Comparison of Seed Predation in the Temperate Deciduous Forest Canopy and Forest Floor

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Abstract

Seed dispersal is an important aspect of forest regeneration. If a granivore encounters a seed, it may either eat the seed immediately or cache the seed for later. The cached seed may be lost and the seed could germinate. A granivore may remove the seed directly from the tree (pre-dispersal) or once the seed has fallen (post-dispersal). My study simulates pre- versus post-dispersal seed removal in a temperate deciduous forest using maple (*Acer* spp.) seeds by using a novel technique to simulate canopy-level seed removals. Ten ground-level and ten canopy-level seed boxes were filled with seeds and left in the field for 23 days. Preference for ground removals over tree removals approached significance, although the number of removals from the trees was unexpectedly high.

Introduction

Seed predation and dispersal are topics of major importance for forest regeneration. By definition, a seed predator encountering a seed is detrimental for the seed, as the seed may be immediately consumed. Occasionally, however, these encounters can be advantageous for the seed, as there is a chance the granivore will cache the seed away for later consumption. If the granivore has imperfect recovery of its seed caches (either losing caches or through loss of territory or death of the granivore), the seeds may germinate, making the granivore a seed dispersal agent rather than a seed predator (Hulme and Benkman 2002). Additionally, the seed may be cached in a highly nutritious refuse pile that may have a better survival and growth rate than a seed that had not encountered a granivore (Levey and Byrne 1993).

In the multi-step process of seed dispersal, seeds exhibit two distinct phases. Phase I dispersal is the movement of a seed from the tree to the first surface it lands upon. Often times, this dispersal is merely gravity sending the seed from the tree to the ground. Phase II includes the horizontal (across surfaces) and vertical (into the ground) movements (Chambers and MacMahon 1994). In tree species such as maple (*Acer* spp.*)*, the seeds are samaras, which have a flattened wing to aid in wind dispersal across greater distances, increasing its phase I and phase II dispersal distances.

Granivores may either be pre-dispersal or post-dispersal seed predators. As the name implies, pre-dispersal predators will go after seeds before they have been dispersed from the parent trees. This group is most often made up of insects whose life cycles are synched up with seed availability. Post-dispersal predators go after the seeds once they have already been dispersed by the tree. These predators, often times vertebrates, will generally exhibit generalist feeding habits (Hulme and Benkman 2002). The primary mammalian seed predators in the University of Notre Dame Environmental Research Center (UNDERC) area are red squirrels (*Tamiasciurus hudsonicus*), eastern chipmunks (*Tamias striatus*), deer mice (*Peromysus maniculatus*), white-footed mice (*Peromyscus leucopus*), meadow jumping mice (*Zapus hudsonius*), woodland jumping mice (*Napaeozapus insignis*), and southern red-backed voles (*Myodes gapperi*) (Hsia and Francl 2007).

Seed caching behavior can be heavily dependent on season. Generally, with mammalian granivores, there is greater caching of seeds in late summer/autumn months (Benhamou 1996). Additionally, Hsia and Francl found much lower rates of caching (5±1%) versus consumption (37±12%) for seeds recovered in their study during June and July (2007). Seed-caching granivores exhibit two caching strategies—larder hoarding and scatter hoarding. Larder hoarding is storing food in one or a few discrete, closely spaced sites. Scatter hoarding is storing either one or a few pieces of food at many different sites. The larders are often very attractive to other granivores, so it must be well protected or defended. The scattered sites are much less attractive, but some sites may be lost (which can lead to tree regeneration) (Vander Wall 1990).

Many previous studies on pre-dispersal predation often excluded studying arboreal vertebrates in the canopy due to difficulty in quantifying their fruit/seed removals (Forget et al. 1999). To solve this problem, Lambert et al. developed a novel system that allows for arboreal vertebrate trapping in a forest canopy (2005). This design was further adapted to study seed removal rates from different heights in the tropical rainforest of Panama (Flagel et al. 2009). My study uses a similar design to compare tree canopy seed removal rates (simulating pre-dispersal seed predation) with ground seed removal rates in a temperate deciduous forest and preferences between two of the most common tree species, *A. saccharum* and *A. rubrum*. While maple (*Acer* spp.) seeds are primarily dispersed by wind, they are still subject to seed predation in the area which functions as a secondary means of dispersal (Hsia and Francl 2007). The specific hypothesis being tested is that there are more seed removals on the forest floor than in the forest canopy.

Methods

In order to assess seed predation at different forest strata in a temperate mixed forest system, I used methods adapted from a similar study in Panama on tropical rainforest seed predation (Flagel et al. 2009). Twenty seed boxes were constructed by gluing panels of Plexiglas together with PL® premium polyurethane construction adhesive and reinforced with duct tape and vinyl electrical tape to form 50cmx15cmx15cm boxes open at one end. Ten of the boxes, designated as tree boxes, had three wire loops attached to the box to form the system to raise the box into the canopy (Fig. 1). To get the seed boxes into the canopy, a rope was attached to a heavy ring bolt, which was thrown over a tree branch to form a simple pulley. One end of the rope was attached to the top of the box and the other attached to the back. A loop of rope was then fed through a loop that was located on the side of the box ~3/4 the way back, allowing for the box to be hoisted into the canopy without spilling seeds. The ground seed boxes were staked to the ground within a five meter radius of the tree the other box was in. Ten total sites were selected that correspond to the general vicinities of the UNDERC deer exclosures.

The seeds used in this study were sugar maple (*Acer saccharum*) and red maple (*Acer rubrum*), which were obtained from TreeHelp.com (Toronto, ON). In order to prevent the introduction of foreign genetics, the seeds were microwaved for 45 seconds to kill the embryos without altering their taste or desirability to granivores (Hsia and Francl 2007). Twenty-five seeds of each species were placed in each box. Additionally, the boxes were laced with pure vanilla extract to serve as an olfactory attractant. The boxes were checked after a few days to determine how many seeds were removed per number of days. When checked, the boxes had their seeds replaced to bring the total number back to twenty-five of each species and more vanilla was added. The rate of replacing the seeds in the seed boxes was varied in order to avoid fixing predation habits of the seed predators (i.e. recharging the box every three days could lead to the predator coming back every three days). The study was conducted for twenty-four days and the number of seeds removed from the canopy level boxes was compared to the number of seeds removed from the forest floor boxes to see if there was a significant difference in the seed predation/removal between the two levels of the forest and/or a seed species preference. The data was analyzed by conducting Wilcoxon signed rank tests in MYSTAT 12.

Results

After having the seeds out for 24 days, a total of 172 seeds were removed from the tree boxes (37 *A. saccharum*, 135 *A. rubrum*) and 345 seeds were removed from the ground boxes (128 *A. saccharum*, 217 *A. rubrum*). The collected data was analyzed with a Shapiro-Wilk normality test, which showed all of the data was non-normal. In comparing the different seed box treatments, a Wilcoxon signed rank test showed differences in mean ground removal rate (1.524 seeds/day) and mean tree removal rate (0.936 seeds/day) approach significance ($p=0.184$) (Fig. 2). Additionally, granivores show a statistically significant preference ($p<0.0001$) for *A. rubrum* seeds over *A. saccharum* seeds. To see if greater removal rates occurred later in the summer, a regression was run comparing removal rate per day versus date and was found to be insignificant ($p=0.253$). Comparison of sites using a Kruskal-Wallis test revealed that differences in removal rates approached statistical significance (0.081).

Discussion

The number of seed removals from the trees found in this study was surprising, as Flagel et al.'s study in Panama showed many more removals from the ground than the trees (361 versus 3) (2009), compared to my study, where there were only roughly twice as many ground removals as tree removals (345 versus 172). While the Wilcoxon test gave a result that approached significance supporting my original hypothesis, the expected disparity was thought to be much greater. Additionally, as the vast majority of the granivores in the study area are thought to be vertebrates, previous studies suggest that much more of the seed predation should be post dispersal and not in the trees (Hulme and Benkman 2002), suggesting that *Sciurids* in the study area are active pre-disperal predators and/or there are invertebrate seed predators in the canopy. A major difference between the Panama seed removal study and my study done at UNDERC is the ecosystem ecology and type of seed used. In Panama, the fruit used was too heavy for arboreal granivores other than arboreal rodents, thereby excluding many other potential granivores such as birds from the study and lowering arboreal removal rates (Flagel et al. 2009), while my study used maple seeds that are likely small enough to be transported by all arboreal granivores (both vertebrate and invertebrate). The observation of seed removal rate discrepancy between the two areas supports previous studies that indicate seed removal rates can greatly vary across year, granivore community structure, and seed species (Moore and Swihart 2008)

Another unexpected result was the strong preference ($p<0.0001$) for *A. rubrum* seeds over *A. saccharum* seeds by the granivores in the study. A previous study (Carson and Royo 2008) ranked small mammal seed preference, lumping *Acer* species together, which suggests little preference between the two. The observed preference could be explained by the larger seeds potentially having a thicker/tougher seed coat, which could cause the granivore to expend more energy trying to extract the edible part of the seed, while the granivore could instead go after the smaller seed that takes less effort to consume (Smith 1970). *A. saccharum* seeds were much larger than the *A. rubrum* seeds (Fig. 3), so, given both seeds in equal densities, the granivores may have opted to select for the seed that would take less effort to consume. This preference could have major implications, as the increased removal of *A. rubrum* seeds could lead to a wider distribution and increased abundance of mature *A. rubrum* trees, changing the future forest composition of the UNDERC area.

While the studies sites were not chosen randomly, they exhibit a variety of forest types with differing tree species diversities and understory vegetation that provides a representation of the UNDERC property as a whole. Had the study been conducted for a longer duration, I would expect to see some site removal preferences shown by the granivores, as the differing forest types likely have different granivore community structures. These differences across the study sites, such as differing amounts of ground-level vegetation, could lead to different removal rates (Carson and Royo 2008).

Future studies in this area could look at canopy versus ground seed removal rates of a single species, such as black cherry (*Prunus serotina*) seeds. This species is fairly common on the UNDERC property, and small mammals prefer to remove it over *Acer* spp. seeds (Carson and Royo 2008), which may yield higher predation rates. Also, the study could be run for a longer duration over the course of several seasons, which would likely give a more significant result with more removals on the ground than in the trees. Additionally, the study would be able to track potential removal preference changes as removal activities shift to more caching behavior in autumn as winter approaches (Benhamou 1996).

A major aspect of this project that future studies could improve upon is the selection of an appropriate tree in which to set the tree box. An appropriate tree had to have somewhat horizontal branches that were roughly canopy height and the branch had to be thick enough to allow for the box to be raised and lowered (if it was too thin, the box caused too much friction on the rope to be raised up). Due to physical constraints, the boxes were not all placed in maple (*Acer* spp.) trees. A future study could improve the design to be able to set the boxes higher in the canopy and get around the problem of having to find horizontal branches

Seed dispersal/removal studies, such as this one, grant limited insight into the seed predation and dispersal process. Additionally, they reveal nothing about final seed fate. However, they are useful in understanding granivore preferences in choosing where and what kinds of seeds granivores go after (Moore and Swihart 2008). While my study cannot give predation rates, it does reveal that there is a significant amount of pre-dispersal seed removal that occurs in a temperate deciduous forest, as well as varying preferences among the seeds of closely related species. When creating models of seed dispersal and seed fate, canopy level granivory must be taken into account in order to have an accurate picture of forest recruitment and regeneration, lest an important facet of seed dispersal be overlooked.

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Figures

Fig. 1 Picture of tree box used in study. The three wire loops (the third is attached to the back) allows for the box to be hoisted into the canopy.

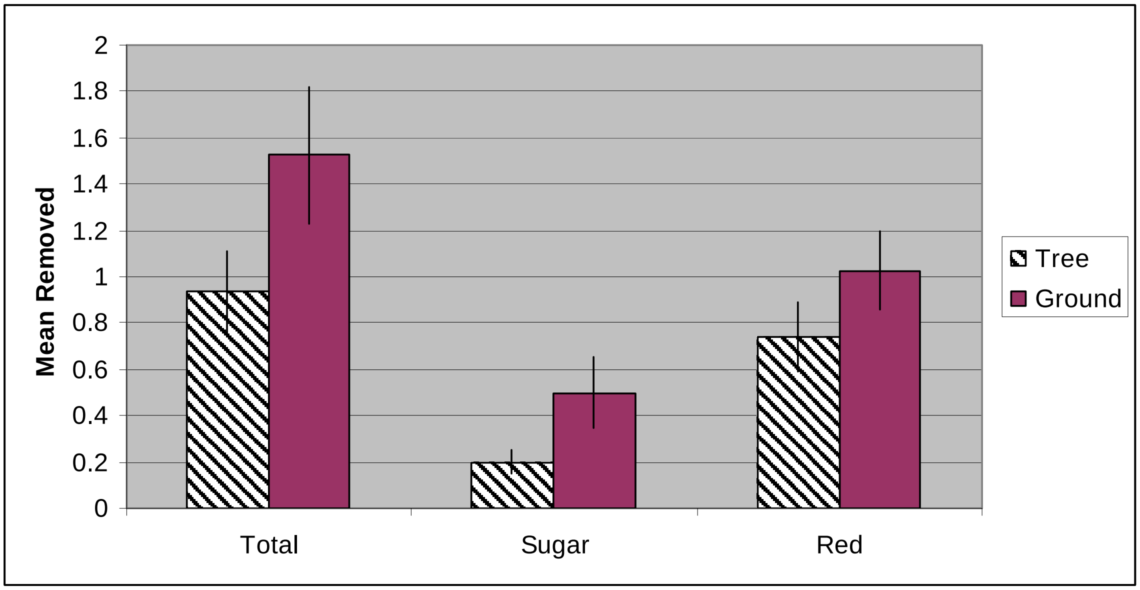

Fig. 2 Mean removals per day of total number of seeds, sugar maple (*A. saccharum*) seeds, and red maple (*A. rubrum*) seeds from the boxes, sorted by treatment. The tree and ground seed removal rate differences approach statistical significance (p=0.184)

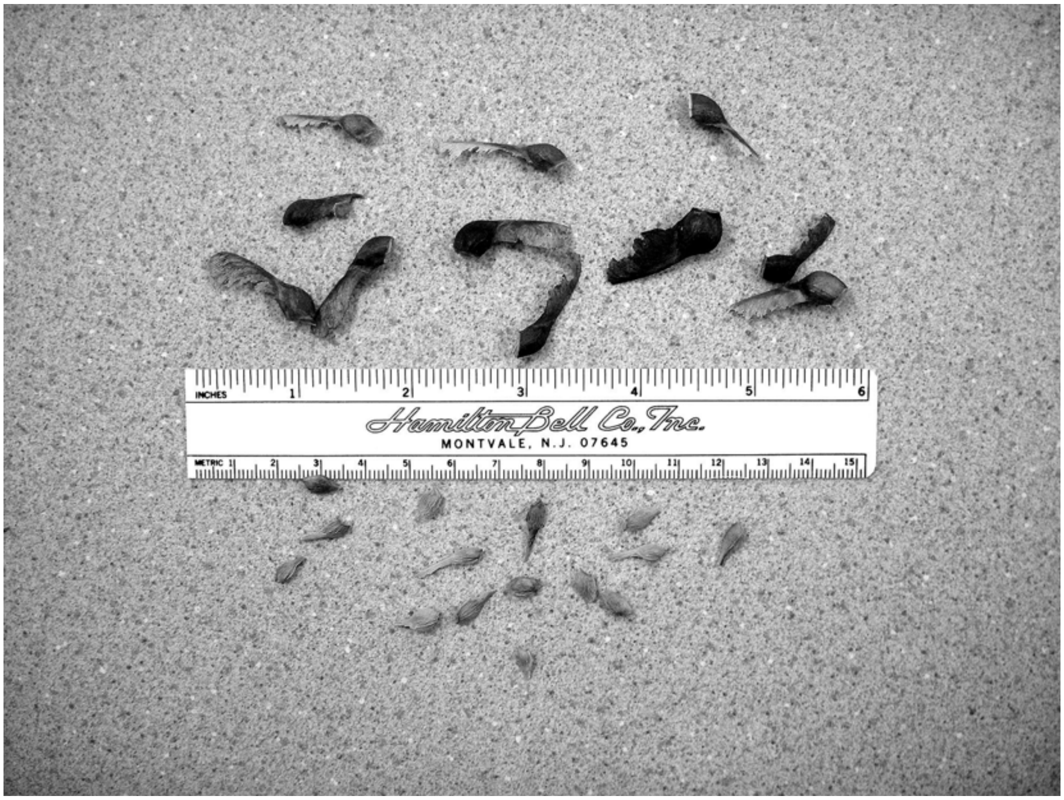

Fig. 3 Picture of seeds used in the study set against a scale. Above the ruler are sugar maple (*A. saccharum*) seeds and below are red maple (*A. rubrum*) seeds.