Mean seed loss (%)	Seed N (%)	Seed C (%)	Sample description
Achillea millefolium	Asteraceae	0	4	0.09	1.9	5.3	53.5	5 infructescences
Arnica sororia	Asteraceae	4	0	0.75	0.0	3.7	52.8	1 head
Balsamorhiza sagittata	Asteraceae	0	4	8.33	26.4	4.5	51.6	1 head
Eriogonum umbellatum	Eriogonaceae	1	4	2.16	18.7	3.7	48.5	5 infructescences
Gaillardia aristata	Asteraceae	4	4	3.92	0.9	3.0	47.7	1 head
Geum triflorum	Rosaceae	4	4	0.77	1.4	4.4	52.5	1 head
Geranium viscosissimum	Geraniaceae	4	4	8.68	59.0	6.4	53.8	5 heads
Heterotheca villosa	Asteraceae	4	4	0.58	12.7	2.6	50.0	5 heads
Lomatium triternatum	Apiaceae	4	4	3.65	26.2	3.2	51.1	1 infructescence
Lupinus sericeus	Fabaceae	1	4	20.92	35.6	8.0	49.5	10 pods
Penstemon procerus	Plantaginaceae	3	4	0.05	0.6	3.0	58.0	5 heads
Potentilla glandulosa	Rosaceae	3	4	0.10	0.3	2.6	55.4	5 heads
Zigadenus venenosa	Melanthiaceae	4	4	1.38	7.1	3.6	56.0	5 heads

in each infructescence. The most common type of damage observed was chewing and the partial destruction of seeds; however, piercing and the near-complete destruction of seeds were also observed. For small-seeded, highly fecund species such as *Achillea millefolium*, *Penstemon procerus*, and *Potentilla glandulosa*, the proportion of seeds damaged was estimated by counting damaged seeds under a dissecting microscope and comparing the number of damaged seeds with the fecundity of a typical inflorescence for that species that had no insect damage. Fecundity was estimated as described in Maron et al. (2018). Briefly, we quantified average per capita seed production by randomly selecting a minimum of five individuals of average size per site (from a minimum of at least four sites; $n > 20$ individuals per species) and estimating fecundity of each individual by counting the number of seeds in one undamaged head or fruiting body and multiplying that number by the total number of heads or fruits produced by that individual. For two target species (*B. sagittata and L. sericeus*), we utilized fecundity estimates (in the absence of herbivory) from our previous work (Amsberry & Maron, 2006; Bricker et al., 2010). For one species, *Zigadenus venenosa*, the damage was estimated by examining chambers on each seed head. If a chamber was damaged, we assumed all seeds inside the damaged chamber were consumed by herbivores. For species with more than one seed head, the

proportion of damaged to undamaged seeds was averaged across each of the seed heads, with the exception of *L. sericeus*, where many pods had opened between collection and analyses. Insect herbivores found in infructescences were identified to determine the most common family feeding on each species. Recruitment reductions due to postdispersal seed predation by rodents were determined using data from a previous study where rodents were experimentally excluded from study plots containing the same focal species that were used in this study (Maron et al., 2018).

Traits

For each focal species, seed weight, seed nitrogen, and seed carbon content were measured as part of a previous study (Maron et al., 2018; unpubl. data). At six sites, we haphazardly selected five reproductively mature individuals of each focal species and collected leaf tissue from each individual. These leaves were air-dried and sent to the Colorado Plateau Analytical Laboratory for determination of %N and %C. Seeds were shipped to the U.C. Davis Analytical Laboratory for determination of seed nitrogen and carbon content, using standard analytical techniques. To determine seed mass, five different samples of seeds were collected (one for each of five different individuals). Depending on the size of seeds, each sample consisted of between 5 and 348 seeds that were counted out and then weighed to determine the weight of each seed, which was then averaged across the five estimates.

Data analysis

To evaluate how seed traits influenced the proportion of seed loss due to insect herbivores, we constructed a linear mixed-effect model. The response variable was proportion seed loss, logit-transformed, which is appropriate for proportional data (Warton & Hui, 2011). Because the logit transformation cannot be executed on zeros or ones, we applied a small correction to the data to remove zeros and ones as follows: $y' = [y(N-1) + 0.5]/N$, where N is the sample size (Smithson & Verkuilen, 2006). As predictor variables, we included $\log_{10}$-transformed seed size (in milligrams), seed nitrogen content (%), and seed carbon content (%). Nonsignificant predictor variables were sequentially dropped from the final model. Species, site, and year were included as random effects to account for the multiple samples measured at each of these levels (Table 1). Models were fit using lme4::lmer (Bates et al., 2015). F values, p values, and df were calculated using the Kenward-Rogers method using lmerTest::anova (Kuznetsova et al., 2017). Marginal and conditional R^2 were calculated using MuMIn::r.squaredGLMM (Barton, 2020; Nakagawa et al., 2017).

To test the relationship between pre- and postdispersal seed predation, we correlated predispersal seed loss with the effect size postdispersal seed predation by rodents. The rodent effect was calculated as the log response ratio of the proportion of seeds that recruited into plots in and out of rodent exclosures (see Maron et al., 2018).

RESULTS

Average seed loss, pooled across all species, was 15.8% (95% CI: 3.5%, 33.6%). There was also considerable variation among species, but this was not predicted by either seed nitrogen or carbon content in the multiple regression, and thus, these traits were removed from the final model. The final model contained only $\log_{10}$-transformed seed size, which was positively related to seed damage (Figure 2a; $F_{1,11.0} = 9.5$, $p = 0.01$). Small-seeded species experienced close to 0% seed loss, whereas many large-seeded species experienced greater than 50% seed loss (Figure 2a). Seed size explained 22.3% of the variation in seed loss among species ($R^2_m = 0.223$). An additional 38.7% of the variation in seed loss was explained by the random effects ($R^2_c = 0.612$). The total variation not explained by $\log_{10}$-transformed seed size was 11.79, which included a residual variance component of =5.91. A substantial proportion of the random-effect variation occurred across species (variance component = 4.93). Less variation occurred across sites (variance component = 0.94), and very little occurred across years (variance component = 0.008). Reductions in recruitment due to postdispersal seed predation by rodents were not correlated with seed loss due to predispersal seed predation by insects (Figure 2b; Pearson's = 0.007, p =0.98).

DISCUSSION

To our knowledge, this is the first examination of interspecific variation in seed loss due to predispersal insect seed predation across a broad suite of co-occurring species in a grassland system. Our goal was to determine background levels of seed predation at the community level and assess whether particular plant traits predicted interspecific variation in predispersal seed predation. If traits correlate with seed loss, then this would enable the prediction of the species that might be most negatively affected by strong interactions with herbivores. We found that at the community scale, the average level of

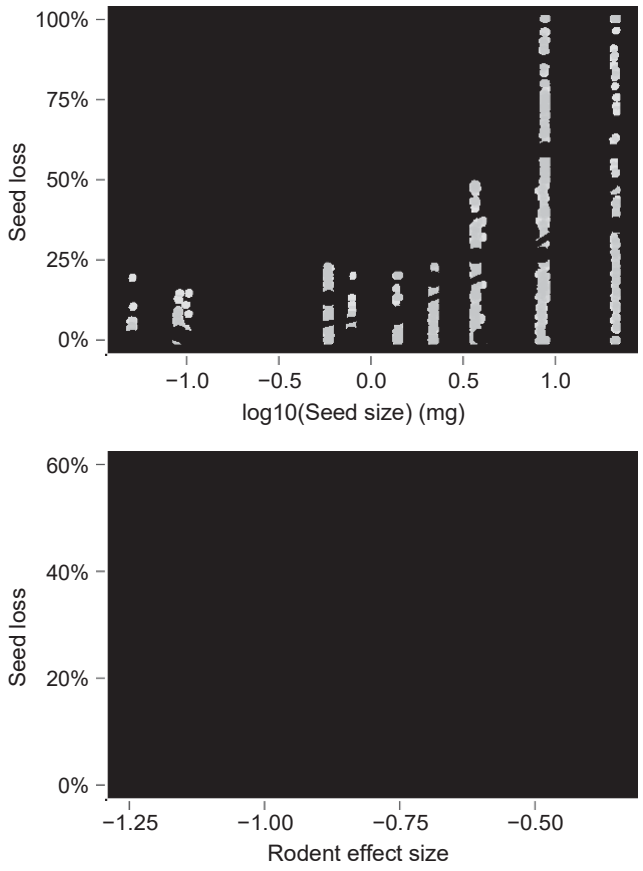

FIGURE 2 (a) Relationship between seed mass (log-transformed) and the percentage of seeds lost to predispersal seed predators (seed loss). Each large black dot represents a different species, and each small dot represents an individual plant. The line is a prediction line from a GLMM fit through the species' means. (b) Relationship between the effect size of postdispersal seed predation by rodents on recruitment. More negative values indicate a greater decrement in recruitment due to postdispersal seed predation by rodents (see section "Methods") and the percentage of seeds lost due to predispersal seed predation (i.e., seed loss)

predispersal seed loss was relatively small (mean = 15.8%), although seed loss was highly variable across species, with some species experiencing near-zero loss, while for others, seed loss was substantial (upward of 50%). Importantly, however, the magnitude of predispersal seed predation was positively correlated with seed size across our 13 co-occurring grassland forb species (Figure 2a). Thus, predispersal seed predation produced clear asymmetries in seed loss among species rather than being a ubiquitous drain on the fecundity of all co-occurring species evenly.

Studies of single species have shown that large-seeded species often suffer from high levels of predispersal seed predation, but that the magnitude of predispersal seed predation can be highly variable even among these large-seeded species (Amsberry & Maron, 2006; Kolb et al., 2007; Kurkjian et al., 2016). Our study expands this body of work by showing that large-seeded species experience consistently higher levels of predispersal seed predation than do co-occurring smaller seeded species in complex grassland communities. Five species (*L. triternatum*, *L. sericeus*, *Eriogonum umbellatum*, *Geranium viscosissimum*, and *B. sagittata*) suffered the highest levels of predispersal seed predation (Table 1). These species were attacked mostly by insects in the families *Curculionidae* (weevils) and *Tenthredinidae* (sawflies) although the species with the highest level of seed loss (mean = 59%), *G. viscosissimum*, was attacked primarily by sawflies. Across all species, weevils were the most commonly observed insect herbivore in the infructescences we dissected. Two relatively large-seeded species, *Heterotheca villosa* and *G. aristata*, experienced surprisingly low levels of predispersal seed predation. It is unclear why this is the case; perhaps these species produce highly defended seeds. Small-seeded species (e.g., *Achillea*, others) experienced near-zero seed predation.

How might declines in seed production due to insect herbivores influence recruitment and future plant abundance? In our system, seedling recruitment among our focal species is strongly seed-limited (Maron et al., 2019). Thus, losses in the number of viable seed due to predispersal seed predation can be expected to directly suppress recruitment and future plant abundance, a result that has been shown in other systems (Baer & Maron, 2018; Combs et al., 2011; Espelta et al., 2009; Louda & Potvin, 1995). Also, since small-seeded species produce more seeds than larger seeded ones, in our system these species experience relatively larger increases in recruitment compared with larger seeded species when safe sites are sufficiently available (Maron et al., 2019). This study suggests that this recruitment advantage is likely enhanced due to differences among these species in the magnitude of predispersal seed predation.

Research examining seed-sized bias in seed predation and its effects on plant recruitment mainly come from studies of postdispersal seed predation by rodents (Brown & Heske, 1990; Larios et al., 2017; Lucero & Callaway, 2018; Maron et al., 2012, 2018; Pearson et al., 2011). These studies show that rodent exclusion promotes enhanced recruitment and establishment of larger seeded species, but not smaller seeded ones. Literature reviews of studies examining seed loss for single species have found a slight negative correlation between seed size and postdispersal seed predation (Moles et al., 2003). These results, however, are potentially misleading because they analyze studies from disparate systems where differences in relative seed size can be extreme. In a recent meta-analysis, Dylewski et al. (2020) found that postdispersal seed predation increases with seed mass until seeds become large enough to limit the ability of seed predators to handle them. In grassland systems, where seeds tend to be relatively small compared with forest systems,

postdispersal seed predation increases predictably with seed mass (Hulme, 1998; Reader, 1993), much like we found for predispersal seed predation.

A previous study in our system (utilizing the same focal species) demonstrated that postdispersal seed predation by rodents more strongly inhibited recruitment of larger versus smaller seeded species (Maron et al., 2018). This begs the question, are the species that experience the greatest reductions in recruitment due to rodent seed predation also those that experience the highest levels of predispersal seed predation? We found that this was not the case. In other words, the effects of rodent seed predation on the recruitment of our focal species were not correlated with levels of predispersal seed predation for those same species (Figure 2b). For instance, *G. viscosissimum* and *L. sericeus* suffered the highest number of seed loss due to predispersal seed predation, but these species do not suffer the highest reductions in recruitment due to postdispersal seed predation. Additionally, *G. aristata*, which, despite being a large-seeded species, experienced very little seed loss due to predispersal seed predation, but the greatest reductions in recruitment due to postdispersal seed predation (Maron et al., 2019). *Zigadenus venenosa* also experienced a large reduction in recruitment due to postdispersal seed predation but had very low levels of predispersal seed predation. Thus, large-seeded species generally are more vulnerable to the negative effects of both pre- and postdispersal seed predators, but particular large-seeded species did not experience a cumulative net effect of both pre- and postdispersal seed predation. The reason why there is no correlation between the magnitude of pre- and postdispersal seed predation at the species level in this system remains unclear. However, this may be because pre- and postdispersal seed predators use different cues when selecting which seeds to predate. More research is needed to fully disentangle these processes.

The magnitude of predispersal seed predation can vary spatially (Kolb et al., 2007; Leimu & Lehtilä, 2006; Maron & Crone, 2006); however, our measurements did not significantly vary among sites. This may be because variation among sites in environmental factors shown to influence the magnitude of predispersal seed predation, such as soil moisture or vegetation height, heat, or rainfall, was not large enough to influence insect populations or how plants respond to seed loss (Denlinger, 1980; Savopoulou-Soultani et al., 2012; Traveset, 1991). This suggests that the magnitude of predispersal seed predation in Western Montana grasslands is better predicted by plant traits such as seed mass rather than abiotic factors that may affect herbivore abundance.

One important caveat to our study is that we assumed that all damaged seed for any given species would eventually be viable if plants were free from predispersal seed predators. However, due to potential resource constraints, it is possible that some damaged seed might have never fully developed. This can only be tested through a manipulative experiment, where herbivores were excluded from some plants and not others and fecundity between treatments was compared. For one of our focal species, *B. sagitata*, Amsberry and Maron (2006) found that predispersal seed predation reduced seed production in *B. sagittata* by an average of 18%, roughly similar to what we found (26%). Thus, it may be that our estimates of seed loss are not grossly overinflated. Additionally, it is possible that some damaged seed may still have been able to achieve germination. However, we believe this is very unlikely because seed predators removed a substantial portion of endosperm in seeds that were attacked.

Our results suggest that large-seeded species should be especially vulnerable to predispersal seed loss by insects in grassland systems. Although overall levels of seed predation in our study were quite moderate, larger seeded species that are often seed-limited (Turnbull et al., 2000) may routinely have their recruitment, and even adult abundance compromised by inconspicuous herbivory.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Palmer, 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.5834845.

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