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Population Matrix Model for American Chestnut (*Castanea dentata*) and the Implications for Re-introduction

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Population Matrix Model for American Chestnut (*Castanea dentata*) and the Implications for Re-introduction

Elise Elwood

Introduction

Biodiversity loss is occurring at an unprecedented and alarming rate; we can no longer ignore the effects of humans on the environment and must take action to reduce our impact (Pimm 1995). Restoration of degraded communities and ecosystems can reduce biodiversity loss (Seddon 2007, Armstrong and Seddon 2008). Restoration strategies, sometimes referred to as the "restoration toolbox," encompass many specific techniques one of which is the re-introduction of individual species (Sodhi and Ehrlich 2010). Re-introductions are the introduction of individuals from a different population of a species to an endemic region of the species, where populations have been eliminated due to natural processes or anthropogenic factors (Sodhi and Ehrlich 2010). Species re-introductions are an important tool in biological conservation; however, they often are unsuccessful or require more resources than expected as it is difficult to predict how a new population will grow (Sarrazin and Barbault 1996, Seddon 2007). California condors (*Gymnogyps californianus*) and the grey wolf (*Canis lupus*) are examples of highly successful re-introductions of animal populations (Wilmers 2003, Ralls and Ballou 2004, Ripple 2001). However, there have been few attempts at re-introducing a plant species. Instead plant re-introductions have largely been used only as a part of whole ecosystem restorations.

American chestnut (*Castanea dentata*; chestnut henceforth) offers a potential for intentional plant re-introduction (Jacobs 2007, Jacobs et al. 2013). American chestnut has been called a foundation species in the Eastern United States because it was important for regulating nutrient cycling and decomposition (Ellison 2005), as well as food web dynmaics (Dalgleish & Swihart 2012). Foundation species are unlike keystone species in that they are high in number and widespread, yet similar in that they are important in determining the structure and stability of local ecosystems (Ellison 2005). Trees are often foundation species in forest ecosystems; the presence or absence of specific plant populations have the potential to strongly affect ecosystem structure and health.

The American chestnut was a prominent tree in eastern forests from Maine to Georgia in early American history (Jacobs et al. 2013). American chestnut trees impact community and ecosystem processes, such as insect, soil, small mammal, and bird communities, as well as tree composition. In 1905, the fungus *Cyphonectria parasitica* was accidentally introduced in New York Zoological Garden and quickly spread throughout the range of the American chestnut infecting adult chestnuts of the estimated three to four billion trees in a period of 50 years (Zhang 2013, Welch 2006). The fungus enters chestnut trees through cracks in the bark which are characteristic of older chestnuts or tree wounds, and spreads to the cambium creating cankers that prevents the flow of nutrients (Welch 2006). Restoring American chestnut with a blight-resistant chestnut tree has been explored by the American Chestnut Foundation and other researchers since the 1920s. Scientists have experimented with multiple possibilities for creating blight resistance in American chestnut trees including crossbreeding with Asian chestnut trees (primarily Chinese chestnut, *Castanea mollissima*), infecting trees with a hypovirulent (non-lethal) strains of the blight, *C. parasitica*, and genetic modification (Jacobs et al. 2013). American chestnut may be important to restoration of forest communities as there is a possibility for the re-introduction of blight resistant chestnut. This is perhaps one of the first opportunities for tree re-introduction and may serve as a model for future plant re-introductions.

Monitoring re-introduction projects and modeling the growth of populations are ways to ensure restoration efforts may be achieved. Matrix population models are size structured models that can be used to project population growth rate for re-introduced populations, and offer specific information on what life stages or transitions are the most important for targeting management to enhance population establishment (Morris and Doak 2002). If the population growth rate is declining, it indicates that the population may not be viable without management action or change in environmental factors (Morris and Doak 2002). The rate of decline could be due to many factors. Sensitivity and elasticity values (prospective analysis of matrix models, (Caswell 2001)) can help determine what life stages and transitions are most important to the population growth rate, and thus how to target management strategies. Population models also offer the ability to mathematically experiment with different re-introduction scenarios (Morris and Doak 2002). While significant population monitoring of growth, survival, and reproduction is necessary to create a viable model, population models that advise management can enhance the success of species reintroductions (Morris and Doak 2002).

My study creates a matrix population model of a young population of American chestnuts with the goal of informing restoration efforts using blight-resistant, back-crossed American chestnut. My research provides a detailed demographic study for a site just north of the historical range of chestnut experiencing similar annual environmental effects that re-introduced populations in the Northeast may face. The goals of my study are 1) to measure growth, survival, and reproduction of a chestnut population under natural conditions 2) to develop a matrix model that can be used to inform restoration, and 3) to use the model to explore possible restoration scenarios.

Methods

Site description

The Atkinson Grove was selected as a study site as it is a reproducing population of American chestnuts largely unaffected by blight located in central ME, around 40 miles north of Bangor. The land is currently owned and managed by the Northeast Wilderness Trust. Prior to the discovery of American chestnut on the property, the land was owned by a logging company (Rea 2008). One of the loggers correctly identified the trees as American chestnut, and saved the trees (Rea 2008). It is unknown whether these chestnuts were originally planted north of their historical range or were dispersed by natural processes (Rea 2008). However, the establishment pattern of the largest trees is not consistent with human planting (Sara Fitzsimmons, personal communication).

American chestnut trees flower in late June and have been observed to flower in early July in an arboretum 70 miles south of Atkinson (Ardeana 2012). Blight has been present at the site in recent years. Blight spread at Atkinson has been slow due to a short growing period each year as cold weather forces the blight into dormancy (Anagnostakis 1984). While blight presence has been recorded at the site, blight presence is minimal enough that it is not included in the population model (Appendix 1).

The population is spread over ~ 6.1 ha of land and has an average rainfall of 43.62 inches per year and an average yearly temperature of 5.3°C (US Climate Data). For the years of the study, 2011-2013 the rainfall has been, 114.02, 120.55, and 116.48 cm per year respectively (NOAA, US Climate Data). The average temperature over each year was 7.28°C (2011), -1.7°C (2012), and 5.9°C (2013) (NOAA, US Climate Data). If there is a hard frost late in the spring, flower buds may be damaged, effecting the timing and extent of flowering (Zon 1904). The last hard frosts in Bangor ME may be before April 2nd or as late as May 10th.

Rabbits and deer are the major sources of herbivory on American chestnut at the site. Young chestnut seedlings waiting for a light gap are most impacted by the effects of herbivory. Winter snow packs may reach several feet in the region, allowing rabbit browse to affect seedlings that would be large enough to otherwise escape browse.

Data collection

Data were collected from the site during the month of July each year: July 30-31 2011, July 18-26 2012, and July 21-29 2013. In 2012 and 2013, a 10 m by 10 m grid was laid down to organize data collection, covering an approximate area of 12.7 acres. All canopy trees with a Diameter at Breast Height (dbh) > 4 in and all chestnuts were tagged and measured. Living trees of 4 in dbh or greater were selected as they are responsible for the vast majority of the canopy competition. Dead trees (snags) were not tagged. Age, root collar diameter (rcd) or the diameter of the sprout where it emerged from the soil, and height were measured for chestnut seedlings (where dbh < 1 in). Chestnut seedlings have distinct terminal bud scars for each year of growth allowing determination of the age of the seedlings by counting the number of terminal bud scars. When there was significant browse and the number of terminal bud scares could not be determined, an age range was estimated using a combination of terminal bud scares, diameter of browsed stems, and expert opinion of chestnut growth. Age was recorded for each plant only during 2012 or 2013 corresponding plant age was then calculated for other years of data. If age was not available for 2012 or 2013, age from 2011 was used. The lower end of the estimated age range was used for analysis.

For trees with a dbh > 0.25 in (2011) or dbh >1 in (2013), dbh was measured instead of or in addition to root collar diameter. A subset of older chestnut trees was cored using an increment borer in order to determine age and growth of older trees. Fieldworkers recorded if plants had split stems and the number of sprouts (usually stump sprouts). When there were multiple sprouts or the tree split before breast height, dbh of the largest sprout was recorded. Browse and other disturbance (i.e., tree knocked over) were noted. On older chestnuts, the presence or absence of catkins (male flowers) in the surrounding area was used as an indication of whether a tree flowered. The location of all of the chestnut seedlings and saplings in addition to all canopy trees (dbh > 4 in) were mapped using a PosTex ultrasonic instrument (Hagloff, Inc.) which provides detailed information on the relative positions of objects studied. In 2013, in approximately 25% of plots established in 2012, chestnuts were re-measured for rcd (or dbh) and height in order to determine growth, stasis, or retrogression (shrinking, often due to browse).

Model structure

In order to create a matrix model, stages were determined based upon differences in probability of browse, survival, growth, age, and reproductive capacity (Morris & Doak 2002). Using demographic data from the entire population, I have broken the population into 9 life stages (Figure 1). The first three stages are age based: Stage 1 seedlings are less than a year old, stage 2 seedlings are 1 year old, and stage 3 seedlings are 2 years old. Stage 4 and Stage 5 are seedlings that are 3 years or older and are under 50 cm or over 50 cm respectively. Stage 6 seedlings are 3 years or older and are taller than 100 cm but not large enough to have a dbh =1. Stage 7 saplings have a dbh between 1 and 4 in and stage 8 trees have a dbh between 4 and 10 in. Finally, stage 9 includes all trees greater than 10 in dbh.

Model parameterization

In order to calculate growth, stasis, and retrogression matrix elements, I first calculated the likelihood of each stage transition occurring for plants that survived. Growth, stasis, and retrogression stage transitions were calculated by taking the quotient of the number of individuals in size class n+1, n, or n-1 in year t+1, respectively, divided by the number of individuals in size class n in year t (Morris & Doak 2002). Growth, stasis, and retrogression stage transitions can be interpreted as the probability each event will occur within a single time step (1 year) if the plant survives. In order to determine the final matrix elements, stage transition values are multiplied by the survival probability of the initial stage.

Ideally, I would use measurements of growth and survival for all stages from our population in ME where all trees are experiencing similar environmental conditions. Due to a low sample size and slow growth of the large trees in our population, additional data regarding the growth of large chestnut trees was used from the work of Zon in 1904 for growth from trees with a dbh between 4 and 10 in to a dbh >10 in (G10, Figure 1). Zon's work with American chestnut, as a forester in MA in the early 1900s provides an age to dbh conversion (Zon 1904 p 24). His data suggest that it would take 11 years for a chestnut to grow from a dbh of 1 to 4, and 23 years for a 4 in dbh chestnut to grow larger than 10 in. Thus for all surviving chestnuts with a dbh between 1 and 4, the likelihood of stasis is Y-1/Y where Y is equal to the total amount of years it takes to grow from a dbh of 1 in to a dbh of 4 in and the likelihood of growth is 1/Y.

In order to determine the probability of survival for each stage class, I calculated the quotient for the number of individuals from the node alive in year t+1 divided by the number of individuals alive in year t. However, due to high survival throughout the population, this gave many survival rates of 1. In order to determine survival probabilities using all of the data available I ran logistic regressions relating height to survival and dbh to survival from 2011-12 and 2012-13 (Morris & Doak 2002). I then determined the midpoint or median height or dbh for each size class (x value), and found the corresponding fitted point from the regression equation (y value). For new recruits, 1st year, and 2nd year seedlings, the median of all of the plants of that age for that stage class was used as the x value input (height). For 2011 there were no new recruits (or plants less than 1 year old) and so the median for 2012 was used as the x value. The fitted points from the logistic regression represent the survival probability between single year transitions for individuals in each stage class. Once I determined the survival probabilities for each size class for both 2011-12 and 2012-13, I averaged the two years to create a single survival vital rate vector. 2011-12 comprises approximately 40% of the data and 2012-13 comprises approximately 60%. Due to a complete survival rate of the large trees in our population, I used the survival rate from a population of healthy American chestnut in MI for chestnuts for our largest size class (Davelos and Jarosz 2004).

In order to calculate fecundity, first I determined the number of trees that were noted in any year to have flowered. Once this total number of flowering trees was determined, I then calculated a mean number of new recruits per year (2012-2013). No new recruits were noted in 2011; due to much smaller sample size and area searched, as well as differences in sampling technique, this year was not included in calculations for the average number of new recruits. In order to determine the fecundity values, the per capita recruitment value is multiplied by the probability of flowering for the trees within the size class.

Model Analysis

I used R and the package popbio to calculate the population growth rate and complete the asymptotic and transient analyses (R Core Team 2012). Deterministic prospective analyses (sensitivities and elasticities) were conducted using Eigen analysis (Caswell 2001) using the function eigen.analysis() from the popbio package (Stubben and Milligan 2007).

The population growth rate (λ) indicates if a population is growing ($\lambda > 1$) or declining ($\lambda < 1$), or stable ($\lambda = 1$). The damping ratio (ρ) is a way of indicating how long there will be transient dynamics before a stable λ is reached (Caswell 2001). The dominant right eigenvector (w) indicates the stable stage distribution and the left eigenvector (v) contains the reproductive values for each stage class (Caswell 2001). The stable stage distribution indicates the expected long-term distribution of the population within the stage classes of the model. Reproductive values indicate "the relative contribution to the future population growth" that is expected of the individuals currently in that class (Morris and Doak 2002). The reproductive values are normalized by dividing each number by the value for the first stage class, so that the lowest stage class always has a reproductive value of 1 (Morris and Doak 2002).

The sensitivity matrix indicates how sensitive λ is to changes in the matrix elements; which elements would have the largest effect on λ, should those elements be changed by the same amount. Matrix elements that represent, growth, stasis, and retrogression are by necessity less than 1, while fecundity values may be quite large making it difficult to compare the impact of matrix elements on λ from sensitivities. Elasticity values are normalized sensitivity values that are more easily comparable to each other. Elasticities sum to 1 and thus can be interpreted as percentages.

Transient analysis was conducted using the pop.projection() function with the observed population vector as the initial vector and a total number of year set at 100 (Stubben and Milligan 2007). The transient analysis examines the dynamics of the model in the short term, before asymptotic dynamics of the model have been reached (Ezard et al. 2010).

In order to model different growth scenarios, re-introduction tactics of introducing 100 plants in either stage 4 or stage 5 were run in the model. In addition, I simulated increased deer management in a restoration context by reducing the number of seedlings (<100cm) that undergo retrogression. I eliminated retrogression from >50cm to <50cm (R1) by setting the matrix element to 0. In addition, to simulate a reduction of browse on seedlings <50 cm and removal of browse as a barrier to growth, I reduced the number of seedlings in stage class 4(<50cm) that survive but do not grow to >50 cm (S1) and increased the number of seedlings growing to >50 cm (G5). In 2011, 11% of seedlings <50 cm and in 2013 17% of seedlings <50 cm were browsed. For this restauration model of aggressive management scenario I reduced the matrix element for stasis of seedlings <50cm, and increased the matrix element for growth >50cm by 0.15, (approximately 15%).

Results

Population description

In 2012, 593 chestnuts were tagged and measured; 8.8 acres were sampled. There were 230 trees measured in 2012 that had been previously measured in 2011. In 2013, 586 chestnuts were tagged or measured, 130 of those were trees previously measured in 2012. In 2013, a total of 499 chestnuts were revisited to determine survival. Blight was witnessed to have infected only 6 trees in the population or a total of 0.51% of the population recorded. However, presence of blight was not collected systematically until 2013. In 2013, 3 of 33 trees large enough to be visibly infected had blight, this is approximately 8.6% of the population of large trees (Appendix 1). There are significant correlations between age and height, rcd, dbh, and height and rcd; the correlation between height and rcd is particularly high with a rho of 0.76 (Appendix 2). Root collar diameter data was not included in the matrix model parameterization because height was determined to be a more useful parameter.

Growth

It appears that seedlings shoot up during their first year of growth and then grow very little for the next couple of years (Figure 2). The median height for seedlings less than 1 year old is 15.1 cm, the median heights for 1 and 2 and 3 year old plants are 15.2 cm, 14.8 cm, and 17.8 cm respectively. Using the age to dbh conversion from Zon, stage transitions can be calculated for the growth of the larger stages. The stage transitions from stage 7 to stage 8 are 0.91 for stasis and 0.091 for growth. The stage transitions from stage 8 to 9 are 0.957 for stasis and 0.043 for growth. The matrix elements calculated using Zon's data for stage 7 to 8 of 0.9 and 0.09 are shifted more towards stasis and less toward growth than the matrix elements calculated from our population of 0.87 (stasis) and 0.13 (growth). The matrix elements calculated from Zon's population are only used as model parameters for the transition between stage 8 and 9 (Appendix 3). Deer and rabbit browse primarily effects seedlings <100 cm tall (Figure 3). Specifically, 69.3% and 87% of browsed seedlings are under 50 cm and 100 cm tall respectively.

Survival

Survival is very high within the Atkinson population. Seedlings less than 1 year old have a much lower survival (0.77) than older seedlings (0.97-1) when calculated by number of survivors out of total seedlings in the stage class. The lowest survival probability calculated via logistic regression was for 0 year old seedlings from 2011 to 2012 (0.86). In 2011-12 stage classes 6-9 all had a survival of 1, and in 2012-13 stage classes 5-9 all have a survival probability greater than 0.99 (Appendix 4). For the matrix population model, I used the logistic parameterization of survival except for the survival of the largest stage (Figure 4). For stage 9 trees, I used the survival rate provided by Davelos and Jarosz (2004): 0.987.

Fecundity

Trees greater than 10 in dbh are known to flower consistently (Davelos 2004, Mattoon 1909) and the smallest flowering tree recorded at Atkinson had a dbh of 4.1 in; thus I set the lower limit for potentially reproducing young trees to stage 8, at a dbh>=4 (Figure 5). Per capita recruitment of 1.412 and 2.917 were observed in 2012 and 2013 respectively with an average per capita recruitment value of 2.167. Trees with a dbh ≥10 in were given a probability of flowering of 1, therefore the F1 matrix element is 2.167. Trees with a dbh ≥4 but <10 have a probability of flowering of 0.32, and a F2 value of 0.693, thus less than 1 new seedling is attributed to each plant in that size class per year (Appendix 5). Stage class 9 is responsible for producing 3x as many new recruits as stage class 8.

Asymptotic analysis

The long-term population growth rate (λ) of the Atkinson population is 1.0319, and the damping ratio is 1.081. The stable stage distribution indicates that the largest class will be stage class 4 (seedlings 3 or older and less than 50 cm), exceeding 50% of all chestnuts in the population (Figure 6). Stages 5 and 6 will be the next largest, however still much smaller than size class 4. In addition, there will be very few trees in stage class 7 (with a dbh >1 and <4), much less than are in stage class 8 or 9. The stable stage distribution has more trees in stage class 4 and stage class 9 than the observed stage distribution. However, the observed stage distribution has more trees in stage classes 7 and 8. Stages 1, 2, 3, 5, and 6 differ only slightly between the observed and stable stage distributions (Figure 6). Fewer trees in stage classes 7 and 8 in the stable stage distribution indicate that there will be fewer intermediate chestnut trees and more, though still very few, large trees.

Comparing reproductive value among stages, 2nd through 4th stage classes will contribute 15 to 39% more to future population growth than the stage 1 class. Stages 5 and 6 will contribute 238 and 419% more than stage 1. However, it is not until stages 7, 8, and 9, the largest reproductive values are found: these stages impact the future population growth 2930%, 3630%, and 4830% more than seedlings less than a year old (Figure 7).

Prospective analysis

The growth from stage 6 to 7 had the largest sensitivity values of 0.726, indicating that an absolute change of this matrix element would affect λ more than a change in any other matrix element (Table 2). The largest elasticity values, and thus the matrix elements that have the largest impact on λ, are 0.262 and 0.204 for the survival of stage class 9 and 8 respectively. As elasticities sum to1, they can be directly compared, thus the next largest elasticity value, 0.152, for the survival of stage class 4, will have a smaller impact on λ than changing the survival of stage class 9 or 8, but a larger impact on λ than any other matrix element (Table 3). The survival of stage class 4 has an impact 7x larger than the growth from stage 4 to 5 (elasticity= 0.023), and nearly twice as large as the impact of survival of stage classes 5 and 6 (elasticities= 0.078 and 0.083).

When elasticities are summed by category, the relative influence of growth, stasis, retrogression, and fecundity may be determined. In the Atkinson population, stasis or survival within one stage class are the state transitions most elastic to λ, with a total of 84.2% of the elasticity. After stasis, growth is the next most elastic to λ, indicating 14.1% of the elasticity. Fecundity and retrogression represent merely 1.5-2% of the elasticity (Table 4).

Transient analysis and restoration scenarios

According to the transient analysis, the population in ME will reach stable dynamics in approximately 80 years (Figure 8). The transient analysis indicates that the population will overshoot the long-term λ and then go below λ before reaching a stable λ after around 80 years.

The transient scenarios demonstrate the impact of different re-introduction strategies, comparing the introduction of 100 stage 4 or stage 5 chestnuts. When chestnut seedlings ≤50 cm are introduced, the λ starts around 0.96, increasing to a high of 1.035 before stabilizing after around 80 years, whereas when chestnut seedlings >50 cm are introduced, the λ starts around 1, briefly drops to 0.98, peaking at 1.04 and then stabilizing after 70 years (Figure 9a ,9b).

In the low-browse analysis, a lambda of 1.05 was reached, which is higher than the lambda without the limits to browse (Figure 9c). This population followed a very similar trajectory of population growth rates as the asymptotic analysis, resulting in a stable lambda after approximately 60-70 years.

Discussion

A λ of 1.03 indicates that the population is growing at 3% per year. According to our model, the population is not likely to decline or be extirpated without outside influence. This is very encouraging for re-introduction, because it indicates that the population will continue to grow and is self-sustaining. The damping ratio close to 1 indicates that the transient phase will be long – i.e., it will take decades to reach stable population growth. Stasis of stage 9 (dbh>=10) and stages 8 (dbh >=4) were the matrix elements with the largest elasticities to lambda; the survival of these large stage classes are driving the population growth. Stage 4 (seedlings <50 cm and 3+ years old) stasis, has the next largest elasticity value and potential to impact λ. Chestnut seedling growth in this population is highly heterogeneous; while seedlings aged 3 to 9 grow very little on average, individuals may greatly increase or decrease in height. Limitations to optimal chestnut growth seem to include retrogression from non-fatal herbivory, and environmental factors such as access to light. Chestnut survival is so high in the Atkinson population, as injured chestnuts re-sprout, that limitations to growth impact stasis values and thus λ greatly. Fecundity has little elasticity to λ. Restoration scenarios indicate that management reducing browse would help increase λ. While there will be a growing chestnut population in the forest, approximately 95% of the population will have a dbh less than 1 in. The observed population is still a young population, and thus it makes sense that there are very few trees in the largest stage class of full adult trees. It is likely that so much of the population is under 50 cm tall due to competition growth constraints and herbivory (Jacobs 2007, Paillet 2002).

The Atkinson population has a higher λ than either of two healthy populations studied in MI by Davelos and Jarosz (2004): λ = 1.005 and 1.012. In addition, elasticities as summed by category (stasis, growth, retrogression, and reproductive) indicate that while stasis is the most elastic vital rate for both sites (Atkinson and the populations in MI), growth and retrogression transitions have larger elasticity to lambda in Atkinson than was reported in MI (Table 4). In addition to differences in elasticity to λ, our model uses a different method of calculating fecundity. What is not reflected in our fecundity calculations is that larger trees not only flower more consistently, but that number of chestnuts per flowering tree increases exponentially with dbh, thus our fecundity estimate of the stage class 8 is likely an overestimation and stage class 9 an underestimation. In Davelos and Jarosz (2004), the number of chestnuts per tree is included in the estimates of fecundity and thus the fecundity of the largest six class is much larger than her other reproducing stages (Davelos and Jarosz 2004).

Although the largest elasticity values are for the survival of trees in stage 8 and 9, this is not necessarily useful information for management. Survival among trees >=4 in dbh is already high, it would be difficult to increase survival of these trees. It would not be feasible to plant trees of this size, and blight management cannot eradicate blight, only lengthen the lifespan of trees in the population by slowing its growth and dispersal. Thus, in order to advise re-introduction, it may be useful to look at the stage class 4, or seedlings <50 cm tall and 3 years or older. The elasticity value for the survival of this class is 0.153 is nearly 2x higher than the next greatest elasticity value. Planting seedlings >50 cm or protecting seedlings that are <50 cm from heavy browse would likely have a positive impact on the population growth rate.

The large elasticities and reproductive values for trees with a dbh >1 and in particular with a dbh >10, illustrate the devastating effects of blight and its rapid demise of the American chestnut. The combined survival elasticities for the largest 2 size classes represent 46.6% of all elasticity to λ .The blight kills the individuals in the population that have the largest expected relative impact on the future growth of the population.

The re-introduction scenarios indicate that the population growth rate will not be stabilized for many years if seedlings greater than 3 years old and either $\leq$ 50 cm or > 50 cm are introduced. The population protected from browse has a higher population growth rate indicating that this population is growing at a faster pace. Thus, while limiting browse would help a struggling population, with a population growth rate above 1 already, the resources required to limit browse may not be worthwhile. However, in a population that had a population growth rate below 1, it may be beneficial to limit browse. Deer can greatly impact community composition and structure, limiting the regeneration of species (Rooney and Waller 2003, Augustine and McNaughton 1998).

Future Directions

Additional opportunities for analysis include incorporating soil, light, spatial locations, and local competition. A subset of plots were sampled for small stem (<0.25 in dbh) diversity and abundance, recording all stems in the plot. This information may be used to determine the forest type and competition faced by American chestnut within the site. In addition, there are tree cores from many larger trees in the population that can be used to calculate growth for the larger size classes and to compare with growth of large chestnuts at the site in ME with Davelos in MI and Zon in MA. Current analyses use averaged data from multiple years, as the data from each year is not complete. However, there are some possibilities to incorporate observed inter annual variation in fecundity, survival, and growth into a stochastic model in order to determine confidence intervals for the population growth rate and stable stage distribution. Finally, adding information on weevils and other predators would make a more complete model. By mapping individual chestnut recruits to the closest or most likely potential parent (flowering adult nearby), and collecting data on burr numbers, I would be able to more accurately determine the difference in fecundity between the different stages or by dbh.

Integral projection models are models that do not break the population into a few discrete size classes, but instead an entire range of stage classes and thereby eliminates artifacts from stage class divisions and accounts for more variation in growth rates. λ of long lived and slow growing species can be greatly impacted by the number and the placement of stage categories. Zuidema and Pieter (2010) conducted a study on different tree species in which they found λ, elasticity values, and age estimates to be highly sensitive to the number of life stages. While λ values varied with different life stage categories in a matrix model, the λ value stabilized with 100-1000 different categories created by an IPM (Zuidema and Pieter 2010). In addition, matrix models often underestimate tree ages, as they offer unrealistically fast progression through the life cycle; IPM's alter tree age estimates significantly, resulting in slight overestimates in Zuidema and Pieter's study (2010). I will continue the study of the Atkinson population through the development of an IPM that I could compare to the matrix model approach.

Conclusions

American chestnut is one of the most studied extirpations due to an exotic fungus, and has the possibility for re-introduction in the near future (Ellison 2005). Exotic pathogens or pests affect many other tree species and American chestnut may serve as a model for other extirpated or declining tree species (Jacobs et al. 2013). Demographic analysis offers the ability to project population growth of reintroduced populations and thus advise management actions through focusing efforts on life stage transitions that have the largest impact on lambda. American chestnut may serve as a model for the use of a demographic study to advice the re-introduction of plant species.

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Tables

Table 1. Matrix elements representing the probability of transition between stages for growth, stasis, and retrogression. For fecundity, matrix elements represent the number of new recruits per capita per 1 year time step. The starting stage is indicated by the row number and the stage in the following year is indicated by the column number. Growth states are green, stasis stages are blue, retrogression stages are pink, and fecundity values are yellow.

t										
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
t + 1	**1**	0	0	0	0	0	0	0	0.693	2.167
	2	0.897	0	0	0	0	0	0	0	0
	3	0	0.911	0	0	0	0	0	0	0
	4	0	0	0.897	0.878	0.228	0.068	0	0	0
	5	0	0	0.042	0.076	0.598	0.136	0	0	0
	6	0	0	0	0.008	0.171	0.773	0	0	0
	7	0	0	0	0	0	0.023	0.866	0	0
	8	0	0	0	0	0	0	0.134	0.957	0
	9	0	0	0	0	0	0	0	0.042	0.987
	Survival by stage class	0.897	0.911	0.939	0.962	0.997	0.999	0.999	0.999	0.987

Table 2. Sensitivity values. Sensitivities indicate an absolute change in growth from stage 6 to stage 7, and from stage 4 to stage 6 would have the largest effect on λ. Largest sensitivities are in bold. Only sensitivities for non-zero elements are shown.

	1	2	3	4	5	6	7	8	9
1	0	0	0	0	0	0	0	0.006	0.006
2	0.018	0	0	0	0	0	0	0	0
3	0	0.018	0	0	0	0	0	0	0
4	0	0	0.017	0.18	0.044	0.034	0	0	0
5	0	0	0.029	0.308	0.076	0.059	0	0	0
6	0	0	0	**0.542**	0.133	0.104	0	0	0
7	0	0	0	0	0	**0.726**	0.099	0	0
8	0	0	0	0	0	0	0.123	0.22	0
9	0	0	0	0	0	0	0	0.293	0.274

Table 3. Elasticity values: the largest elasticities are the stasis values for stages 9, 8, 4, 7, and 6 in descending order, indicating that a proportional change in stasis of stage 8 would have the largest proportional effect on λ. Fecundity, growth, and retrogression values are less elastic to λ. Largest elasticities are in bold.

	1	2	3	4	5	6	7	8	9
1	0	0	0	0	0	0	0	0.004	0.012
2	0.016	0	0	0	0	0	0	0	0
3	0	0.016	0	0	0	0	0	0	0
4	0	0	0.015	**0.153**	0.01	0.002	0	0	0
5	0	0	0.001	0.023	0.044	0.008	0	0	0
6	0	0	0	0.004	0.022	**0.078**	0	0	0
7	0	0	0	0	0	0.016	**0.083**	0	0
8	0	0	0	0	0	0	0.016	**0.204**	0
9	0	0	0	0	0	0	0	0.012	**0.262**

Table 4. Comparison in the importance of different elasticities by category between healthy populations of American chestnut in MI and in the Atkinson population. Each site's model is parameterized differently.

Site	Growth	Retrogression	Stasis	Reproduction
Healthy population in MI (Davelos and Jarosz 2004)	0.076	0.009	0.903	0.012
Atkinson Population	0.141	0.02	0.824	0.015

Figures

Figure 1. Life cycle diagram illustrating the different life stages of the population model and all observed stage transitions with a year. Stage 1 seedlings are less than a year old, stage 2 seedlings are 1 year old, and stage 3 seedlings are 2 years old. Stage 4 and Stage 5 are seedlings that are 3 years or older and are under 50cm or over 50cm respectively. Stage 6 seedlings are 3 years or older and are taller than 100cm but not large enough to have a dbh =1. Stage 7 saplings have a dbh between 1 and 4 in and stage 8 trees have a dbh between 4 and 10. Finally, stage 9 includes all trees greater than 10 in dbh.

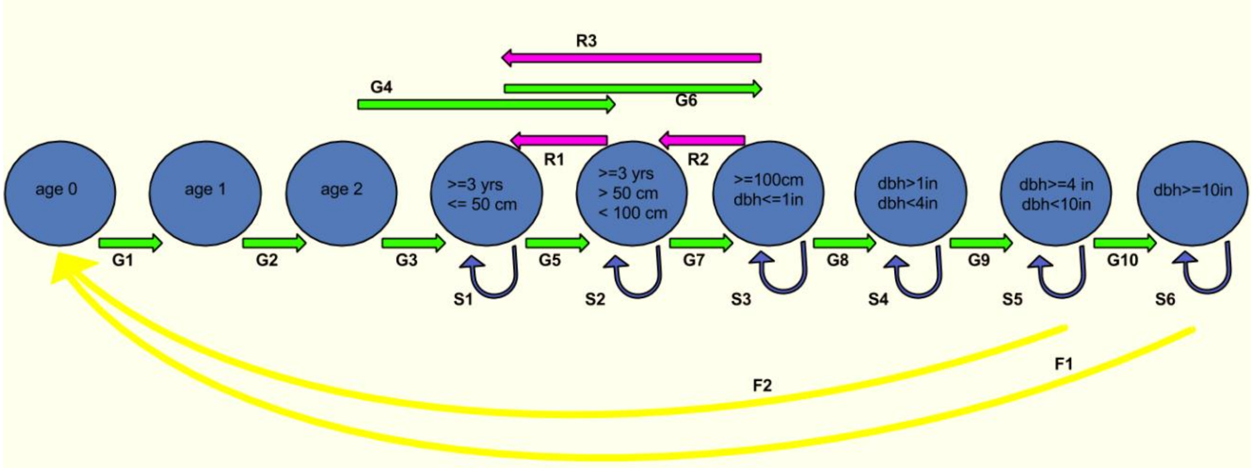


Figure 2. Growth rate by age of plant, includes all years of data but each tree is only represented one time all years.

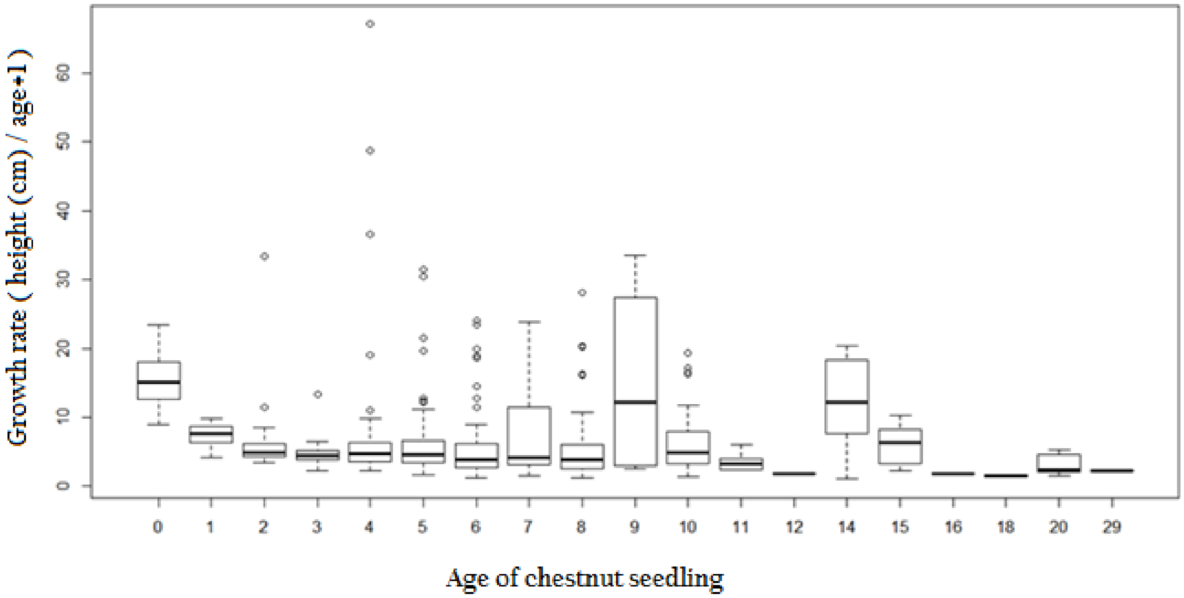


Figure 3. Logistic regression of the probability of browse, probability of browse decreases significantly once seedlings are 100 cm tall. Marks on the bottom of the graph indicate the observed heights of all seedlings. *P* = 0.010

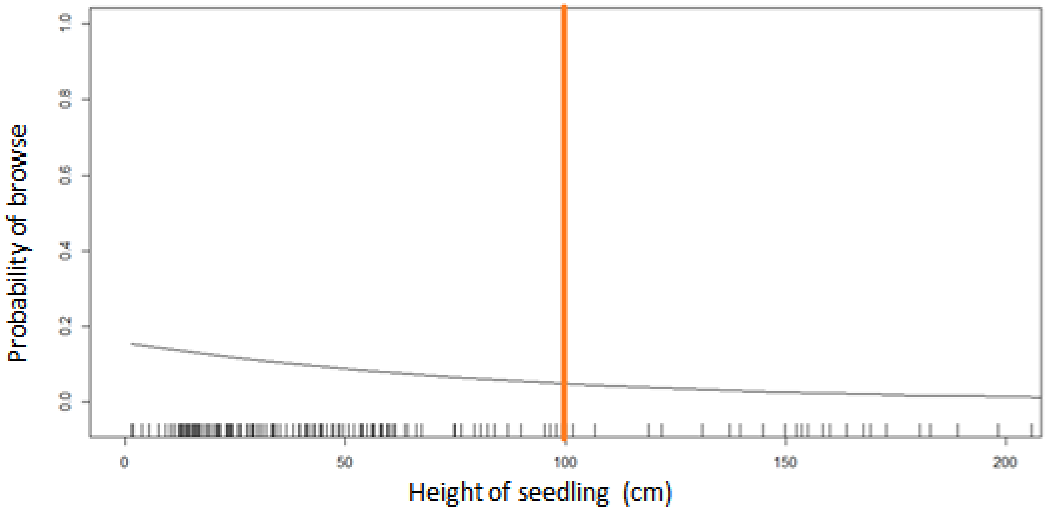


Figure 4. Logistic regressions used to calculate Survival Vital rates by stage class. a) survival by height (cm) 2012-13, b) survival by dbh(in) 2012-13, c) is survival by height (cm) 2011-12, and d) survival by dbh (in) 2011-12; there were no trees with a dbh found dead in 2012 and thus no regression.

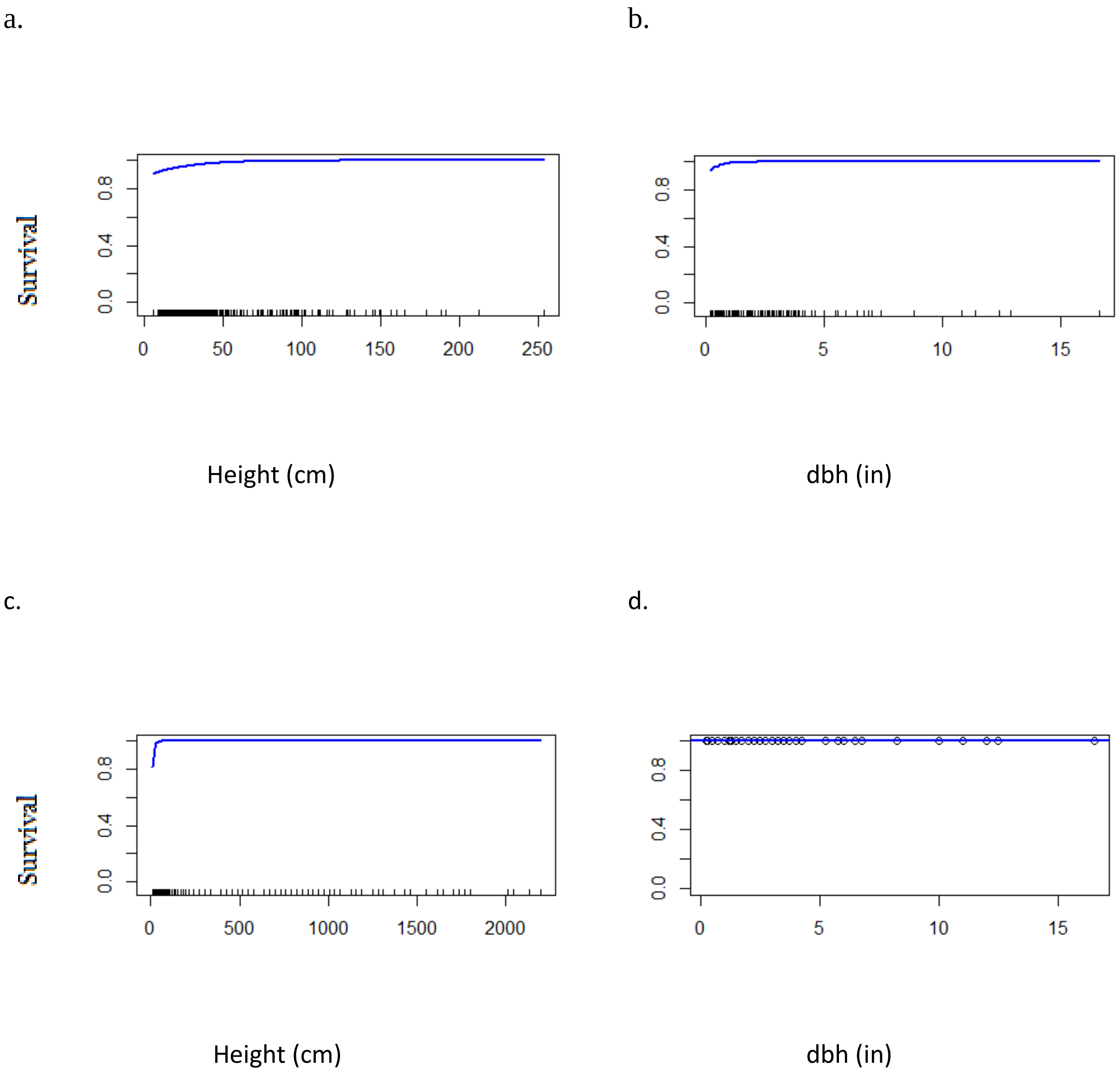


Figure 5. Histogram of large chestnut trees at Atkinson. Dbh for trees noted to be flowering in 2013 are purple, while trees not noted to be flowering are blue. The earliest a trees were observed to flower is with a dbh of 4.1. Calculations of fecundity, determined by per capita seedlings and total trees with a dbh. (Trees with a dbh >=10in are presumed to always flower).

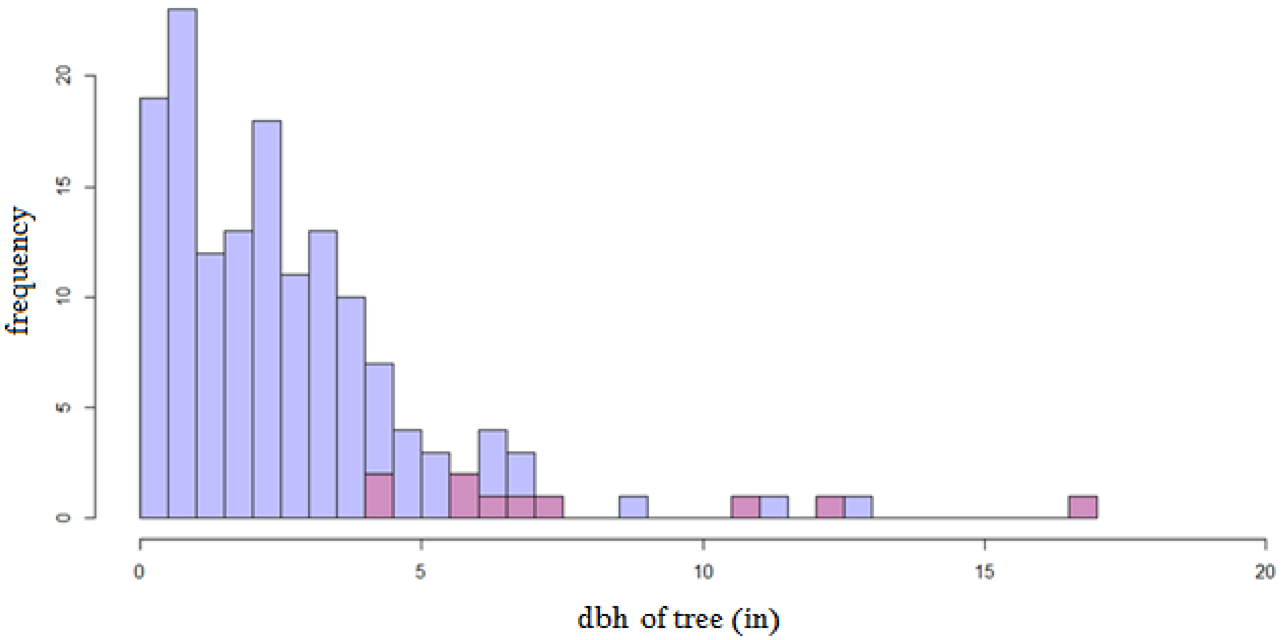


Figure 6. Observed Stage distribution 2011-2013 (red) and Stable Stage Distributions (blue) distribution via asymptotic analysis.

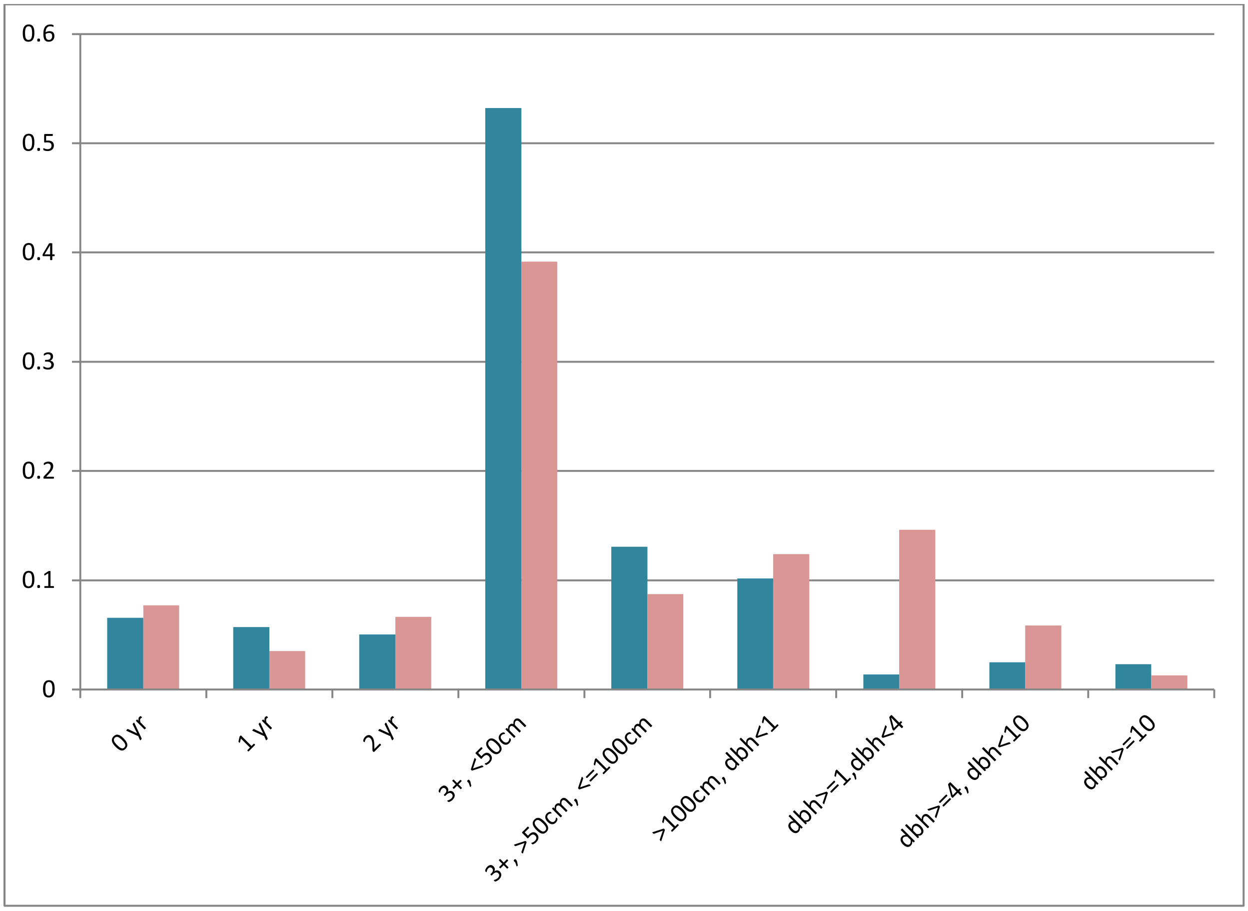


Figure 7. Reproductive Values (w) indicate the potential reproductive ability and importance of each stage, where stage 1 is normalized to 1. The older stage classes have a far greater reproductive importance.

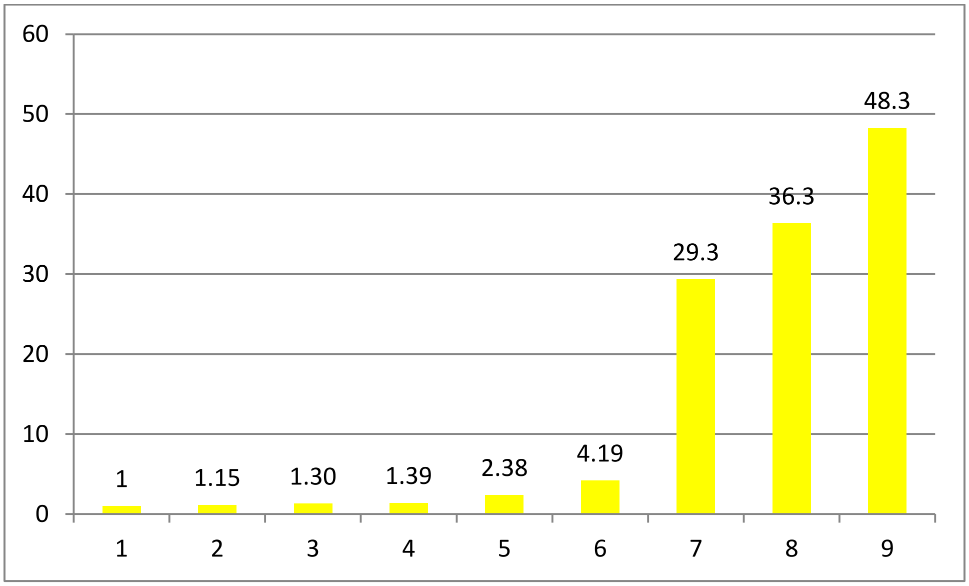


Figure 8. Transient Dynamics, the y axis is the annual or single time step lambda value and the x axis is the # of iterations or years. The purple line indicates the stable population growth rate. The population overshoots the population growth rate before reaching a stable growth rate in approximately 80 years.

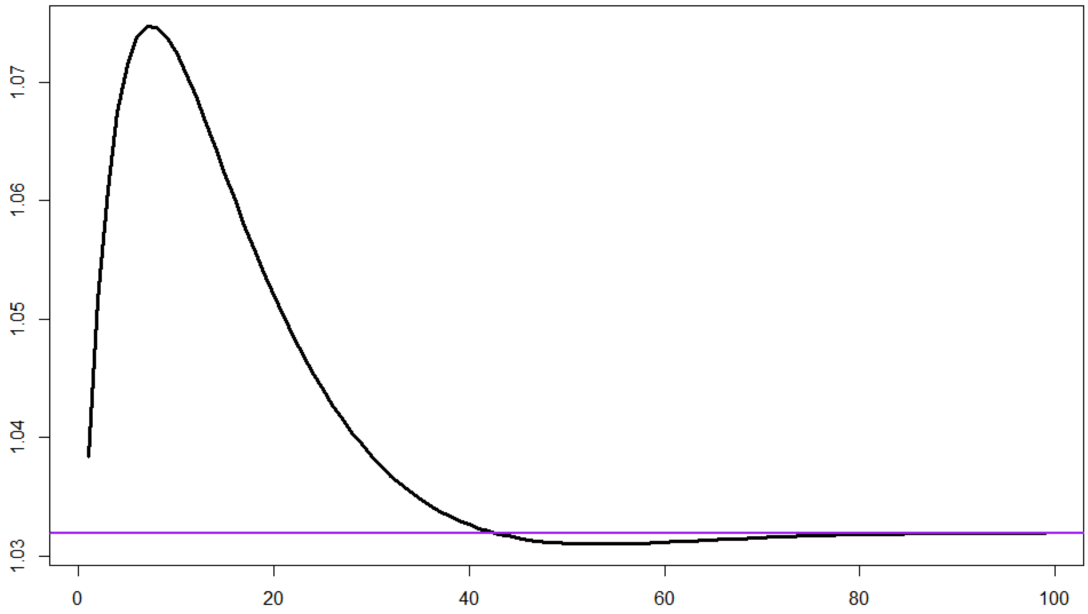
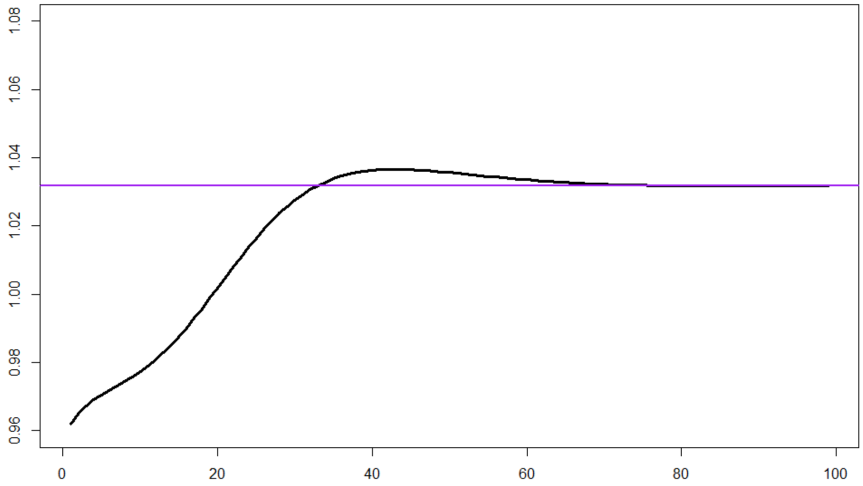
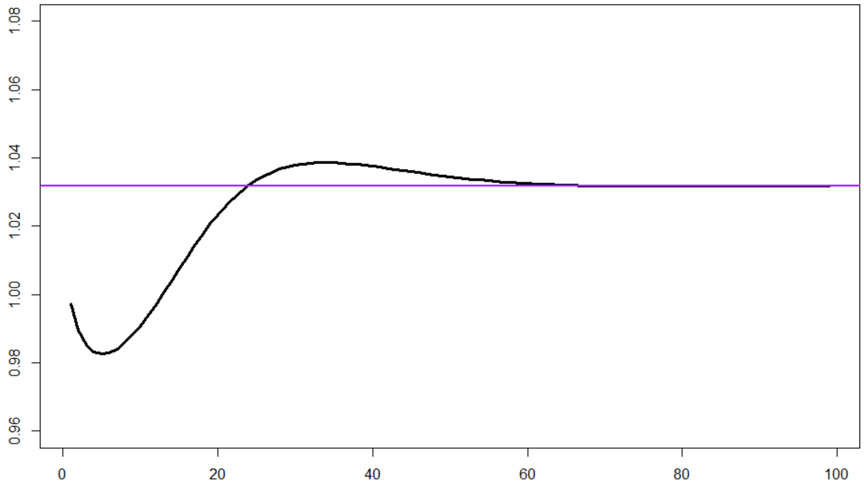


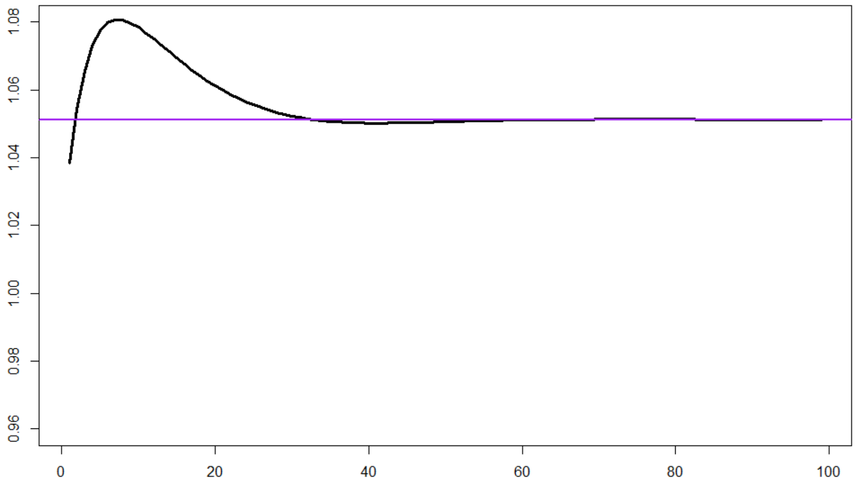
Figure 9. Transient Scenarios: Change in lambda over 100 years for a potential reintroduction scheme of 100 chestnuts a) seedlings <50cm and 3+ years old b) seedlings >50cm and <100cm. c) Change in lambda over for a potential management scheme of protecting seedlings from browse. This model uses the observed distribution as the original size vector (λ = 1.051255).



a.



b.



c.

Appendix

Appendix 1. Prevalence of Blight at the sight. Blight prevalence was not systematically recorded in 2011 or 2012. It is unlikely that trees with a dbh < 4 would be visibly infected by blight.

	# of trees observed to have blight	%
Entire population	6	6/1166 = 0.51% of total population
Trees in 2013 resampled area with a dbh >= 4in	3	3 / 33 = 8.57% of trees with a dbh >=4

Appendix 2. Correlations between different measured characteristics. Values are rho from correlation test where * $p < 0.05$, ** $p< 0.001$, *** $p<0.0001$.

	age	Height	rcd	dbh
age	1	0.43***	0.53***	0.35**
height		1	0.76***	NA
rcd			1	NA
dbh				1

Appendix 3. Growth, stasis, and retrogression values of surviving plants were calculated by taking the quotient of the number of individuals in size class n+1, n, or n-1 in year t+1 divided by the number of individuals in size class n in year t respectively.

Stage in yr t -> Stage in yr t+1	2011		2012		N (2011+2012)	N (total in stage in year t)	Mean Value
	N	N (stage in year t)	N	N (stage in year t)			
3 -> 4	23	24	20	21	43	45	0.955556
3 -> 5	1	24	1	21	2	45	0.044444
4 -> 5	4	68	6	58	10	126	0.079365
4 -> 6	1	68	0	58	1	126	0.007937
5 -> 6	5	28	1	7	6	35	0.171429
6 -> 7	1	36	0	8	1	44	0.022727
7 -> 8	5	47	4	20	9	67	0.134328
8 -> 9	0	16	0	1	0	17	0
4 -> 4	63	68	52	58	115	126	0.912698
5 -> 5	17	28	4	7	21	35	0.6
6 -> 6	29	36	5	8	34	44	0.772727
7 -> 7	42	47	16	20	58	67	0.865672
8 -> 8	16	16	1	1	17	17	1
9 -> 9	5	5	1	1	6	6	1
5 -> 4	6	28	2	7	8	35	0.228571
6 -> 5	3	36	3	8	6	44	0.136364
6 -> 4	3	36	0	8	3	44	0.068182
7 -> 8	Supplemental Data from Zon 1906 (p24).						.091
7 -> 7							.909
8 -> 9							.043
8 -> 8							.957

Appendix 4. Two methods of calculating survival vital rates were used; the proportion of trees that survive from yr t to yr t+1 (far right) and the use of fitted values from logistic regressions on survival and tree size(columns 2-4). Survival is very high for our population.

Size Class	Median or Midpoint value of class (x value)	Survival Values via logistic regression (y value)	Mean Survival Value via logistic regression	Survival values via division (survivers yr t+1/# of individuals yr t)
1	2011 12.6 cm	0.8632548	0.8971127	0.769
	2012 12.6 cm	0.9309706		
2	2011 15.24 cm	0.8942102	0.91062515	1
	2012 11.2 cm	0.9270401		
3	2011 20.42 cm	0.9401821	0.93859325	1
	2012 14.9 cm	0.9370044		
4	2011 25 cm	0.9657283	0.96191395	0.974747
	2012 25 cm	0.9580996		
5	2011 76.2 cm	0.9999199	0.99737195	0.979592
	2012 75 cm	0.994824		
6	2011 198 cm	1	0.99974995	1
	2012 130 cm	0.9994999		
7	2011 2.5 dbh	1	0.9998753	1
	2012 2.5 dbh	0.9997506		
8	2011 5.75 dbh	1	0.99999995	1
	2012 5.5 dbh	0.9999999		
9	2011 14.25 dbh	1	1	1
	2012 12.4 dbh	1		

Appendix 5. Calculations of Fecundity, determined by Per capita seedlings and total trees with a dbh.

* Trees with a dbh >=10in are presumed to always flower

Stage class	# flowering trees	# flowering trees/ Total # trees in class (Probability of Flowering)	Fecundity (probability of flowering * average per capita recruitment)
Dbh>=4in and <10in	8	0.32	0.693
Dbh>=10in	3	1*	2.1667