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Laboratory Performance and Two-Year Field Assessment of the Seed-Feeding Beetle Algarobius Prosopis Against Recruitment of Invasive Prosopis Juliflora in Oman

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ABSTRACT

Mesquite [Prosopis juliflora (Sw.) DC.] is among the most problematic invasive woody plants in Oman; its prolific seed production drives spread and recruitment. We evaluated the seed-feeding beetle Algarobius prosopis (LeConte) (Coleoptera: Chrysomelidae: Bruchinae) in laboratory experiments and a two-year field comparison in Barka, South Al Batinah Governorate. Across 100 paired mature-pod samples, mean sample mass declined from 133.48 ± 5.15 g before beetle exposure to 67.02 ± 2.60 g after exposure (mean loss 66.46 ± 2.58 g, or 49.79 ± 0.19%; Wilcoxon signed-rank test, $P < 0.001$). Adult emergence holes averaged 15.81 ± 2.22 per sample but were not associated with mass loss (Spearman $\rho = 0.118$, $P = 0.241$). Reproduction succeeded in all four mature-pod cages and in none of four immature-pod cages (Fisher exact test, $P = 0.029$), and F1 adults emerged in all 90 single-pair containers provisioned with two, four, or eight mature pods, approximately 60 d after exposure. No F1 adults emerged from chickpea (Cicer arietinum L.), faba bean (Vicia faba L.), or common bean (Phaseolus vulgaris L.) in nine replicated exposures. Following release of 17,360 laboratory-reared adults at four sites, recent mesquite recruitment was not detected at any release site during two years of monitoring, whereas it was present at all three untreated control sites, particularly after rainfall (Fisher exact test, $P = 0.029$). These results indicate that A. prosopis can be mass-reared on mature mesquite pods and that its release was associated with reduced mesquite recruitment under Omani field conditions. Because the field comparison involved few sites and lacked pre-release seedling counts, and because non-target screening was limited to three crop legumes, the findings should be regarded as preliminary evidence justifying expanded host-range testing, seed-viability assessment, and replicated field trials before A. prosopis is incorporated into integrated mesquite management programs.

INTRODUCTION

Species of the genus Prosopis sensu lato, commonly called mesquite, are among the most widespread and damaging woody invaders in arid and semiarid regions worldwide (Shackleton *et al.*, 2014). Originally introduced for fuelwood, fodder, shade, and sand-dune stabilization, mesquite has formed dense thickets across parts of Africa, Asia, Australia, and the Arabian Peninsula, where it reduces native plant diversity, depletes groundwater, obstructs access to grazing land and water points, and has been associated with allergenic pollen (Hussain *et al.*, 2020; Pasiecznik *et al.*, 2001; Shackleton *et al.*, 2014). Recent taxonomic work has transferred Prosopis juliflora (Sw.) DC. to the genus Neltuma (Hughes *et al.*, 2022); we retain the name P. juliflora here because it remains the name used in management and regulatory literature in the region.

In Oman, P. juliflora is recognized as an invasive alien species that occurs across a wide range of habitats, including wadis, farmland margins, roadsides, and coastal plains (Patzelt *et al.*, 2022). In the neighboring United Arab Emirates, invasion by P. juliflora reduced native species richness and altered soil properties beneath its canopy (El-Keblawy & Al-Rawai, 2007). Mechanical clearing and herbicide treatments are costly, must be repeated because of resprouting and recruitment from the soil seed bank, and are difficult to apply across extensive or inaccessible areas (Shackleton *et al.*, 2014). In addition, mesquite provides fuelwood, fodder, and shade to some rural users, which creates conflicts of interest that complicate control programs (Shackleton *et al.*, 2015).

Mesquite produces large numbers of hard-coated seeds that are dispersed by livestock, wildlife, and water, and this reproductive output is a principal driver of its spread (Pasiecznik *et al.*, 2001; Shackleton *et al.*, 2014). Because agents that attack seeds do not destroy the useful woody biomass of established trees, seed-feeding bruchine beetles have been the first choice for biological control of mesquite in several countries (Moran *et al.*, 1993; Zachariades *et al.*, 2011). In South Africa, Algarobius prosopis (LeConte) was released in 1987, established rapidly, and destroyed substantial proportions of the annual seed crop, although its impact was constrained where livestock consumed pods before beetles could complete development (Impson *et al.*, 1999; Zachariades *et al.*, 2011; Zimmermann, 1991). Interspecific competition among introduced bruchids also influenced which species persisted (Coetzer & Hoffmann, 1997; Hoffmann *et al.*, 1993). In Australia, where biological control of mesquite has also been pursued (van Klinken *et al.*, 2003), A.

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prosopis attacks seeds both before and after dispersal, including seeds that pass through livestock dung (van Klinken & White, 2011, 2014). The general consensus from these programs is that seed feeders can reduce seed input substantially but should be integrated with other methods rather than used alone to control established infestations (Zachariades *et al.*, 2011; Zimmermann, 1991). Whether seed predation translates into reduced plant recruitment depends on the degree to which populations are seed-limited (Maron & Crone, 2006). Evaluating an agent therefore requires evidence at several levels: the ability of the agent to develop and reproduce on the target, the plant stages it can exploit, its safety for nontarget plants, and its effects on recruitment in the field (Schwarzländer *et al.*, 2018; Sheppard *et al.*, 2005). Host specificity is especially important in the Arabian Peninsula, where the native ghaf tree [Prosopis cineraria (L.) Druce] is culturally and ecologically valued and is congeneric with the target in the traditional sense (Pasiecznik & Felker, 2006). Although direct nontarget attack by weed biological control agents is uncommon and largely predictable from host-range testing (Hinz *et al.*, 2019), testing plans should follow the centrifugal phylogenetic approach and prioritize close relatives and economically important species (Schaffner, 2001; Wapshere, 1974).

To our knowledge, no published study has evaluated the laboratory performance and field effects of A. prosopis against P. juliflora in Oman. The objectives of this study were to (1) quantify changes in pod sample mass and adult emergence following beetle exposure; (2) determine whether successful reproduction depends on pod maturity; (3) confirm development across different numbers of pods per beetle pair; (4) conduct a preliminary screen of three locally important crop legumes; and (5) compare recent mesquite recruitment between release sites and untreated control sites over two years in Barka, Oman.

Finally, although no offspring developed on chickpea, faba bean, or common bean, the beetle has not yet been tested on the native ghaf tree (Prosopis cineraria) or on a wider range of native legumes. Further releases outside the current study area should therefore await the results of expanded host-range testing and approval from the relevant national authorities.

Management Implications

Mesquite spreads mainly through seed, and each new cohort of seedlings becomes a future stand that is expensive to remove mechanically or chemically. This study shows that the seed-feeding beetle Algarobius prosopis can be multiplied in large numbers on mature mesquite pods in a local laboratory and released into invaded sites in Oman. During two years after release of 17,360 beetles, no recent mesquite recruitment was found at any of the four release sites, whereas new seedlings appeared at all three untreated sites, especially after rain. For land managers, the beetle is therefore best viewed as a low-cost, self-sustaining tool that targets the seed stage and may slow the establishment of new plants, not as a means of killing established trees.

Practitioners should combine beetle releases with existing measures that remove or suppress established trees, so that seed production and recruitment are reduced at the same time as standing biomass. Because the beetle reproduced only on mature pods, releases are most likely to succeed when timed to coincide with mature pod availability, and removing pods before they mature would reduce the resources the beetle needs. Because livestock and wildlife readily eat mesquite pods, managers should also consider how grazing and pod collection interact with beetle populations.

MATERIALS AND METHODS

Study Organism and Colony Establishment

A seed-beetle population identified as A. prosopis was recovered from mesquite pods collected in Al Musannah, South Al Batinah Governorate, Oman. Adults were multiplied in the Biological Control Research Laboratory on mature mesquite pods before experimental use and field release. Colonies were maintained in closed rearing cages under laboratory conditions, and adults from this colony were used in all experiments and field releases.

Pod Mass and Adult Emergence

One hundred mature-pod samples were each weighed on a laboratory balance immediately before beetle exposure and again after the exposure and emergence period. Adult emergence holes were counted on each sample. Absolute mass loss was calculated as initial mass minus final mass, and percentage mass loss as 100 × (initial mass − final mass)/initial mass. All masses were measured directly; no values were imputed. No beetle-free control samples were included in this experiment.

Pod Maturity Experiment

Immature (green, tender) and mature mesquite pods were compared in closed wooden cages. Each cage contained 100 pods and 26 male–female pairs (52 adults). Each treatment was replicated four times, with replicates conducted independently across two years. Successful reproduction was recorded as a binary cage-level response based on emergence of F1 adults, and the cage, not the individual pod, was treated as the experimental unit.

Pod-Number Exposure and Developmental Period

A single male–female pair was confined in each container with two, four, or eight mature pods. Each treatment had 30 independent containers (90 in total). Successful F1 emergence was recorded for each container. The interval from exposure to emergence of the next adult generation was approximately 60 d; this was an overall observati

Chickpea, faba bean, and common bean were selected because they are cultivated legumes of local economic importance. Each crop was represented by three independent replicates, and each replicate was exposed to six male–female pairs (12 adults) in a container holding seeds of the test crop. Successful reproduction

was defined as emergence of F1 adults. Beetles used in the screen came from the same laboratory colony that reproduced successfully on mature mesquite pods in the experiments described above.

a Each pod-maturity cage contained 100 pods. Pod maturity: two-sided Fisher exact test, P = 0.029. Pod-number treatments were not compared statistically because all units produced F1 adults. Nontarget screen: chickpea, Cicer arietinum; faba bean, Vicia faba; common bean, Phaseolus vulgaris; one-sided 97.5% exact upper bound for reproduction probability = 0.34 (0/9 overall).

Field Release and Post-release Monitoring

Following laboratory multiplication, 17,360 adult A. prosopis were released at four mesquite-invaded sites in Barka, South Al Batinah Governorate, Oman: Site A, 5,400 adults; Site B, 2,560; Site C, 5,780; and Site D, 3,620. Three additional mesquite-invaded sites in Barka without beetle release served as untreated controls. All seven sites were monitored for two consecutive years through repeated site visits for the presence or absence of recent mesquite recruitment, defined as the presence of newly emerged mesquite seedlings that had established during the monitoring period. New recruitment following rainfall events was also recorded. The site was the experimental unit for the field comparison to avoid pseudoreplication (Hurlbert, 1984).

Statistical Analysis

Analyses followed recommendations for weed science research (Onofri *et al.*, 2010; Ritz *et al.*, 2015) and were conducted in Python v. 3.11 with SciPy v. 1.17 (Virtanen *et al.*, 2020). Continuous variables are reported as mean ± SD. Normality of the paired mass differences was assessed with the Shapiro-Wilk test. Because the differences departed from normality (W = 0.910, P < 0.001), the Wilcoxon signed-rank test was used as the primary test of pre- versus post-exposure mass, with effect size expressed as $r = Z/\sqrt{n}$; the paired t-test and the 95% confidence interval (CI) for mean mass loss are reported as a sensitivity analysis. The association between emergence-hole counts and absolute mass loss was assessed with Spearman rank correlation (primary) and Pearson correlation (complementary). Two-sided Fisher exact tests were used for the 2 × 2 comparisons of successful reproduction by pod maturity and of recent recruitment by field treatment because of small sample sizes. For outcomes with zero or complete success, exact (Clopper-Pearson) one-sided 97.5% binomial bounds were calculated to indicate the precision of the observed proportions. Significance was assessed at $\alpha = 0.05$.

RESULTS AND DISCUSSION

Pod Mass Change and Adult Emergence

Mean pod sample mass declined from 133.48 ± 5.15 g before beetle exposure to 67.02 ± 2.60 g after exposure (Figure 1). Mean loss was 66.46 ± 2.58 g (95% CI, 65.95 to 66.97 g; median 67 g, interquartile range 64 to 69 g), corresponding to 49.79 ± 0.19% of initial mass. The Wilcoxon signed-rank test indicated a significant difference between pre- and post-exposure mass (W = 0, P < 0.001; r = 0.87), and the sensitivity analysis led to the same conclusion (paired t99 = 258.02, P < 0.001) (Table 2). These results show a substantial reduction in pod mass during beetle exposure. However, because no beetle-free control samples were weighed over the same period, part of the loss may be attributable to moisture loss rather than to larval feeding alone, and the magnitude of beetle-induced loss cannot be isolated from these data. Future experiments should include paired unexposed pods held under identical conditions and should measure seed destruction directly, for example as the proportion of seeds with emergence holes and the germination of intact and attacked seeds.

Adult emergence holes averaged 15.81 ± 2.22 per sample (range, 12 to 19). The number of holes was not significantly associated with absolute mass loss (Spearman $\rho = 0.118$, P = 0.241; Pearson r = 0.137, P = 0.174) (Figure 2). Emergence holes therefore document adult production but should not be used as a surrogate for pod mass loss in this system. This is plausible biologically, because each emergence hole represents one seed destroyed by one larva, whereas pod mass also includes the sugary mesocarp and endocarp, which make up most of the pod mass and are not the primary larval resource.

Effect of Pod Maturity and Pod Number

Successful reproduction occurred in all mature-pod cages (4/4) and in none of the immature-pod cages (0/4) (two-sided Fisher exact test, P = 0.029) (Table 1). With four replicates per treatment, this is the smallest P value attainable, and the one-sided 97.5% exact lower bound for the probability of reproduction on mature pods was 0.40. The result indicates strong dependence on pod stage under the conditions tested and agrees with earlier work showing that A. prosopis is most damaging to seeds in mature pods and that complementary agents may be needed to attack earlier pod stages (Moran *et al.*, 1993). In practical terms, the dependence on mature pods implies that beetle populations will build up only when mature pods are available, and that release timing should be matched to the pod-ripening period.

All 90 single-pair containers produced F1 adults, irrespective of whether they contained two, four, or eight pods (30/30 in each treatment) (Table 1), and the next generation emerged approximately 60 d after exposure. Because no variation occurred among treatments, no statistical comparison was made. These results confirm that a single pair can complete a generation with as few as two mature pods, which is useful for designing economical mass-rearing systems. However, because F1 numbers were not recorded, the data do not allow comparison of offspring production among pod densities; counting offspring per container would allow optimization of rearing density in future work.

Preliminary Nontarget Crop Screening

No F1 adults emerged from chickpea, faba bean, or common bean (0/3 replicates for each crop; 0/9 overall) (Table 1). This is a positive initial result under the conditions tested, but its precision is limited: with nine replicates, the one-sided 97.5% exact upper bound for the probability of reproduction on these crops combined was 0.34, and with three replicates per crop it was 0.71. The screen therefore does not establish host specificity. Internationally accepted risk assessment for weed biological control agents requires a structured test plant list selected by phylogenetic relatedness, ecological overlap, and economic importance, together with concurrent positive controls on the target plant (Schaffner, 2001; Sheppard *et al*., 2005; Wapshere, 1974). In Oman, the priority should be the native P. cineraria, which is the closest native relative of the target and has considerable cultural and ecological value (Pasiecznik & Felker, 2006), followed by native Acacia sensu lato and other mimosoid legumes, and additional crop legumes. The generally favorable safety record of weed biological control worldwide (Hinz *et al*., 2019) does not remove the need for this site-specific testing.

Field Recruitment after Release

During two years of monitoring, recent mesquite recruitment was not observed at any of the four release sites (0/4), whereas all three untreated control sites (3/3) supported new recruitment, particularly after rainfall (two-sided Fisher exact test, $P = 0.029$) (Table 3). This pattern is consistent with suppression of recruitment at release sites and with the biology of A. prosopis as a seed predator that can destroy a large proportion of mesquite seed before and after dispersal (van Klinken & White, 2011, 2014; Zimmermann, 1991). It is also consistent with the expectation that seed predation reduces recruitment most strongly in seed-limited plant populations (Maron & Crone, 2006).

Several limitations constrain causal interpretation of the field result. First, only seven sites were included, allocation of sites to treatments was not randomized within a formal experimental design, and presence or absence of recruitment is a coarse response. Second, no pre-release seedling counts, seed-bank estimates, or measures of beetle establishment and pod infestation at release sites were available, so differences among sites in stand age, soil moisture, grazing pressure, flooding, or seed rain could have contributed to the observed pattern. Third, the number of beetles released differed among sites, and the small sample size did not permit analysis of release intensity. Given these constraints, the field comparison should be interpreted as correlative evidence that is consistent with, but does not prove, a causal effect of A. prosopis on recruitment.

Implications and Future Research

Taken together, the laboratory and field results link seed-stage performance of A. prosopis with recruitment outcomes in the field and support its evaluation as a component of integrated mesquite management in Oman. Experience in South Africa indicates that seed-feeding bruchids can destroy large quantities of seed but are unlikely on their own to reduce the density of established mesquite stands, and that their effect is reduced where livestock consume pods before beetle development is complete (Impson *et al*., 1999; Zachariades *et al*., 2011; Zimmermann, 1991). Beetle releases should therefore be combined with mechanical, chemical, or utilization-based control of established trees and with grazing management.

Priorities for future work are (1) expanded, phylogenetically structured host-range testing that includes P. cineraria and native mimosoid legumes, with concurrent positive controls; (2) direct measurement of seed destruction and seed viability in exposed and unexposed pods; (3) replicated, randomized field trials with pre- and post-release counts of seedlings, pod infestation, and beetle abundance, and with release rate as a factor; and (4) assessment of interactions between beetle populations and livestock consumption of pods.

CONCLUSION

This study provides the first evaluation of the seed-feeding beetle Algarobius prosopis against invasive Prosopis juliflora in Oman. The beetle was readily multiplied in a local laboratory on mature mesquite pods, completed a generation in approximately 60 d, and reproduced with as few as two pods per pair, but it failed to reproduce on immature pods. Beetle exposure was accompanied by a substantial reduction in pod mass, and no offspring developed on chickpea, faba bean, or common bean. Over two years after the release of 17,360 adults, recent mesquite recruitment was absent from all release sites but present at all untreated control sites. These findings are important because they indicate that a low-cost, self-sustaining agent acting on the seed stage could limit the formation of new mesquite stands without removing the fuelwood, fodder, and shade that established trees provide to rural communities. The conclusions are nevertheless constrained by the small number of field sites, the absence of randomized site allocation and pre-release seedling counts, the lack of beetle-free control pods, and a nontarget screen limited to three crop legumes. Accordingly, A. prosopis should be regarded as a promising complement to, rather than a replacement for, mechanical, chemical, and grazing-based management of established mesquite, with releases timed to coincide with mature pod availability. Before wider deployment, it is recommended that phylogenetically structured host-range testing, including the native ghaf tree (Prosopis cineraria) and other native mimosoid legumes, be completed; that seed destruction and seed viability be measured directly; and that replicated, randomized field trials quantify recruitment, pod infestation, and beetle establishment. Releases outside the current study area should proceed only with approval from the relevant national authorities.

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Table 1 : Experimental design and principal reproductive outcomes of Algarobius prosopis in laboratory experiments.[a]

Experiment	Treatment	Experimental unit (n)	Adults per unit	Units with F1 emergence
Pod maturity	Immature pods	Cage (4)	52 (26 pairs)	0/4
	Mature pods	Cage (4)	52 (26 pairs)	4/4
Pod number	2 mature pods	Container (30)	2 (1 pair)	30/30
	4 mature pods	Container (30)	2 (1 pair)	30/30
	8 mature pods	Container (30)	2 (1 pair)	30/30
Nontarget screen	Chickpea	Replicate (3)	12 (6 pairs)	0/3
	Faba bean	Replicate (3)	12 (6 pairs)	0/3
	Common bean	Replicate (3)	12 (6 pairs)	0/3

[a] *Each pod-maturity cage contained 100 pods. Pod maturity: two-sided Fisher exact test, P = 0.029. Pod-number treatments were not compared statistically because all units produced F1 adults. Nontarget screen: chickpea, Cicer arietinum; faba bean, Vicia faba; common bean, Phaseolus vulgaris; one-sided 97.5% exact upper bound for reproduction probability = 0.34 (0/9 overall).*

Table 2 : Statistical summary of the pod mass, emergence, pod maturity, and field recruitment outcomes for Algarobius prosopis.[a]

Outcome	Estimate	Statistical test	Interpretation
Pod sample mass (n = 100)	133.48 ± 5.15 g before; 67.02 ± 2.60 g after	Wilcoxon signed-rank W = 0, P < 0.001; r = 0.87	Significant pre–post decrease
Absolute mass loss	66.46 ± 2.58 g (95% CI, 65.95–66.97); 49.79 ± 0.19%	Paired t99 = 258.02, P < 0.001 (sensitivity analysis)	Same conclusion as primary test
Emergence holes	15.81 ± 2.22 per sample (range, 12–19)	Descriptive	Adult emergence documented
Emergence holes vs. mass loss	Spearman ϱ = 0.118; Pearson r = 0.137	P = 0.241; P = 0.174	No significant association
Pod maturity	0/4 immature vs. 4/4 mature cages	Fisher exact P = 0.029	Reproduction depended on pod stage
Field recruitment	0/4 release vs. 3/3 control sites	Fisher exact P = 0.029	Recruitment differed by treatment

[a] *Values are mean ± SD unless stated otherwise. CI, confidence interval; r (Wilcoxon), effect size calculated as Z/√n. All Fisher exact tests are two-sided.*

Table 3 : Release intensity of Algarobius prosopis and presence of recent Prosopis juliflora recruitment during two years of monitoring at seven sites in Barka, Oman.[a]

Site	Treatment	Adults released (no.)	Recent recruitment
A	A. prosopis release	5,400	Absent
B	A. prosopis release	2,560	Absent
C	A. prosopis release	5,780	Absent
D	A. prosopis release	3,620	Absent
Control 1	Untreated	0	Present

Control 2	Untreated	0	Present
Control 3	Untreated	0	Present
Total		17,360	

[a] *Recruitment at untreated control sites was particularly evident after rainfall. Release vs. control: two-sided Fisher exact test, P = 0.029.*

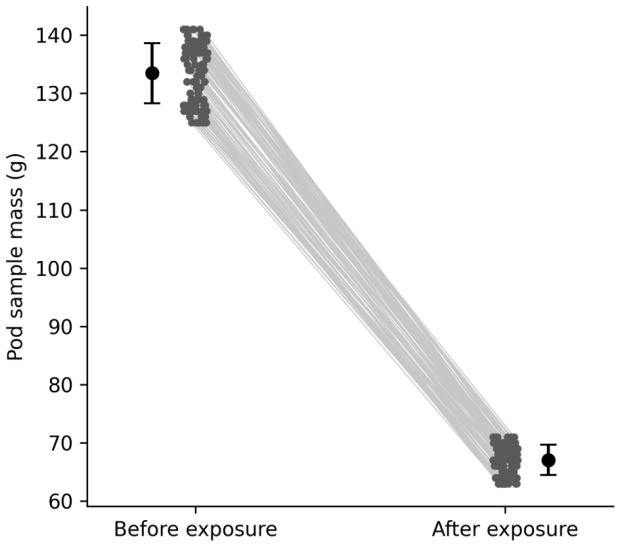


Figure 1: Mass of mature Prosopis juliflora pod samples before and after exposure to Algarobius prosopis (n = 100 paired samples). Gray lines connect paired measurements; black symbols show means ± SD. Wilcoxon signed-rank test, P < 0.001.

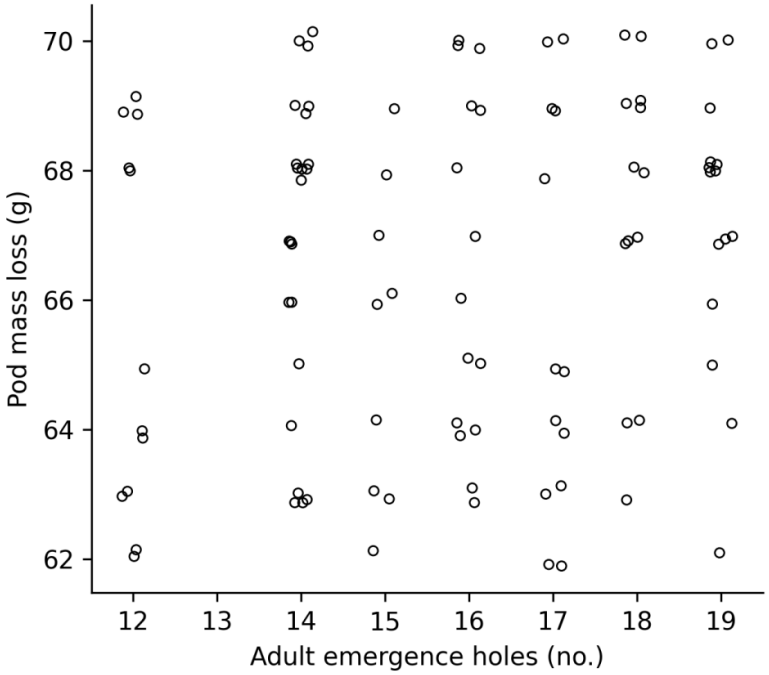


Figure 2: Relationship between the number of Algarobius prosopis adult emergence holes and absolute mass loss of Prosopis juliflora pod samples (n = 100). Points are jittered slightly to reduce overlap. Spearman ϱ = 0.118, P = 0.241.