Selection, Caching and Consumption of Hardwood Seeds by Forest Rodents: Implications for Restoration of American Chestnut and Allegheny Woodrat Conservation

Current Status
Third year of a three-year project

Funding Sources and Partners
DNR Division of Fish & Wildlife, Wildlife Diversity Program; Purdue University; The Nature Conservancy

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Background and Objectives
The American chestnut (Castanea dentata) once was the foundation species of much of the Eastern deciduous forest, numerically dominating and defining the ecological structure of these habitats. The American chestnut

A fox squirrel investigates a tray of tagged seeds and selects a black walnut.
was unique among mast producers (trees that produce nuts) in both the high quantity and the palatability of its seed crop. In 1904, the accidental introduction of the fungal pathogen chestnut blight (*Cryphonectria parasitica*), most likely as an unintended consequence of importing Japanese chestnut (*Castanea crenata*) trees, led to the near extinction of the American chestnut over a 40-year period, as the pathogen spread throughout the species' range.

In response to the rapid removal of the American chestnut from forest ecosystems, a pulse of light, water, and nutrients enabled the expansion of other tree species. Oaks (*Quercus spp.*) were most successful in filling the niche vacated by American chestnut. With the loss of chestnuts, many wildlife species increasingly became reliant on energy-rich acorns for survival through the dormant season. With transitioning forest species composition came a shift in patterns of mast availability because oaks are much more prone to occasional “bumper crop” (highly productive) years among intervening years of average to low acorn production.

American chestnuts generally produce large numbers of chestnuts every year.

In an effort to restore the ecological niche once filled by American chestnut, The American Chestnut Foundation (TACF) began an intensive research and breeding program to develop a blight-resistant American chestnut by crossing American chestnuts with blight-resistant Chinese chestnuts. Ultimately, TACF bred a chestnut that is 94 percent American chestnut, yet resists blight. These blight-resistant chestnuts are in the final stages of plantation evaluations. Limited reintroductions already are underway in national forests in Ohio and Tennessee.

Although the blight-resistant chestnuts are primarily made of American chestnut, questions remain regarding their ecological properties, particularly as they pertain to granivores (animal species whose diets consist largely of seeds). It remains unknown whether blight-resistant chestnuts represent an ecological surrogate for American chestnuts as a desirable and abundant food source for granivores (such as fox squirrel, gray squirrel,
chipmunk, white-footed mouse, white-tailed deer, wild turkey, American crow, blue jay and tufted titmouse). Additionally, biologists have little understanding of the likely responses of granivore populations to the re-establishment of a consistent and prodigious mast producer. Also, preferential seed consumption by granivores (e.g., the preference of blue jays for acorns from black oaks over those from other oak species) can have profound impacts on species composition of the forest. Therefore the shifts in the relative abundances among granivore species and relative preferences of these species for nuts from blight-resistant chestnuts may have important implications for either promoting or limiting expansion of the blight-resistant chestnuts from reintroduction sites.

Given the limited understanding of how the establishment of blight-resistant chestnuts and ensuing increases in mast availability will drive changes among the populations of granivore species, a series of field trials are in progress that aim to reveal:

1) The preference by granivores for blight-resistant chestnuts relative to other sources of mast (white oak, chestnut oak, Northern red oak, black oak, shagbark hickory, pignut hickory and black walnut) commonly available within the historic range of the American chestnut within Indiana;

2) Whether blight-resistant chestnut seeds represent an ecological surrogate for American chestnut as a desirable food source for granivores;

3) Granivore preferences for blight-resistant chestnuts relative to other sources of mast, how these preferences then relate to whether a blight-resistant chestnut is more likely to be consumed or cached, and the implications of seed consumption/caching for blight-resistant chestnut establishment after reintroduction;

4) The conditions under which rodents may facilitate or hinder reintroduction of chestnut into natural forest stands; and

5) How restoration of consistent and prodigious mast resources may impact Allegheny woodrat population dynamics.

Methods
To meet these objectives, we are conducting the following independent and complementary seed trials: 1) hard-mast preference trials, 2) searches for tagged seeds removed during preference trials, 3) frequency-dependent mast preference trials, and 4) response of population dynamics of Allegheny woodrats to mast supplementation. All studies are being conducted throughout forested regions in Harrison and Tippecanoe counties in Indiana.
Mast preference trials are addressing patterns of preference by granivores for blight-resistant chestnuts relative to other locally available hard-mast food items from white oak, chestnut oak, Northern red oak, black oak, shagbark hickory, pignut hickory and black walnut. For these trials we established 30 stations, each consisting of a seed tray monitored with a motion-activated camera. At the start of each trial, we presented an array of 63 seeds consisting of equal numbers of the seven seed species listed. We used the motion-activated cameras to document the pattern and rate at which the seeds were removed by members of the granivore community. Trays for squirrels and chipmunks were available during daylight hours; trays for mice were available throughout the night. Restricting tray availability to either day or night allowed us to independently identify preferences of each type of granivore in the community (squirrels and chipmunks during the day vs. mice during the night).

After a granivore removes a seed from the tray, it must either immediately consume the seed or save (cache) it for later consumption by burying it in leaf litter or some other available substrate. While we infer preference for the various species of seeds by the pattern of removal from the tray, these two differing seed fates (consumed vs. cached) have important implications for forest regeneration.

A seed that is immediately consumed is gone, whereas a cached seed could be “forgotten” and grow into a new tree. Accordingly, we “tagged” nuts of each species to evaluate the fate of the seeds after removal from the tray. Tagging consisted of drilling a small hole through the top of the seed and inserting a wire tied to a piece of fluorescent-colored tape. Seeds were color-coded according to the granivore species for which they were available (squirrels and chipmunks vs. mice). After the seeds were taken from the trays, we visually searched for the tags in the surrounding leaf litter. If a tag was found without a seed, we assumed the seed was eaten. An intact seed was identified as cached.

Patterns of seed preference among granivores have been shown to vary in response to the relative availability of seeds. Therefore, in our frequency-dependent mast preference trials, we evaluate changes in seed consumption rates in response to variation in the presented ratios of acorns and chestnuts. These trials will reveal how the restoration of American chestnut is likely to impact the relative preference for other mast resources.

As chestnuts are returned to the landscape, two scenarios of seed preference are possible: 1) consumers may prefer common mast items such as acorns, which would reduce chestnut consumption rates and promote chestnut expansion after initial introductions, or 2) during initial restoration efforts consumers may consume novel chestnuts at a disproportionately high rate, hindering restoration efforts by slowing the establishment rate of the new trees and expansion out of introduction sites.

To evaluate this question, we used methods similar to those described for seed preference trials, but instead of presenting equal numbers of each species of seed on the trays, we evaluated preferences among three seed species (chestnut, Northern red oak and white oak) when presented at different ratios. Specifically, we conducted paired trials for each of these three species (chestnut vs. red oak, chestnut vs. white oak, red oak vs. white oak), evaluating shifting patterns of preference across five different presentation ratios (1:9, 3:7, 5:5, 7:3 and 9:1). The sequence of seed removal by granivores will allow us to assess whether consumer selection of chestnuts is frequency-dependent (i.e., dependent upon the number of seeds available relative to other types of seeds) and what impact frequency-dependent preference will have for chestnut reintroduction efforts.

As the final component of these seed trials, we are evaluating the relationship between the extirpation of the American chestnut and the decline of the Allegheny woodrat. Allegheny woodrats are endangered in Indiana and are a species of conservation concern throughout their range. One factor hypothesized to be contributing to the range-wide decline of woodrats is a loss of hard-mast food resources, which woodrats heavily depend upon for survival through winter months. Because oaks are prone to years of acorn production failure in contrast
to American chestnuts—which consistently produce an abundance of seeds—it is possible that the restoration of American chestnut could facilitate the recovery of Allegheny woodrats.

To evaluate the relationship between hard-mast availability and woodrat recovery, we are supplementing the winter caches of woodrats by depositing 1 kg of acorns in occupied woodrat den sites. Specifically, we divided eight woodrat populations equally among the four different mast supplementation treatments: 1) supplemented both years (2011 and 2012), 2) unsupplemented in 2011 and supplemented in 2012, 3) supplemented in 2011 and unsupplemented in 2012, and 4) unsupplemented in both 2011 and 2012.

Monitoring of woodrat populations through 2011, 2012 and 2013 allowed us to identify the effect of mast supplementation on such traits as reproductive success, over-winter survival, individual condition and population growth. Receiving this pulse of acorns simulates a highly productive oak mast year or expected mast availability once chestnut has been fully restored. To gain additional insight into woodrat seed preferences, we conducted an extra set of seed preference trials specifically targeting woodrats. Seed stations were set up outside occupied den sites, and we documented the pattern and rate of seed removal again.

**Progress to Date**

We have completed all seed preference and frequency-dependence trials along with seed-tag searches. Mast supplementation at woodrat den sites was conducted in both 2011 and 2012. Allegheny woodrat live-trapping for population monitoring was conducted in 2011, 2012 and 2013 among all sites that were incorporated in the hard-mast supplementation study. We expect to publish final results by mid-2014 at docs.lib.purdue.edu.

**Challenges Encountered**

The main challenge associated with beginning the series of seed trials has been developing a station infrastructure. Because of the large scale of the station grid setup, we needed equipment that was manageable to carry yet robust enough to support a foraging squirrel or exclude a persistent one and withstand inclement weather. Fine-tuning the motion-activated cameras also presented some difficulty. In order to get the quality of images needed to document seed selection events, we had to fine-tune camera focal distances and the placement of seed trays under the cameras over several successive test runs.

Once our stations were up and running, attracting visitors to them proved difficult. While mice visited several stations, squirrels and chipmunks scarcely appeared. In 2012, we ran our trials at sites where diurnal granivores were known to be present in greater abundance, and we established fewer stations in any given site in order to farther spread the trials in space and time.

After conducting preference trials for fox squirrels and gray squirrels, we found that certain seed types were more difficult to recover than others. In particular, hickories were recovered at lower rates than most acorns and chestnuts, and black walnut seeds were almost never recovered. We suspected that this problem had to do not with our ability to find tags for these seeds but that they were being taken farther outside our 30m-radius search area. To confirm, we conducted mock tag searches as single blind experiments in which we “cached” seeds or left tags on the surface, and a separate “blind” technician conducted searches for them.

We had high recovery rates of tags (average 83%), but found that our ability to detect a tag was indeed distance-dependent (i.e., the farther a tag is taken by a squirrel, the less likely we were to find it). We were therefore able to make assumptions about fates of seeds taken outside our search area. This may be important if the distance a seed is taken indicates the perceived value of a seed to a granivore. In addition, we are planning a follow-up study that includes an expansion of our search area to assess whether these assumptions were valid.