The Continued Spread of a Wild Population of American Chestnuts

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Abstract - We monitored the reproduction, dispersal, and regeneration of a wild population of *Castanea dentata* (American Chestnut), established from 4 seed-bearing trees planted in a western Maine forest in 1982. The 40-year-old parent trees, sourced from wild stock of a relict population in northern Michigan, show no obvious signs of blight and have been producing viable seeds now for >20 years. Over the course of 2 surveys conducted in 2019 and 2020, we mapped and measured 1348 offspring, varying in size from seedlings to nearly mature trees. As of October 2020, the natural spread of this population had expanded to at least 370 m from the parent trees, with an average dispersal distance of 124 m. While previous publications have focused on the scatter-hoarding behavior that gave rise to this expanding wild population, we report on possible factors affecting their spread, their fate, and prognosis for the future. Given the absence of other reproductive populations of American Chestnut in the immediate vicinity, our data provide rare insights into natural seed dispersal from a known point of origin while documenting the return of a functionally extinct species to a northern hardwood forest ecosystem.

Introduction

Castanea dentata (Marsh.) Borkh. (American Chestnut), once a culturally and ecologically significant component of eastern hardwood forests (Davis 2006, Paillet 2005), has been considered functionally extinct due to the rapid spread of *Cryphonectria parasitica* (Murrill) M.E. Barr (Chestnut Blight), a fungal pathogen introduced in the early 20th century (Russell 1987). While remnant sterile stump sprouts of American Chestnut remain scattered throughout its historic range (Paillet 1988, 2002), reproductive populations have been almost entirely absent from the landscape for over 100 years, except for occasional localized refugia (Brewer 1995). The near elimination of American Chestnut presents a challenge for those seeking to study its ecology using modern techniques, and to those who hope to restore eastern hardwood forests to pre-blight conditions. In response to this challenge, Paillet (2005:42) identifies the "study of naturalized stands of American Chestnut established beyond the range of the blight" as one potential strategy to gain a better understanding of the role of American Chestnut in pre-blight hardwood forests. While historically rare in the northeastern US (Thompson et al. 2013), recent studies suggest that American Chestnut's range of suitable habitat may continue to expand north due to climate change (Barnes and Delborne 2019, Noah et al. 2021). Should reintroduction efforts become successful, American Chestnut is expected to

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become established in areas beyond its historic range, including the foothills of the Appalachians in northern New England where our study site is located (Fig. 1).

Fagaceous trees such as *Quercus* (oaks) and *Castanea* (chestnuts) in eastern North America are primarily dispersed by scatter-hoarding, a mutualism that has not only shaped historical distribution of nut-bearing trees (Pesendorfer et al. 2016) but may also play a role in migration and restoration efforts in the face of climate change (Wright et al. 2022). Among scatter-hoarding seed predators, corvids and *Cyanocitta cristata* (L.) (Blue Jay) in particular, have been known to play a crucial role in dispersal of the American Chestnut as they can carry up to 3 nuts at a time for distances greater than 1.2 km (Bosema 1979, Pesendorfer et al. 2016, Wright et al. 2022). Our results provide a rare glimpse of these seed-dispersal dynamics and their role in establishing a growing population of healthy American Chestnuts originating from a single known point source.

Origin and establishment of the wild population

In 1982, we purchased 15 wild-stock American Chestnut seedlings from the Wexford County Soil Conservation District in Wexford, MI, and planted them in a clearing on York Hill in Franklin County, ME. (see Fig. S1 in Supplemental

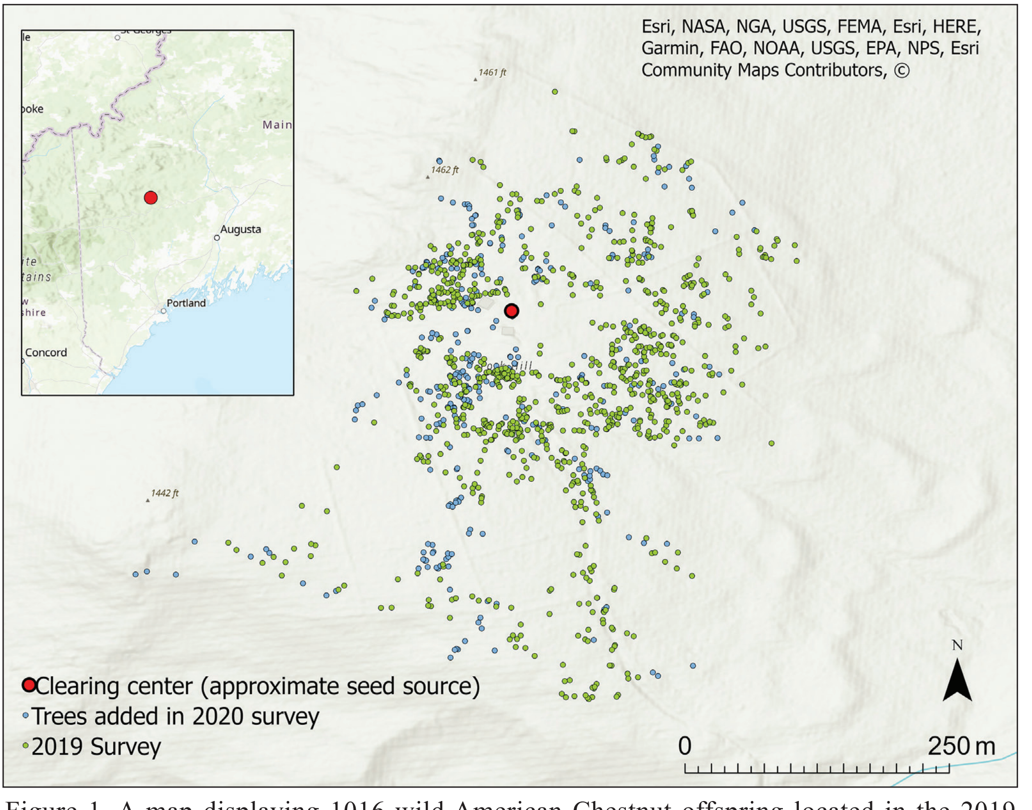

Figure 1. A map displaying 1016 wild American Chestnut offspring located in the 2019 survey in green and the additional 332 trees added to the survey in 2020 in blue. The red dot represents the center of the clearing where the four original parent trees had been planted in 1982.

File 1, available online at https://www.eaglehill.us/NENAonline/suppl-files/n29-3-N1960-Heinrich-s1, and for BioOne subscribers, at https://www.doi.org/10.1656/N1960.s1). Of those 15 seedlings, 4 survived to maturity and by 2003 had begun producing viable annual seed crops, displaying no obvious sign of fungal infection (Heinrich 2014). The surviving mature trees are located 10–20 m from the permanent residence of one of the co-authors, and therefore we have had a unique opportunity to witness their growth for nearly 4 decades from an unobstructed vantage point. The proximity of the residence to the parent trees has allowed for frequent observation of their phenology, health, ecology, and eventual recruitment of a second generation. Many of the observations related to this population have been detailed in prior publications (Heinrich 2014, 2015).

When the parent trees began producing fruit in 2001, Blue Jays and *Tamiasciurus hudsonicus* (Erxleben) (Red Squirrel) were identified as the primary seed dispersers (Heinrich 2014). Blue Jays were observed harvesting the seeds as the fruits were opening, and then dispersing them into the surrounding forest in caches of up to 3 nuts, the presumed maximum number they could carry at one time (Heinrich 2014). Red squirrels made multiple trips to the same cache, creating a point source of up to 20 seedlings sprouting at 1 location (Heinrich 2014, 2015). An initial survey in 2013 revealed a population of 238 wild offspring in the forest surrounding the clearing (Heinrich 2014).

Since the last survey in 2013 up until 2019, the parent trees have remained blight-free, and have typically flowered and produced viable fruit every year. In 2014, two of the 4 surviving planted trees were felled due to extensive damage from *Erethizon dorsatum* (L.) (Porcupine), and while vigorous stump sprouts have since grown from their root stocks, they have not yet begun to flower. In 2018, the 2 remaining flowering trees began to show signs of infection by *Armillaria* sp. (honey fungus) near the base of the trunk, and both produced a notable bumper mast crop later that year. In 2019 however, the 2 mature trees did not appear to flower or bear any fruit. Typical bright white inflorescences were never observed, and no husks appeared to develop at any time during the 2019 growing season. Seed predators were notably absent from the tree's canopy during the fall. Upon confirming the absence of a mast in 2019, we recognized an opportunity to revisit the wild population, and follow-up on the survey conducted 6 years prior.

The primary purpose of our unplanned natural experiment was to reassess the size of the wild population, map its approximate distribution, and set a precedent for future monitoring by collecting information on each seedling. We aim to repeat this protocol in future surveys to determine the rate at which the population has grown, and understand which conditions are most favorable for sustaining a wild population. Due to the rarity of naturally regenerating populations of American Chestnut, we are aware of only several instances in which natural dispersal and regeneration of such a large population have been documented (Paillet and Rutter 1989), and we are unaware of any studies that have monitored the expansion from a single, known seed source.

Site Description

The parent trees are located at the southern edge of a clearing on an otherwise forested hilltop in Franklin County, ME, at an elevation of ~430 m (see Fig. S2 in Supplemental File 1). The forest surrounding the clearing is comprised of a mix of hardwoods and conifers, with *Acer saccharum* Marshall (Sugar Maple), *Acer rubrum* L. (Red Maple), *Fagus grandifolia* Ehrh. (American Beech), *Pinus strobus* L. (White Pine), *Abies balsamea* (L.) Mill. (Balsam Fir), *Picea rubens* Sarg. (Red Spruce), *Betula papyrifera* Marshall (Paper Birch), and *Betula alleghaniensis* Britt. (Yellow Birch) as principal components. The landowners perform occasional thinning of the overstory within the survey area just to the east of the clearing in what was once a sugarbush. Thickets of young, dense Balsam Fir regeneration dominate portions of the survey area to the south, and to the north and west of the clearing are shallow-to-bedrock rocky knolls dominated by mature spruce and fir.

The survey area consists of 89% sandy loams with a drainage class categorized as moderately to well drained, and an estimated 1.1 percent of the surface area comprised of cobbles and boulders (NRCS 2021). Average slope is 3–15%, and average depth to the water table is 43–86 cm. Mean annual precipitation is 79–241 cm, with a mean annual air temperature of -2.8 to 11.1 °C, and a frost-free period of 90–160 days (NRCS 2021).

Methods

We conducted year 1 surveys on 28 and 29 October 2019 during a brief phenological window in which most deciduous trees and shrubs had shed their leaves, yet American Chestnut still bore green foliage. This timing ensured stark contrast of the green chestnut leaves against the otherwise dormant understory, thereby allowing us to locate and confidently identify American Chestnut seedlings with relative ease (see Fig. S3 in Supplemental File 1). Working in a group of 5, we surveyed the property, moving outward from the clearing in parallel transects while recording a GPS track to determine where the team had already been. As we moved away from the clearing, our records of new trees became more infrequent, and after we suspected that we had reached the furthest extent of the distribution, we continued searching for an additional 20 m before turning back toward the clearing. We continued our search until we had hit a saturation point and could no longer find any unmarked Chestnut trees.

When a wild stem was located, we first confirmed that it was an American Chestnut, and then placed a surveying flag directly adjacent to it and assigned a placemark number in sequential order using black permanent marker. We recorded the geographic location of each flagged tree using the averaging function in the Avenza Maps Pro iphone app (Avenza Systems, Inc., Toronto, ON, Canada). We measured the height of each seedling to the nearest cm with a 1-m foldable ruler, except for several larger individuals that we measured using a clinometer. If more than 1 seedling was present growing at each location, we measured the height of the tallest individual. We estimated age of the seedlings based on the number of nodes on each individual stem. We estimated canopy cover with the naked eye on a scale from 0 to 3, with 0 representing full sun (~0-25% canopy cover), 1 representing partial shade (~25–50% canopy cover), 2 representing partial sun (~50–75% canopy cover), and 3 representing full shade (~75–100% canopy cover).

We re-assessed the population in 2020 to estimate seedling mortality and provide an updated estimate of population size. As the parent trees did not bear fruit in 2019, we were confident that any unmarked individuals in 2020 must be at least 1 year old, and therefore could be added into the total population dataset from the year prior. Follow-up surveys were completed on 8 October 2020 during the same phenological window as 2019. During this follow-up survey, we repeated the search using the same methods, relocating as many flagged trees as possible, and adding flags to trees that we had missed the year prior. Using ArcGIS (ESRI, Redlands, CA), we measured dispersal distance from a central point within the clearing, equally distant from each of the 4 original parent trees, for all 1348 recorded stems.

Data were first plotted in Microsoft Excel 16.62, and all statistical analyses were performed using JMP® Pro 15 (SAS Institute Inc., Cary, NC, 1989–2021). After testing for normality, we found our mean height data to be not normal. A Wilcoxon's signed rank test was performed to test for significant differences in mean height between 2019 and 2020. We performed a Kruskal-Wallace H test to detect significant differences in height between canopy cover classes.

Results

During the 2019 survey, we located 1016 stems, all within 370 m of the clearing (Fig. 1). Of these, we estimated that 564 were less than 1 year old (Table 1). Therefore, we estimated that ~55.5% of the known population consisted of seedlings that had been initiated during spring of 2019 following the sizable mast of 2018. In 2020, we recorded 332 newly observed individuals all of which were determined to be at least 1 year old, for a total count of 1348. Since no seed crop was produced in 2019, we assumed that these 332 added specimens had been present the year prior but could have been easily overlooked if their leaves had already senesced, or the stem had been browsed before the 2019 survey began. An updated breakdown by age class in 2020 is displayed in Table 1 accounting for both the newly observed specimens and subtracting those that were confirmed dead or missing (though it should be noted that by 2020 the trees in each age class would have advanced a year since 2019, so that, for example, the first group of 795 trees would in 2020 have been age class 1–2).

Dispersal and distance from seed source

We determined an average (± SE) dispersal distance of 123.6 ± 2.0 m. The furthest tree surveyed measured 371.3 m from the center of the clearing, and most of the surviving offspring were observed in clusters between 50 and 150 m from the original seed source, just beyond the forest edge (Figs. 1, 2).

Table 1. Survey results displaying the estimated age (number of growing seasons based on number of nodes), average height (± SE), and number of trees in each age class for a wild population of *Castanea dentate* (Americna Chestnut) in Franklin County, ME.

Estimated age class (yrs)	Average stem height (cm)	Stems counted in 2019	Stems added in 2020	Stems re-located in 2020	Confirmed dead in 2020
0–1	15.8 ± 0.2	564	276	840	45
1–2	29.5 ± 1.2	178	39	217	11
2–3	72.3 ± 4.5	125	6	131	0
3–4	116.7 ± 0.8	68	4	73	0
4–5	178.9 ± 13.5	54	1	55	0
5–6	226.5 ± 22.3	18	3	21	0
6–7	368.6 ± 23.1	3	2	5	2
7–8	291.7 ± 204.2	3	0	3	0
8–9	-	0	0	0	0
9–10	-	0	0	0	0
10–11	-	0	0	0	0
11–12	-	0	0	0	0
12–13	-	0	0	0	0
13–14	-	0	0	0	0
14–15	865.0 ± 115.0	2	0	2	0
15–16	950.0	1	0	1	0

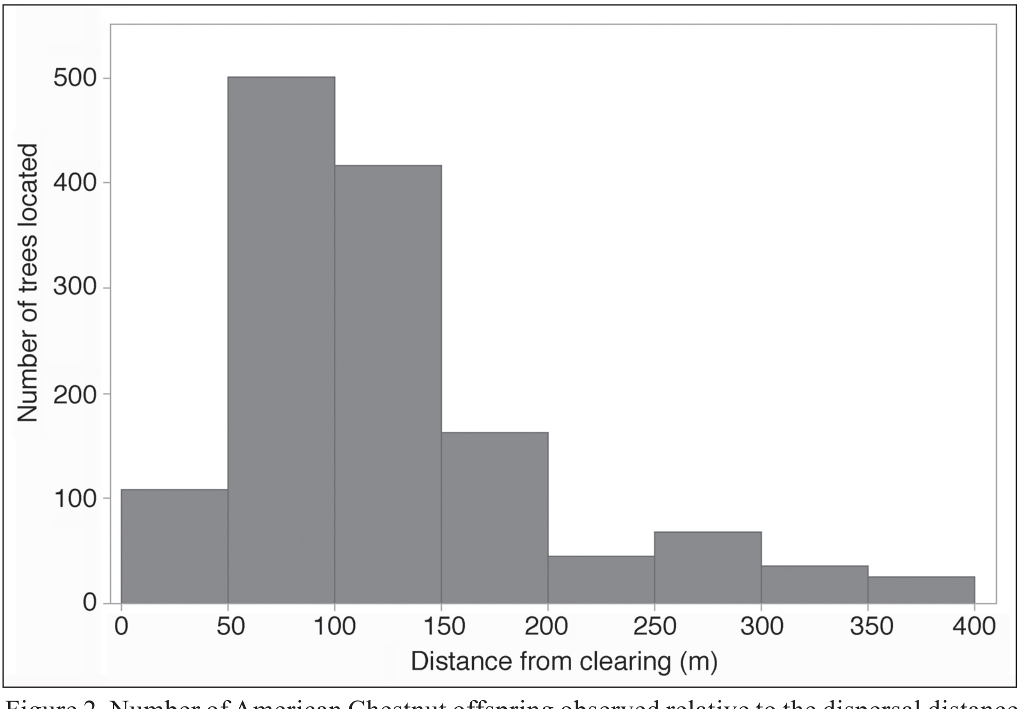

Figure 2. Number of American Chestnut offspring observed relative to the dispersal distance in meters. Most offspring were dispersed between 50 and 150 m from the clearing center with an average dispersal distance of 123.6 ± 2.0 m.

Seedling mortality

During the follow-up survey in 2020, we successfully relocated 808 of the 1016 individuals that we had marked the year prior. Of the 808 flags that we revisited, 750 were found to have the associated trees still present, alive, and apparently healthy, while 58 were reported as dead or missing (Fig. 3) Therefore, the mortality rate between 2019 and 2020 for all age classes is estimated to be ~7.2%. Of the 58 trees determined to have been killed between survey years, 46 belonged to the cohort initiated in 2019. We estimate seedling mortality of this cohort to be ~10.4% during their first year. Of all 1348 specimens observed during the 2 surveys, we reported 62 as showing obvious signs of browse.

During the 2020 survey, we were unable to locate 208 of the flags that we had placed the year prior. Many of these were scattered throughout dense thickets of young balsam fir where visibility was poor even within several meters of the placemark location. Others may have had the flag disturbed by wildlife or weather. Since we were unable to determine the condition of those individuals, we did not include them when estimating mortality and survivability.

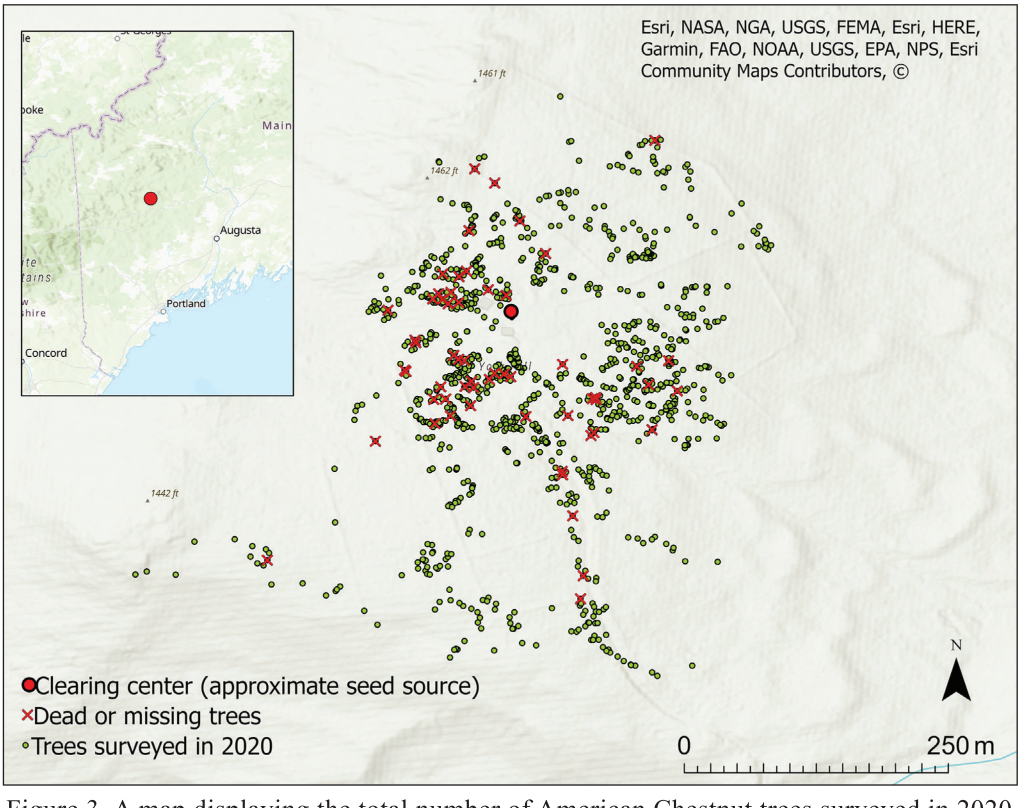

Figure 3. A map displaying the total number of American Chestnut trees surveyed in 2020, the green points representing trees that were still present and alive, and the red "X" marks representing 58 trees that were determined to be missing or dead. The large red dot represents the center of the clearing where 4 original parent trees had been planted in 1982.

Average height

In 2019 mean (± SE) stem height was calculated to be 48.8 ± 2.6 cm. In 2020, mean height increased by 3.8 cm to 52.6 ± 2.1 cm (Wilcoxon's signed rank $Z = 3.31$, $P = 0.0009$). When comparing height to the amount of available sunlight between both survey years, a Kruskal–Wallace H test revealed statistically significant differences in mean height between canopy-cover classes ($H = 141.63[3]$, $P < 0.0001$). Our results suggest that wild trees tended to exhibit the most growth under 25–50% canopy cover with an average height of 112.5 cm. Those growing under 0–25%, 50–75%, and 75–100% canopy cover yielded average heights of 64.2 cm, 51.8 cm, and 30.4 cm, respectively (Fig. 4).

Discussion

While our surveys in 2019 and 2020 yielded 1348 offspring, it is important to note that this represents a minimum, as subsequent walks through the forest

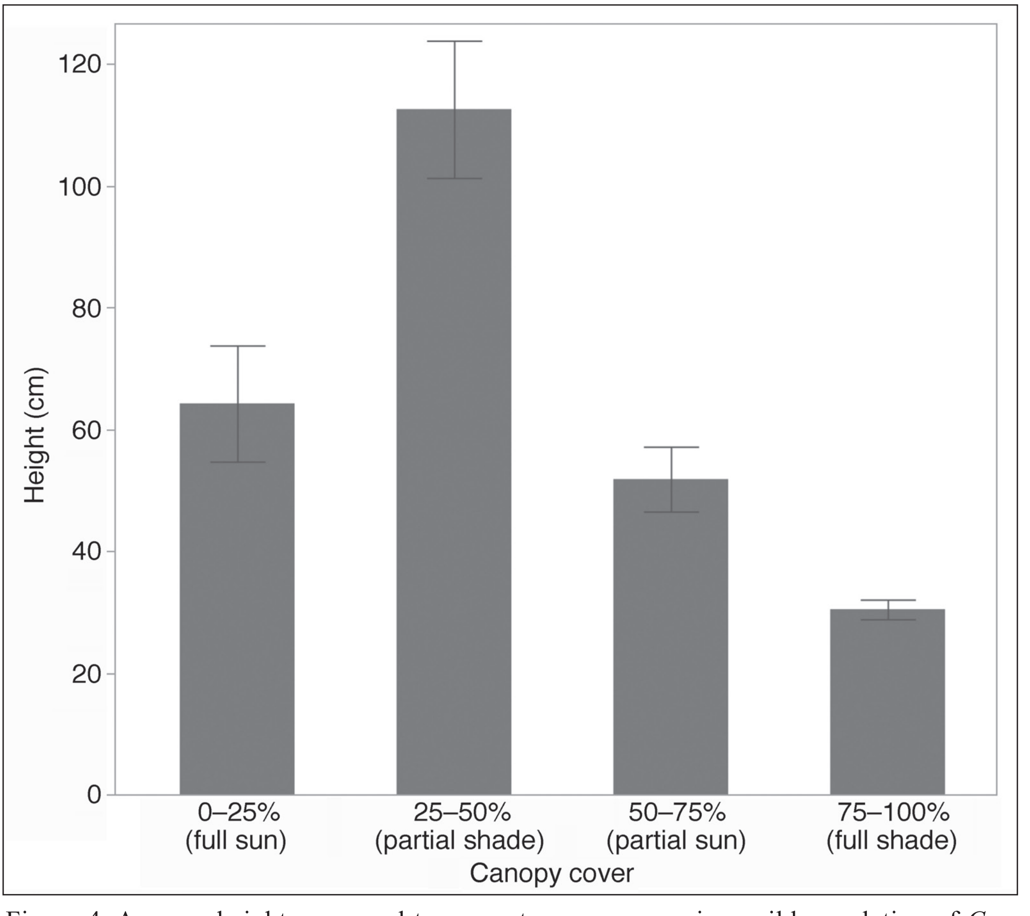

Figure 4. Average height compared to percent canopy cover in a wild population of *Castanea dentata* (American Chestnut) in a western Maine forest. A Kruskal–Wallace H test revealed statistically significant differences in mean height between canopy cover classes (H=141.63[3], $P < 0.0001$).

continue to uncover more that were not marked and counted. During our surveys, we searched ~500,000 m^2 of sloping, forested terrain. While we timed the surveys to maximize the visibility of seedlings, we still expected that some stems would remain undetected. Many of the newly discovered trees were small, and if in the shade often had a single leaf. Others had likely been browsed at the time of our surveys and had later grown a new stem. Several accounts reported seedlings growing beyond our survey area, up to ~800 m from the clearing center; however, since these were incidental sightings reported after our survey had been completed, we did not include them in our results. Given that the frequency of stems was shown to drop precipitously after moving beyond 200 m from the clearing center, and none had been located beyond 371.3 m in either year of our surveys (Figs. 1, 2), we suspect that these incidental observations represent outliers. Other such outliers are very likely to exist beyond our measured maximum dispersal distance of 371.3 m, as jays have been recorded traveling up to 1.6 km with nuts of similar weight (Bosema 1979). However, systematically surveying a much larger area on foot to include what we consider a relatively small fraction of the population was impractical given the timeframe of our survey. The continued discovery of trees that been previously undetected underscores the importance of future follow-up surveys and continued monitoring to update the estimated size of the population.

Estimated age classes and mean stem height

Given the size of our sample population and the diversity of site conditions across the property, we believe that our measurements represent average growth and regeneration to be expected in a typical mixed forest setting in western Maine. This information could be useful when informing restoration efforts and predicting how many growing seasons an established seedling may take to reach the canopy and begin flowering. While we detected a significant relationship between estimated age and mean stem height (Fig. 5), age alone may not be the most reliable indicator of stem growth. We also found a significant relationship between stem height and canopy cover (Fig. 4). Those under favorable conditions with ample sunlight will undoubtedly grow faster and have greater odds of reaching maturity, whereas those in unfavorable conditions may never grow beyond a meter tall and may never flower, described by Paillet as remaining in a “perpetually juvenile” state (Paillet 1993). Given the relatively high survival rate that we observed among seedlings despite browse pressure, it is possible for many of those initiated in the large 2018 cohort to persist for decades, putting on little to no growth until they are released by a canopy opening (Paillet 1993, Wang et al. 2013).

It is worth noting that our methods for determining age were purely estimates. As most of the stems were seedlings or saplings, using an increment borer was not a practical option for determining age. Estimating age by node distribution, a method employed by Paillet and Rutter (1989) in a similar study, can be performed quickly in the field, though may not be an accurate representation for stems that had been browsed or re-sprouted. However, most trees we surveyed were determined to be less than 1 year old, confirmed by the fact that many still had intact nuts attached, thereby adding confidence to our age estimate for the youngest cohorts. Partially decomposed remnants of nuts were occasionally found near the base of stems that we estimated to be 1–2 years old, but it was clear that they had not germinated that season. For specimens more than ~1 m tall, we found it relatively easy to count the number of years of growth on the stem.

Mortality and browse pressure

The seedling (age 0–1) survival rate of ~89.6% between growing seasons was much higher than anticipated given drought conditions across the region in 2020 and significant browse pressure from *Odocoileus virginianus* (Zimmermann) (White-tailed Deer), *Alces alces* (L.) (Moose), and *Lepus americanus* Erxleben (Snowshoe Hare) and other small mammals throughout the year. However, these survivability estimates fall within the reported values of 80–93% seedling survival after 1 year in nursery settings (Wang et al. 2013). Our findings are consistent with studies suggesting that browse pressure seems to have relatively little effect on survivability due to the American Chestnut's remarkable ability to resprout (Elwood et al. 2018). Therefore, the greatest factors contributing to recruitment are likely related to seed predation (Elwood et al. 2018) or adequate site conditions at cached locations where germination can occur (Wang et al. 2013).

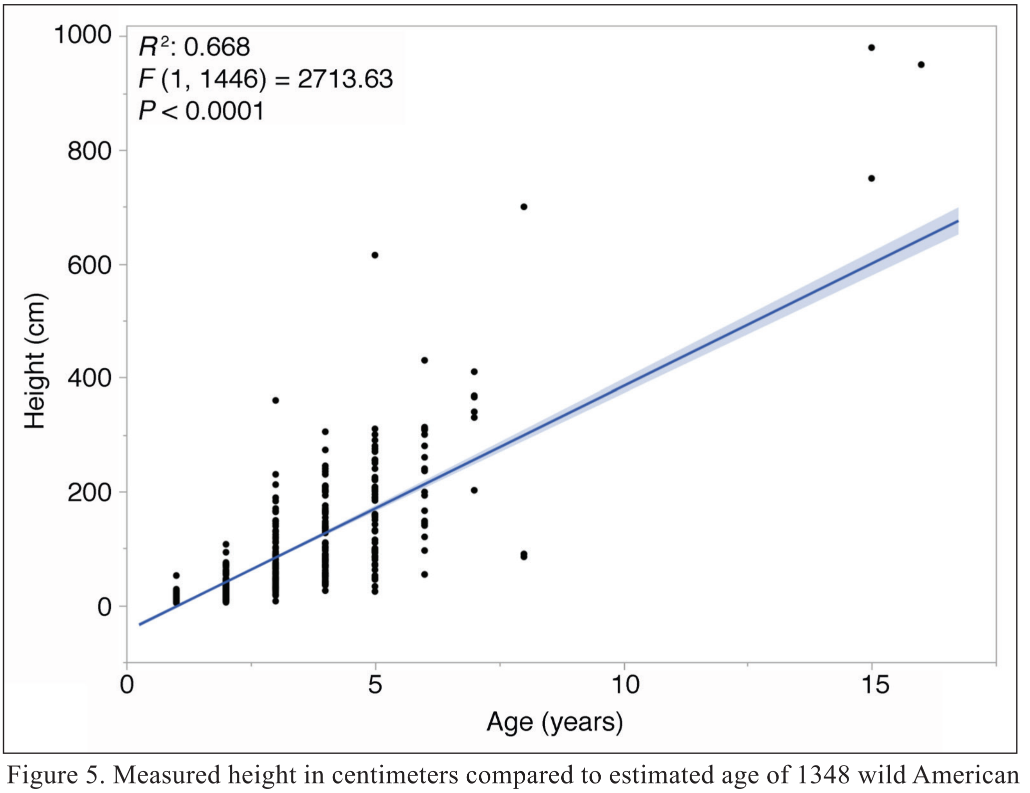

Figure 5. Measured height in centimeters compared to estimated age of 1348 wild American Chestnuts surveyed in a western Maine forest. Note that the individual points overlap, particularly in the youngest cohorts where many stems were measured at similar or equal heights.

Natural resistance

It is unknown whether the general health and fecundity of the surviving parent trees can be attributed to isolation from the blight, or to some degree of natural resistance. Our study site in Franklin County, ME, is located just north of American Chestnut's historic range (Little 1977), and therefore it is unlikely that an infected population exists within the distance required for wind-borne transmission (Rigling and Prospero 2018). However, *Quercus* (oaks) and *Acer* (maples) have been observed as "minor incidental hosts" to Chestnut Blight (Rigling and Prospero 2018), and both genera are widespread throughout the study area.

The original wild stock planted in 1982 were purchased from the Wexford County Soil Conservation district in Michigan (see Fig. S1 in Supplemental File 1), which conducts a search every fall for relict populations of seed-bearing trees to rear their stock. Populations found near the extreme western edge of American Chestnut's range have reported to exhibit resilience to the blight, continuing to produce viable seeds despite developing the typically fatal cankers characteristic of Chestnut Blight (Brewer 1995).

Seed dispersal and distribution of offspring

Most of the surviving trees were located 50–150 m beyond the edge of the clearing where the parent trees had been planted (Figs. 1, 2), and many of these are suspected to have been cached by Red Squirrels, as rodents have rarely been observed transporting seeds more than 100 m (Pesendorfer et al. 2016). Offspring were noticeably absent in the clearing directly adjacent to the seed trees, despite having access to almost full sun (Figs. 1, 3). A similar distribution pattern was also described in Paillet and Rutter's (1989:3457) study of a population in Wisconsin, in which they state that "chestnut seedlings and small saplings are more numerous along woodland edges and in recently disturbed soil, they are rare in the interior of ungrazed pasture". We believe that this distribution can be attributed to several factors, primarily the scatter-hoarding dispersal mechanism itself. Prior to the surveys, we observed scatter-hoarding behavior of both Red Squirrel and Blue Jay. Red Squirrels snip whole fruits from the live branches, which they then gather from the ground and take to a "safe" location just beyond the forest edge to be cached (Heinrich 2015), whereas jays remove the nuts while the fruit is still on the tree and carry them away from the seed source (Heinrich 2014, Pesendorfer et al. 2016). These behaviors leave few viable seeds remaining in the clearing. Chestnuts are particularly vulnerable to frost and desiccation (Paillet 2005), and therefore are less likely to germinate without the favorable microclimate that is provided by caching behavior (Vander Wall 1993), so those left within the clearing would have a greater chance of succumbing to these stressors. Additionally, much of the clearing remains unmowed, and is therefore dominated by dense vegetation throughout the growing season. Despite access to near full sun conditions due to the lack of canopy cover, any nuts that were to germinate may have difficulty becoming established due to competition from aggressive grasses, ferns, and other forbs that would starve the seedling of both light and nutrients. There may also be greater browse pressure from small rodents that are more abundant within the clearing than in the surrounding forest (B. Heinrich, pers. observ.).

While there is a distinct lack of recruitment within the clearing, a small population of young seedlings near the base of the parent trees persists, though none were estimated to be more than 2 years old. These young trees likely contribute to the relatively low mean height recorded among stems with access to full-sun conditions (Fig. 4). Beyond the clearing, most surviving trees tended to be clustered around areas where they would have access to partial sunlight, and especially along roads and forest edges. A linear grouping of American Chestnut trees running southeast from the clearing became established along the edge of a driveway (Fig. 1), and clusters of offspring just to the east of the clearing appeared to benefit from the overstory thinning that occurs within the former sugarbush. These observations correspond with those described by Paillet and Rutter (1989:3457) , in which they mention that "the general pattern of chestnut distribution indicates the importance of woodland edges in chestnut propagation".

Those seedlings found at the southern edge of our survey population were located along the top of a dry, south-facing ridge, and the northern and western limitation of the distribution appears to be limited by conifers. White Pine, spruce, fir, and occasionally *Tsuga canadensis* (L.) Carrière (Eastern Hemlock) dominate the rocky, shallow-to-bedrock knolls to the north and east of the clearing. Offspring were noticeably sparse in these regions, and almost entirely absent in areas dominated by dense Balsam Fir regeneration. The dispersal of any seedling beyond this range can likely be attributed to jays, the only birds that have been observed scatter-hoarding chestnut seeds at this location (Heinrich 2014, Johnson et al. 1997). Given that jays have been known to carry similarly sized nuts such as acorns over 1.6 km from their seed source (Bosema 1979) and are suspected to travel tens of kilometers while carrying seeds (Pesendorfer et al. 2016), it is highly likely that more seedlings have become established far beyond the extent of our study area.

Conclusion

As climate change and increasing globalization accelerate the spread of forest pests and other stressors (Frankel et al. 2012, Weed et al. 2013), understanding the dynamics behind natural regeneration is crucial to inform reintroduction efforts of American Chestnut (Paillet 2005, Noah et al. 2021). With nation-wide efforts underway to restore populations of both hybridized and pure American Chestnuts, it is worth examining our findings in the context of climate change and biodiversity conservation. We now know that 4 healthy seed-bearing trees can initiate a reproductive population of over 1000 individuals within a span of only 30–40 years. Furthermore, we now have a clear picture of the seed-dispersal patterns resulting from scatter hoarding, and we can estimate the average distance in which a single chestnut's genetic material can travel from a known point of origin with scatter-hoarding as the primary method of dispersal. Beyond chestnut reintroduction, these findings may also contribute to our understanding of similar species such as oaks, which also rely on scatter hoarding as their primary dispersal mechanism (Bosema

1979) and have ranges that are also expected to expand in response to climate change (Barnes and Delborne 2019, Janowiak et al. 2018).

From the perspective of biodiversity and wildlife conservation, the reintroduction of American Chestnuts to hardwood forest ecosystems would benefit wildlife in several ways. By flowering mid-summer and producing a reliable annual mast crop, American Chestnuts serve as a source of food in the form of nectar and pollen for pollinating insects, as a larval host for 93 known species of Lepidoptera (Robinson et al. 2010), and as a reliable forage for seed predators. Paillet (2005) estimates that the introduction of American Chestnut to hardwood forests would increase total nut production by 20–50%. For nearly 2 decades, these seed-bearing trees have filled an ecological niche that had been missing from eastern hardwood forests for over a century. As of July 2021, the first known offspring have reached reproductive maturity (see Fig. S4 in Supplemental File 1), giving rise to the likelihood that a third generation of seedlings may become established in the coming years. Continued study of this population in subsequent decades will provide further insight into the efficacy of fostering resilient wild populations and may offer a better understanding of the rate at which naturally dispersed American Chestnut may become established as its range continues to expand.

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