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Brian M. Connolly
Gonzaga University, connollyb@gonzaga.edu

Francesca Lanni
Hamilton College

John L. Orrock
University of Wisconsin-Madison

Peter W. Guiden
Hamilton College, pguiden@hamilton.edu

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Seed coatings containing capsaicin reduce seed removal on temperate woody species

Francesca Lanni[1]
Brian M. Connolly[2,3]
John L. Orrock[4]
Peter W. Guiden[1,*]

1. Biology Department, Hamilton College, Clinton NY 13323
2. Biology Department, Gonzaga University, Spokane WA 99258
3. Biology Department, Eastern Michigan University, Ypsilanti MI 48197
4. Department of Integrative Biology, University of Wisconsin, Madison, WI 53706

*Corresponding author: pguiden@hamilton.edu

Abstract

Coating seeds in taste-averting chemical defenses (e.g., capsaicin from *Capsicum* spp.) can reduce rodent seed predation, and thus might promote plant establishment and forest regeneration. However, the efficacy of such seed coatings remains unknown for many woody plant species, and seed coatings have not been evaluated across different habitats where forest managers might seek to promote forest regeneration. We used two complementary seed-removal experiments in closed-canopy forests (Michigan) and an old field undergoing reforestation (New York) to examine whether coating seeds of four native tree species (*Acer rubrum*, *Fagus grandifolia*, *Pinus banksiana*, *Pinus resinosa*) with chili powder reduces seed removal by rodents. In all species and habitats, control seeds were removed more than seeds treated with capsaicin (94% more in the closed-canopy forest, 17% more in the old field). Seed coatings containing capsaicin may provide a generally effective tool to support native tree recruitment and promote restoration success.

Keywords:

Chemical defense; Forest regeneration; Reforestation; Rodent; Seed coating

Introduction

Seed survival is an essential component of tree recruitment that ultimately impacts the abundance, composition, and diversity of forest communities (Ward et al. 2018, Hansen and Turner 2019, Hoecker et al. 2020, Magee et al. 2021). Promoting the seed-to-seedling transition is often necessary to maintain resilient high-quality forests or reforest previously disturbed forest habitats (Hansen and Turner 2019, Hoecker et al. 2020, Miller et al. in press). Accordingly, broadcast seed sowing can be a cost-effective management option, but requires minimizing barriers to seed survival to ultimately promote successful forest regeneration (Brooks et al. 2009). Seed predation by rodents may be one important factor limiting the establishment of tree seedlings from seed (Sullivan 1978, Dylewski et al. 2020, Boone et al. 2022, Moore et al. 2022). However, reducing rodent seed predation via fencing (e.g., Orrock et al. 2009), rodent trapping, or rodent poisoning (Salmon and Dochtermann 2006), and diversionary feeding (Sullivan 1979) can be costly, ineffective, and may have undesirable non-target effects on other species (Salmon and Dochtermann 2006, Roos et al. 2021). Forest management and restoration efforts could therefore benefit from strategies that reduce the negative effects of rodents on seed survival (Sullivan et al. 2001), especially if those strategies can be executed at large spatial scales necessary to meet management objectives.

One potential approach to reducing seed predation is to coat seeds with taste-averting chemical defenses derived from other plants (Pearson et al. 2019). For example, capsaicin is the naturally occurring compound in chili peppers (*Capsicum* spp.) that gives these fruits their characteristic spice, which likely evolved in chilis to protect them from mammalian seed predation (Tewksbury and Nabhan 2001). Seed coatings containing capsaicin can substantially reduce both herbaceous and woody seed predation by rodents in temperate grasslands (Pearson et al. 2019) and savannas (Nolte and Barnett 2000). However, little is known about whether seed coatings containing capsaicin might similarly reduce seed predation on temperate North American tree species. Captive feeding studies have shown that capsaicin can reduce both herbivory and seed predation of tree species by a wide range of mammals commonly found in temperate forests (including rodents and deer; Wagner and Nolte 2000, Willoughby et al. 2011). However, it remains unclear whether capsaicin coatings reduce rodent predation on woody tree seeds in ecological communities, including closed-canopy forests where tree recruitment is low (Miller et al. in press) or early-successional habitats undergoing reforestation (Brooks et al. 2009). Addressing this knowledge gap by examining the effect of capsaicin coatings on seed removal (which is often the first step in the process of seed predation; Brehm et al. 2019), in multiple forest contexts could provide forest managers with new tools to promote the regeneration of existing forests or to improve the efficacy of reforestation from seed.

Seed-removal studies often vary in their duration, which may affect the insight they provide. A recent global meta-analysis of seed removal suggests that the median exposure time used in seed removal studies was <20 days, with a maximum of 210 days, and that longer exposure time generally leads to higher estimates of seed removal (Chen et al. 2021). Therefore, conducting seed removal experiments with both long and short durations of exposure to seed predators can provide important insight about the cumulative risk of seed removal over time (i.e., across multiple seasons; Moore et al. 2007, Guiden and Orrock 2021).

We evaluated whether coatings containing capsaicin (hereafter referred to as “capsaicin coatings”) reduce seed removal in two independent, but complementary experiments. In the first study, we assessed whether the effect of capsaicin coatings on seed removal differed among tree species in existing closed-canopy forests. In the second study, we investigated whether capsaicin coatings deter seed removal of a single woody species in an old field habitat undergoing reforestation. We also examined in the second experiment whether the effect of capsaicin coatings depended upon the duration of seed exposure. Combined, these two studies evaluate the efficacy of capsaicin coatings in multiple species and habitats, providing insight into the potential effectiveness of capsaicin coatings for increasing survival of woody tree species.

Methods

We conducted a series of seed removal experiments in two different habitat types to evaluate the influence of capsaicin coatings, seed species identity, and time on seed removal. In all trials, we used capsaicin powder from ghost pepper (*Capsicum chinense* x *frutescens*) for our capsaicin coatings. This powder is readily available at a low cost and has a high concentration of capsaicin (>1,000,000 Scoville Heat Units), making it a potentially effective deterrent against rodents (Pearson et al. 2019).

Seed removal of woody species in closed-canopy forests (Michigan study)

The first seed removal experiment took place at five forest sites in Ypsilanti, Michigan (mean annual temperature: 9.1°C mean annual precipitation: 801 mm; Fick and Hijmans 2017). Michigan forest sites were continuous forest patches nested within a larger urban matrix. At each forest site, three plots (i.e., seed removal stations) were established. Plots within a forest site were separated by a minimum of 150 meters and plots were located a minimum of 15 meters from the forest edge. Forest canopy dominants at all Michigan sites included oaks (*Quercus* spp.), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and associated conifers (e.g., *Pinus strobus*, *Pinus resinosa*).

We examined the effects of capsaicin on the seed removal of red maple (*Acer rubrum*), red pine (*Pinus resinosa*) and jack pine (*Pinus banksiana*), as these represent common native woody species in southeastern Michigan. Samaras were present on *A. rubrum* seeds to mimic the structure of natural dispersed seeds and not artificially alter seed handling time by granivores. Using a spray bottle, we directly applied ~8 mL 50% pepper extract in solution with ethanol (see Supplementary Material for details) to seeds of each species in 3.8 L white, translucent buckets. The control seeds received ~8 mL of ethanol. We agitated the seed depots for 2 minutes to ensure that the seeds were evenly coated with the pepper extract with a fan blowing directly into the seed depot under full sun to promote rapid volatilization of the ethanol from the seed's surface. The seeds were dry in 20-30 seconds and evenly coated in the pepper extract residue

To quantify the effect of capsaicin coatings on seed removal in closed-canopy forests, we deployed 2 seed depots (i.e., buckets) at each plot (n = 30 depots total). Seed depots consisted of translucent plastic 3.8 L plastic seed depots. Each seed depot had 5 × 5 cm holes cut into opposite sides of the seed depot to permit rodent entry and was filled with a thin layer of sand. At each site, we placed one pair of seed depots: one of the two seed depots received 30 ethanol-treated seeds (10 seeds each of the 3 species), whereas the other seed depot in the pair received 30 capsaicin-treated seeds (10 seeds each of the 3 species coated with ghost pepper extract). Seed depots were placed approximately 1 m apart and each seed depot was covered with a lid to prevent disturbance from wind, rain, and larger animals. Seed depots were deployed in the field from 3-June-2021 to 7-June-2021, at which time the remaining intact seeds in each seed depot were counted and signs of seed consumption were noted (e.g., the presence of scat, seed coat fragments).

Seed removal of woody species in an old field (New York study)

This study was conducted at a 17-acre old field habitat in the Hamilton College Experimental Forest in Clinton, NY (average annual temperature: 7.5°C, average annual precipitation: 1086 mm; (Fick and Hijmans 2017). Historically, the field was used for corn and soybean row-crop agriculture until 2019, when soybeans were planted to increase soil nitrogen before reforestation began in the summer of 2020. Common plant species included wild rye (*Elymus* spp.), goldenrods (*Solidago* spp.), and asters (*Symphyotrichum* spp.). We divided the field into 9 blocks of approximately equal area to capture different microhabitats present in the field (i.e., some blocks were closer to forest edge). Two study plots were randomly placed in each block (n = 18 plots total). On average, the two study plots within each block were separated by 30 ± 5 m (mean ± 1 s.d.), while the distance between nearest study plots in adjacent blocks was 77 ± 11 m. These distances far exceed the typical home range of *Microtus pennsylvanicus* (Madison 1980, Bowers et al. 1996), which is the dominant rodent species in this habitat. In June 2021, 250 saplings were planted on the field's southwest quadrant in protective tubes as part of a reforestation project; four plots were placed where seedlings were planted and the remaining 14 plots were placed among exclusively herbaceous vegetation.

We coated seeds of American beech (*Fagus grandifolia)*, a dominant late-successional species in forests surrounding the study area, with capsaicin powder to quantify the effect of capsaicin coatings on seed removal. Seeds were coated using a modified version of the seed coating technique described by Pearson et al. (2019). 10 g of ghost pepper powder was combined with 70 ml of a non-toxic seed moisturizer made from the pine resin (Wilt-Stop; Bonide in Oriskany, NY), giving it adhesive properties. This was then mixed into a slurry, in which half of the seeds were immersed overnight ("treated seeds"). The other half of the seeds were treated similarly, but with only 70 ml of Wilt Stop and no capsaicin powder ("controls"). The seeds were then set out to dry for 48 hours until dry.

To quantify seed removal, we placed two 3.8 L translucent plastic seed depots at each plot (n = 36 seed depots), with paired depots approximately 2 m apart. Each seed depot had a 7 cm by 7 cm hole cut into it to allow rodents to enter. Each seed depot was filled with 3 cm of sand, and 10 treated seeds and 10 control seeds were placed on top of the sand, leading to a split-plot design. At each site, one of the seed depots was covered with a lid to prevent access from larger mammals (e.g., deer) and birds. This allowed us to compare how allowing access to multiple consumer guilds increased seed removal of treated versus control seeds. The seed depots were placed in the field on October 29, 2021. One set of seed depots from each of the plots was collected on November 17, 2021, after 19 days in the field. To test the effect of capsaicin over longer timescales, the remaining seed depots were collected on March 15th, 2022 after 137 days in the field. Once the seed depots were collected, we counted the number of intact seeds remaining in each treatment. Capsaicin-treated seeds remained visually distinct in all trials, as they were still covered with red powder.

Data analysis

All analyses were conducted using generalized linear mixed effects models (lme4) in R version 4.1.2 (Bates et al. 2015, R Core Team 2021) with a binomial error structure. The response variable in our models, unless otherwise stated, represents the proportion of seeds removed from each seed depot. We present results as model estimated marginal means (expressed as the proportion of seeds removed) obtained from the "emmeans" package and a 95% confidence interval (Lenth 2022).

For the Michigan dataset, we modeled the proportion of seeds removed from a seed depot as a function of species identity (*Acer rubrum, Pinus banksiana*, *Pinus resinosa*), seed coating (treated vs. control), and a species × coating interaction. We included a random intercept term for plot, nested within site, to account for potential non-independence among data points at the same plot and site.

For the New York dataset, we modeled the proportion of seeds removed from a seed depot as a function of seed coating (treated vs. control), cover treatment (seed depot covered or uncovered), and duration in the field (short versus long). Our model included all possible interactions, but we removed the insignificant three-way coating × cover × duration interaction term from our model to increase model parsimony. We also included random intercept terms for coating treatment nested within cover treatment nested within sampling point to account for our split-plot design. In order to ensure that our replicates were spatially independent, we also calculated Moran's I (Valcu and Kempenaers 2010) using the mean proportion of seeds removed in a study plot (averaged across covered and uncovered depots).

Results

Seed removal of woody species in closed-canopy forests

We monitored a total of 900 seeds over this experiment (300 seeds per species), 534 of which were removed (59%). During our seed removal study conducted in closed-canopy forests, the proportion of uncoated seeds removed (mean: 0.828, 95% confidence interval: 0.694 – 0.911) was almost double the proportion of capsaicin-treated seeds removed (0.425, 0.261 – 0.608; χ^2 =

104.07, $P < 0.001$, Figure 1), averaged across all species. There was also a strong effect of species on seed removal: on average, *P. resinosa* had the lowest proportion of seeds removed (0.403, 0.241 – 0.590), followed by *A. rubrum* (0.654, 0.469 – 0.802), followed by *P. banksiana* (0.841, 0.708 – 0.920; $\chi^2 = 87.69$, $P < 0.001$). There was no significant species × treatment interaction ($\chi^2 = 3.61$, $P = 0.16$).

Seed removal of woody species in an old field

We monitored a total of 800 seeds over this experiment, 536 of which were removed (67%). During our seed removal study conducted in an old field, the proportion of uncoated seeds removed (0.809, 0.688 – 0.891) was 17% greater than the proportion of coated seeds removed (0.691, 0.542 - 0.808; $\chi^2 = 4.17$, $P = 0.04$; Figure 2, Figure S5), averaged across cover treatments and study duration. The duration seeds were left in the field also had a large effect on seed removal, as the proportion of seeds removed in the long-term trial (0.888, 0.798 – 0.940) was 62% greater compared to the proportion of seeds removed in the short-term trial (0.545, 0.395 – 0.688; $\chi^2 = 30.21$, $P < 0.001$; Figure 2, Figure S5). Whether seed depots were covered or not also influenced seed removal, as the proportion of seeds removed in covered seed depots (0.820, 0.701 – 0.898) was 21% greater compared to uncovered seed depots (0.675, 0.527 – 0.795; $\chi^2 = 5.17$, $P = 0.02$; Figure 2, Figure S5). We detected no significant effect of coating treatment × cover treatment interaction ($\chi^2 = 0.15$, $P = 0.69$), coating treatment × duration interaction ($\chi^2 = 0.25$, $P = 0.61$), or cover treatment × duration interaction ($\chi^2 = 0.88$, $P = 0.34$). We found no evidence of spatial autocorrelation in seed removal (Moran's I = -0.085, expected I under complete spatial randomness = -0.111; z = 0.229, P = 0.81).

Discussion

Seed predation can significantly reduce the establishment of tree seedlings (Schnurr et al. 2002, Dylewski et al. 2020, Boone et al. 2022, Moore et al. 2022). Here, we show that coating seeds of eastern temperate tree species in capsaicin significantly reduced seed removal, the first step in the process of seed predation, in studies ranging from 4 to 137 days (Figures 1-2). This protection from seed removal occurred consistently in four temperate forest tree species (*A. rubrum, F. grandifolia, P. banksiana, P. resinosa*), suggesting that a diverse range of species can benefit from capsaicin coatings. Moreover, we observed that capsaicin coatings consistently reduced seed removal in both closed-canopy forests and old fields, regardless of the specific coating technique used. Broadcast seed sowing can be a viable management intervention that can promote native tree recruitment (Li et al. 2021, Greet et al. 2022) or accelerate reforestation in previously degraded habitats (Di Sacco et al. 2021). Our results suggest that capsaicin coatings might increase the success of broadcast seed sowing to meet both goals. Together these studies show the consistent and lasting benefits of capsaicin seed coatings across several species, different habitat types, and different geographic regions, supporting the idea that such coatings could be a generally viable tool for habitat restoration (Pearson et al. 2019).

We found no significant interaction between capsaicin coating and study duration in the old field experiment. This suggests that the effects of capsaicin seed coatings persisted throughout winter and spring (Figure 2), seasons in which small-mammal seed removal can be a significant source of seed mortality (Moore et al. 2007, Guiden and Orrock 2021). However, it is important to note that the effect size of capsaicin coating appeared to be larger for seeds exposed to seed removal for a short duration compared to seeds exposed to a long duration (Figure 2). Therefore, the weak capsaicin coating × duration interaction observed here could be due to low statistical power, especially given the very strong main effect of study duration (i.e., mean proportion of seed removal across all other treatments was 0.888 ± 0.035). More studies are needed to understand how duration of exposure and weathering affect the efficacy of capsaicin coatings (Pearson et al. 2019).

We also found strong differences in seed removal among the three species used in the closed-canopy forest seed removal experiment. *Pinus resinosa* seeds were least likely to be removed, followed by *Acer rubrum* seeds and then *P. banksiana* seeds (Figure 1). Possible explanations for this interspecific variation in seed removal include differences in physical or chemical traits influencing the net rewards of foraging gained by rodents (Dylewski et al. 2020, Moore et al. 2022), as well as preferences of different small-mammal species (Cramer 2014). Despite the differences in rodent preferences implied by these results, capsaicin coatings still consistently decreased seed removal (Figure 1). Examining how capsaicin coatings affect large-seeded species such as walnuts (*Juglans* spp.), oaks (*Quercus* spp.), or chestnuts (*Castanea* spp.) will be an important extension of this work, as these species are often directly planted in reforestation projects (Hall et al. 2019).

Our old field experiment also found that cover type significantly influenced seed removal. While the cover treatment was designed to manipulate access from different consumer guilds (e.g., rodents versus large mammals or birds), covered seed depots experienced greater seed removal than uncovered seed depots. This was contrary to what we would expect since the lids were designed to prevent additional seed removal, but instead they experienced more. One potential explanation for this pattern could be that rodents perceived lower predation risk under the cover of the seed depot, similarly to when they are covered by vegetation, and therefore are more likely to spend time in covered seed depots consuming seeds (Mattos and Orrock 2010). Interestingly, we did not observe an interaction between cover treatment and capsaicin coating (Figure 2), suggesting that capsaicin coatings increase survival even in microhabitats where we expected the highest seed removal. Given the additive effects of capsaicin coatings and cover treatment, and the fact that predation risk for rodents can exhibit substantial spatial variation within habitats (Guiden and Orrock 2017, Gaynor et al. 2019), identifying higher-risk microhabitats and selectively adding capsaicin-coated seeds to these sites may maximize seed survival and invite the potential for greater seedling recruitment.

Our results raise several questions that highlight important future directions for studies of seed removal. For example, seed removal is notoriously context-dependent (Maron et al. 2014), as seed traits (e.g., chemical defenses, size; Dylewski et al. 2020), habitat conditions (e.g., rodent community composition; Cramer 2014), and temporal variation (e.g., high- versus low-mast years; Moore et al. 2022) may all affect seed removal. Capsaicin is also one secondary compound among many that can deter seed predation: essential oils or activated carbon, for example, can also effectively deter rodent seed predation (Taylor et al. 2020). Future studies that measure removal of seeds with different experimental coatings could be replicated along these dimensions, which will help determine the value of these chemical defenses in different environmental contexts. Furthermore, applying these findings to bolster forest regeneration will require testing the practical aspects of our methods. Some examples of these practical aspects include comparing germination of coated versus uncoated seeds (Pearson et al. 2019), or testing how coating techniques stand up to variation in weather (e.g., rain versus snow) to help maximize land managers' returns on investment. Finally, the relationship between seed removal and seedling establishment is complex. Seed removal might better reflect seed dispersal, rather than seed predation, in some plant species (Vander Wall et al. 2005), implying that in some cases increased seed removal might promote seedling establishment. Additionally, other filters on community assembly, such as competition or environmental limitations, may mask the effects of seed predation on seedling establishment, or vice versa (Brown and Vellend 2014). Pairing seed removal studies with seed-addition studies, where seeds are sown or buried (Pearson et al. 2019, Bogdziewicz et al. 2020, Dylewski et al. 2020), or tracking seed fate after removal (Vander Wall et al. 2005, Guiden and Orrock 2017) will help clarify links between seed removal and establishment. These future studies will be important for understanding whether the promising results we present here will provide a cost-effective means for increasing tree recruitment and promoting forest sustainability in the future.

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Competing interests statement

The authors declare there are no competing interests.

Data availability statement

Data analyzed in this paper can be found on FigShare: https://doi.org/10.6084/m9.figshare.22773542.v1

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Figure Captions

Figure 1:

The results of the closed-canopy forest seed removal experiment depicting the number of treated (orange) and control (blue) seeds of each species removed at the end of the trial. Small open points represent raw data. Large closed points represent estimated marginal means predicted from our binomial generalized linear mixed model, and error bars represent 95% confidence intervals.

Figure 2:

The results of the old field seed removal experiment depicting the number of treated (orange) and control (blue) *Fagus grandifolia* seeds removed at the end of both the short-term (19 days) and long-term (137 days) trials. Small open points represent raw data. Large closed points represent estimated marginal means predicted from our binomial generalized linear mixed model, and error bars represent 95% confidence intervals.

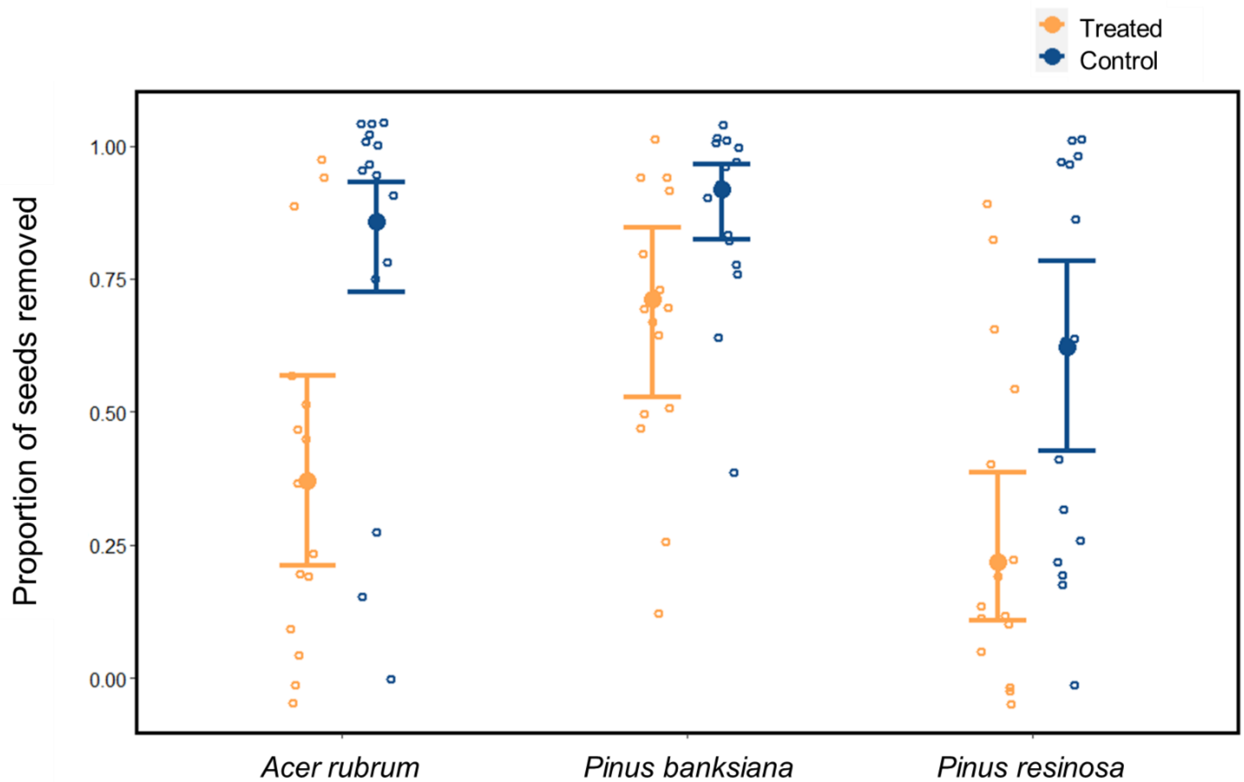
Treated
Control
Proportion of seeds removed
1.00
0.75
0.50
0.25
0.00
Acer rubrum
Pinus banksiana
Pinus resinosa

Figure 1

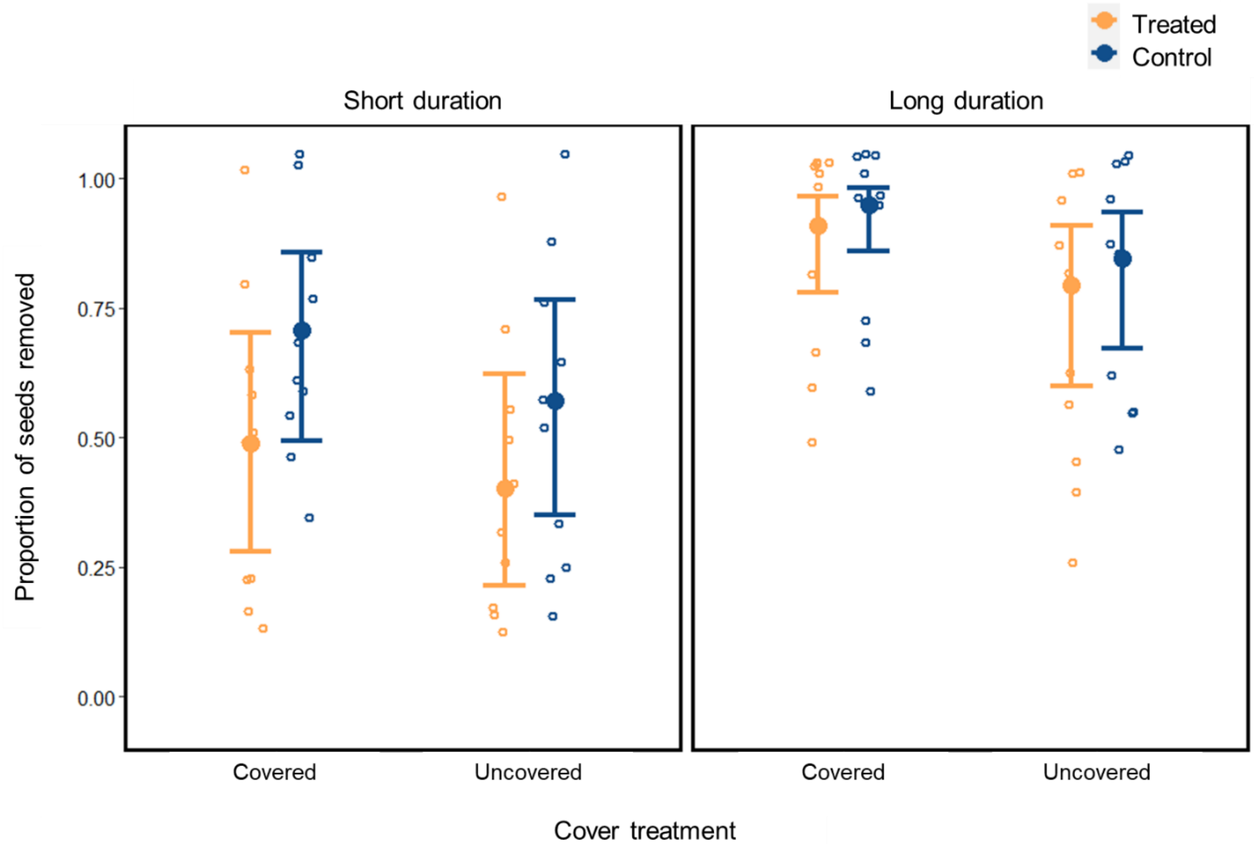
Treated
Control
Short duration
Long duration
Proportion of seeds removed
1.00
0.75
0.50
0.25
0.00
Covered
Uncovered
Covered
Uncovered
Cover treatment

Figure 2