II: THE DEMOGRAPHY OF A NATIVE MONTEREY PINE (*PINUS RADIATA*)

FOREST AND THE POTENTIAL CONSEQUENCES OF ECTOMYCORRHIZAL

SUCCESSION ON FOREST GROWTH

INTRODUCTION

A key challenge in plant ecology is to gauge the strength and direction of factors that influence plant growth and structure plant populations. Since A.B. Frank's 1885 publication hypothesizing the role and ubiquity of the ectomycorrhizal and plant symbiosis, ecologists have increasingly investigated the degree to and mechanisms by which mycorrhizal fungi affect the growth and mortality of plants (Frank 1885, 2005). Mycorrhizal fungi associate with nearly eighty percent of all plant species (Wang and Qiu 2006) and while they may fall along a continuum of effect on their plant hosts, they are generally regarded as beneficial (Johnson et al. 1997, Karst et al. 2008, Hoeksema et al. 2010).

Plant hosts may benefit from mycorrhizal colonization through both lower incidence and severity of diseases caused by plant pathogens (Sylvia 1983) as well as provide some degree of drought tolerance at moderate levels of water stress (Boyd et al. 1986). Additionally, mycorrhizal fungi forage the soil for nutrients that may then be passed along to the host plant. Ectomycorrhizal pines can receive up to 3.2 times more phosphorus and 1.8 times more nitrogen than their non-mycorrhizal counterparts (Bowen 1973). The benefits provided by mycorrhizal fungi consequently influence plant survival and growth; however, mycorrhizal species differ in their ability to perform these services

and in their responses to plants (Allen and Boosalis 1983, Parke et al. 1983, van der Heijden et al. 1998, Sikes and Klironomos 2009). Consequently, spatial or temporal variation in mycorrhizal community composition may significantly influence plant population dynamics and plant community structure. Moreover, land managers and conservation practitioners may require information on the potential ramifications of variation in mycorrhizal fungal community composition for plant population dynamics to make informed and practical decisions to address applied problems (Klironomos et al. 2011).

Two mycorrhizal types, the arbuscular mycorrhizal and ectomycorrhizal (EM) fungi, have received the most attention in the ecological literature, largely because of the ubiquity and consequent ecological importance of their primary plant hosts, herbaceous and woody plants, respectively (Read 1991). Efforts to quantify the effects of variation in arbuscular mycorrhizal fungal composition upon plant populations have been largely successful, observing significant effects upon plant community structure including changes in plant diversity (van der Heijden et al. 1998, Hartnett and Wilson 1999, Klironomos et al. 2000, O'Connor et al. 2002), community composition (van der Heijden et al. 1998, Hartnett and Wilson 1999, O'Connor et al. 2002), and productivity (van der Heijden et al. 1998, Klironomos et al. 2000). In contrast, similar studies on ectomycorrhizal plant populations and communities have been stymied due to the long life span and delay in reproduction of many ectomycorrhizal hosts. Additionally, even shorter-term experiments may be readily contaminated by non-target EM fungi. Hence, studies on the effects of EM fungal variation have necessarily remained in the realm of the short-term.

Ideally, the long-term effects of variation in ectomycorrhizal fungal composition would be experimentally tested in the field; however, the logistics of effectively manipulating ectomycorrhizal fungal community composition for the periods necessary to study its long-term effects upon woody, perennial populations, make this approach unrealistic. Alternatively, by adjusting demographic data to reflect observed effects of ectomycorrhizal fungi in empirical short-term studies, models can be used to project and compare the long-term effects of ectomycorrhizal fungal community differences on various plant population parameters. Similarly, the incorporation of the observed demographic data into projection models can allow researchers to systematically perturb each demographic parameter at each stage/age individually, thereby generating data about the relative contribution of each demographic parameter of each stage/age to population growth. In generating these values, we can determine those phases of the perennial plant life-cycle where the effects of variation in ectomycorrhizal fungal community composition upon plant survival and growth are likely to have the greatest effect upon forest plant population. While this approach requires extrapolation beyond observed mycorrhizal effects, it is one step closer towards understanding the consequences of variations in ectomycorrhizal community composition for plant populations. The ability of modeling to estimate the long-term response of plant communities makes it well suited to address the effects of temporal variation of ectomycorrhizal fungal communities, or succession, upon plant populations.

The succession of ectomycorrhizal fungal communities has been demonstrated within a number of forest ecosystems (Fleming 1983, Fleming et al. 1985, Fox 1986, Visser 1995, Nara et al. 2003, Twieg et al. 2007, Yamashita et al. 2008). As the forest

matures and plant roots converge, vegetative growth of the mature forest ectomycorrhizal fungi creates a common mycorrhizal network (CMN) connecting the roots of these plants together. Seedlings may establish in the understory of these forests, connecting directly into these pre-existing CMNs, likely avoiding many of the carbon costs necessary to build their own (Simard and Durall 2004). Conversely, when seedlings in the forest understory are prevented from accessing CMNs, they are typically colonized by early-successional fungal species, whose total carbon cost must be paid by the seedlings themselves. Plants connected to the CMNs may create a "guild of mutual aid" making resources available to all regardless of identity or size (Perry et al. 1989, Egerton-Warburton et al. 2007). Resources that may be limiting to plant growth and survival, including water (Egerton-Warburton et al. 2007), nitrogen (He et al. 2003, He et al. 2005), and carbon (Simard et al. 1997) have been shown to move from plant to plant through CMNs; however, showing that CMNs affect the growth and survival of competing plants has proven difficult.

A recent manipulative experiment conducted in the native and mature Monterey pine (*Pinus radiata D. Don*) forest demonstrated a large, positive effect of CMNs on seedling survival. At the end of the two-year study, Booth and Hoeksema (2010) calculated a negative competitive effect of mature plant roots on seedling survival of -65% and a CMN mitigation of seedling mortality of +56%. This positive CMN effect on seedling survivorship may or may not have significant consequences for demographics of the forest, i.e. forest plant structure and population growth rates.

My study had three objectives. First, to summarize demographic information representative of the monodominant mixed-size class stands of Monterey pine in

Cambria, California. Second, to understand the potential consequences of ectomycorrhizal succession (and the consequent formation of CMNs) for forest structure and population growth rates by comparing model estimates of observed demographic growth rates to hypothetical "non-CMN" forests. I hypothesized that the large differences in seedling mortality (-56%) between the observed and hypothetical non-CMN models would translate to significant differences between model estimates of the finite rate of growth, λ. Third, to identify those demographic parameters most influential upon population growth rates so future studies may seek to address the relationships between mycorrhizal ecology and these phases in the life cycle of long-lived, perennial plants.

METHODS

Field Site

Cambria, California is host to the southernmost of three native California stands (35° 32' 25.21" N 121° 05' 29.57" W) of Monterey pine (*Pinus radiata*), covering *c.* 1400 hectares. The Kenneth S. Norris Rancho Marino Reserve (KNRMR) is located at the southern reaches of the Cambria stand and home to approximately 91 hectares of native Monterey pine forest. The KNRMR receives *c.* 460 mm of annual precipitation on average, most during the winter months, at which time most seedling recruitment and plant growth occur (Rogers 2002). Average temperatures range between 9° C and 18° C. The forest soil consists mainly of deep sandy loam (Carpenter and Storie 1933) which is low in organic matter (8 -15 cm) and easily erodes. The sandy soils and low summer precipitation are indicative that water and soil nutrients are the factors most limiting to

plant growth and/or survival (Booth and Hoeksema 2010). Monterey pine is the

dominant tree species with only one other hardwood associate: Coast Live Oak (*Quercus*

agrifolia).

Monterey pine is a short-lived species, with a mean generation time of eighty or

ninety years, infrequently living beyond one hundred and fifty years. Cambria Monterey

pine average 30-37 m tall, may root as deep as soil or clay permit (~1.7 m in deep soil),

and have extensive lateral spread (9 – 12 meters) (Roy 1966). Additionally, Monterey

pine are semi-serotinous such that fire stimulates massive seedling recruitment though

cones also open and release seeds in response to seasonally warm, dry weather, so

seedling establishment is common in the forest understory.   Due in large part to

encroaching urban and recreational development, the historic fire regimes of the

California Monterey pine forests have been severely altered, the few occurring presently

likely caused by accident or the occasional lightning strike (Rogers 2002). This shift

from the natural fire regime within KNRMR in Cambria may be particularly stark, with

no major fires occurring since at least 1940 (nearly a full generation for this species), and

only a few small fires (~ 1 hectare) (Canestro Pers. Comm.). Therefore, the importance

of the less prolific, but more constant and gradual seed rain from the semi-serotinous

cones has shifted in its relative importance to the maintenance of these stands.

Collection of demographic data and data management

The demographic data used to determine size classes and to parameterize

estimates of growth, survival, and mortality were collected from plots in two stand types

representative of the Cambria forests, one a monodominant mixed size class stand of

Monterey pine (93 m x 10 m, MSC), and the other a stand of relatively equal proportions of coast live oak and Monterey pine (93 m x 20 m, OP) (Figure 2-1). Within each plot, the height of trees ranging from 1.4 – 3.0 meters tall was recorded, as was the diameter at breast height (1.40 meters, DBH) for all trees 1.4 meters tall or greater. In addition, height measurements of all trees shorter than 1.4 meters were recorded in a three-meter strip adjacent to the MSC plot and within five-meter strips on each side of the OP plot. Each tree was tagged and mapped along the plot for repeated annual measurements. DBH of all trunks was recorded when multiple trunks of an individual grew to 1.4 meters tall. Estimates of cone number, signs of disease, and mortality were recorded for all censused pines. When mortality was recorded, trees were reassessed for two additional census periods to ensure the tree was, in fact, dead. Full sampling efforts occurred in 2002, 2003, 2004, 2007, and 2009. An additional sampling bout in which only seedling recruitment was measured occurred in 2005.

Sources of data for matrices

Biological information chosen for inclusion in a Lefkovitch size class matrix model was collected largely from the monodominant MSC plot. To improve accuracy regarding growth and mortality data reflective of trees greater than 6.5 cm DBH, I incorporated data for those trees from both the MSC and OP stands. I chose these demographic data specifically since those two plots most accurately represent the sites in which Booth and Hoeksema (2010) conducted their study determining the relationship of CMNs and seedling survivorship rates in a native Monterey pine forest understory.

To accurately gauge the effects of CMNs on long-term population growth rates and stable size class structure, creating early size classes representative of one-year-old recruits and two-year-old individuals was crucial. Therefore, in delimiting size classes for these aged individuals, I only used data collected in consecutive years ('02 – '03, '03 – '04, and '04 – '05) in which I knew the age of one- and two-year old plants.

To utilize the demographic data of plants ≥ 140 cm tall to the fullest extent, where census periods were separated by a year or more of no data collection, growth was assumed to have occurred evenly over the intervening years. In these intervening years of no census, if mortality occurred, I had no knowledge if that death occurred in year J or J+1. Although mortality data of individuals ≥ 140 cm in height in successive years suggests the probability of death to be more likely to occur in year J + 1, I constructed two matrices from the original data, one in which all unknown mortality occurred in year J and the other in which all death occurred in year J + 1. Estimated values of λ for the resultant matrix projections of these two extremes did not differ appreciably and so only the results from the latter scenario are reported.

Finally, although the data showed instances in which DBH actually contracted slightly from one year to the next, for purposes of modeling, no trees were allowed to transition to smaller size classes. Additionally, for trees with multiple stems, I calculated a total DBH following the calculation:

EQ 1: Total DBH $= \sqrt{DBH_a^2 + DBH_b^2 + DBH_c^2 + DBH_n^2} \ldots$

where DBH_{a-n} are DBH measurements on multiple stems a-n.

Size Class Determination and Matrix Construction

Size classes defined by high mortality rates

One of the primary objectives of this chapter was to compare the growth rates and size class structure between the observed demographic data and an adjusted dataset in which the CMN effect (an increase in seedling survival rate after two years of 56%) observed by Booth and Hoeksema (2010) was removed. The boundaries of size classes one and two, representing first year recruits and second year individuals, were determined from the mean heights of individuals of that age ± two standard deviations. The upper bound of the 1st size class determined in this manner overlapped the lower bound of the second size class slightly, but the second size class had an upward-skewed distribution, so I set the upper bounds of the first class as the lower bounds of the second.

Often, one and two year olds were observed in the data to remain in their respective size class for additional years; therefore, the 1st size class included 2-,3-, and 4-year-old individuals, and the 2nd size class included 3-,4-,5-, and 6-year-old individuals." Theoretically, a small proportion of the first and second size class individuals could remain in these size classes indefinitely, but it would be impractical to create a matrix model to account for this possibility, so I set a 0.005 probability limit to stop including additional age matrices within the 1st or 2nd size classes. In this model, the final age a plant could be and still remain in a size class was determined by multiplying the probability of stasis in a size class by itself until this probability was < 0 .005.

Creation of discrete size classes required a concise point at which I was to start classifying individuals into size classes based upon DBH, rather than height. Hence, the fourth size class was determined by taking the mean height ± two SD of individuals growing more than 140 cm tall into the next year. The third size class included those

individuals falling in size between size classes 2 and 4. Caswell (2000) suggests

choosing size class groupings that correlate strongly with some biologically relevant life

characteristic (e.g. probability of death, growth rate, reproductive effort). Additional

support was lent for the first four size classes as the likelihood of mortality to individuals

from year to year differed strongly between these groups (Table 2-1). Due to occasional

gaps between sampling years, I based the probability of death of these earlier classes on

individuals for which I had data in successive years (2002-2003, 2003-2004).

Size classes defined by cone production

Cone production correlated strongly with DBH (0.856, p< 0.001); therefore, cone

production was used as the defining feature of the mature size classes. Two reproductive

groups were defined by determining the two highest DBH quartiles from those cone-

producing trees (DBH $\geq$ 55 cm and 42 $\geq$ 55 DBH cm). Due to large disparities between

minimum and maximum cone production of trees DBH $\geq$ 55.0 (10 – 301 cones), this

group was further delineated by median cone production into two groups, 55 – 61.4 and >

61.4 cm DBH. Fecundity estimates were calculated under the assumption that

contribution to recruitment was equal to cone production of each size class relative to

total cone production of the documented population, divided by the mean annual number

of individuals with each size class, multiplied by the mean annual recruitment number:

EQ 2: *Recruits attributable to size class S individual in year J +1 = ((Size class S*

cone production in year J / total population cone production in year J) / N individuals in

*size class S) * N recruits in year J +1*

Size classes defined using Vandermeer-Moloney algorithm

Individuals >140 cm tall but less than 42 cm DBH showed less distinctive correlations with biologically relevant life characteristics. To partition these individuals into size classes for the model, I employed the Vandermeer-Moloney algorithm as suggested by Caswell (2000, pg. 169) and outlined by Moloney (1986). Vandermeer (1978) developed this algorithm to reduce two kinds of error involved in choosing size classes, standard error (SE) and distribution error (DE). The SE occurs as size classes become too narrow, reducing the number of individuals within each size class, creating error in the estimates of biological parameters used in the model. In contrast, DE is caused as size classes become increasingly large and growth information of individuals is lost. Vandermeer's solution to this problem of conflicting errors was to develop an algorithm to pinpoint size classes where the sum of these errors is minimized. Therefore, the choice of these intermediate size classes, with no clear biological division, was determined by choosing increments that reduced the summed value of SE and DE.

Modeling

Modeling of observed forest data

All relevant biological parameters (stasis, growth, mortality, recruitment contribution; Table 2-1, Figure 2-2, Figure 2-3) from the observed demographic data were entered into a matrix, and multiplied by an arbitrary starting point of 1 individual in each size class, to estimate the population growth rate by calculating the finite rate of increase, λ, and determining the stable size class structure of the population. I used a

modified form of the traditional bootstrapping technique (described below) to calculate 95% confidence intervals for λ.

Regardless of the initial population size in each size class (which is multiplied by the estimated demographic parameters entered into the matrix), the population will always converge on the same stable size class structure and value for λ; however, the number of iterations required to converge upon these values will vary. If observed data for current size class structure is used for the initial population sizes, then the number of iterations required for convergence may be indicative of the degree to which the current structure deviates from the predicted stable size class structure. Therefore, using the observed size class distributions of the 2009 demographic data as a multiplicative starting point against the observed data matrix, I calculated the number of iterations (years) required before the proportional distribution of every size class was within one percent of the stable size class structure.

Elasticity Analysis

Elasticity analysis is conducted by perturbing each value within the projection matrix equally, one at a time, and comparing the relative effect these changes have on the resultant λ (de Kroon et al. 1986, Silvertown and Charlesworth 2001). In doing so, I sought to determine those size classes of the Monterey pine tree life cycle where small changes in demographic parameters are most likely to affect population growth rates. It is likely these size classes where differences in plant responses to variation in ectomycorrhizal fungal community composition will have the greatest effects upon plant population dynamics and community structure (Caswell 2000).

Elasticity values sum to one to allow for comparisons between demographic parameters; however, it is known that larger/older trees grow more slowly than smaller or younger trees (Gower et al. 1996). Additionally, the final size class in a projection matrix has no additional size class to grow into meaning that the calculation of the stasis parameter for this size class includes demographic information applicable to growth and stasis. By summing stasis and growth elasticities, and dividing by an estimated maximum residence time (MRT) of each size class, we may calculate an adjusted survivorship elasticity. This metric is a proxy for the elasticity of annual survivorship and is, perhaps, a more accurate descriptor of the importance for survivorship in a size class. This adjusted annual survivorship elasticity is only comparable between adjusted annual survivorship elasticities of other size classes or to the unadjusted survivorship elasticity values and not to the elasticities of fecundity, stasis, or growth. Although this treatment of elasticity data is rarely conducted upon stasis and growth information in other demographic studies, I felt it was important to do so in order to gain additional perspective on how annual survivorship within size classes potentially affects population growth rates and juxtapose this information with the elasticity values for the unadjusted survivorship values.

Modeling of the hypothetical, non-CMN forest: adjusted models

To investigate the long-term effect of ectomycorrhizal fungal succession and consequent development of CMNs upon forest populations, I developed two models that remove the CMN reduction of seedling mortality observed by Booth and Hoeksema (2010). In their paper, mortality was reduced by 56% at the end of the two-year study.

In fact, this net two-year reduction in mortality was distributed unevenly over the study, with a 14.4 % reduction in the first year, and a 26.6% reduction in mortality for the individuals remaining in the study after the first year. It is possible that these reductions in mortality were age or size specific and so additional age classes within size classes 1 and 2 were incorporated, and CMN-related survival benefits were removed from those age classes in two different ways:

Model A: The first and more conservative of these two models removes CMN-related survival benefits only from the 1st (-14.4%) and 2nd year (-26.6%) age classes in size class 1, and from the 2nd year age class in size class 2 (-26.6%), but not from the other additional age classes in size classes 1 and 2. This model aims to understand the ramifications of the Booth and Hoeksema (2010) observed CMN-related survivorship benefits on population growth rates, assuming that their results apply to one and two year olds, regardless of the size of these plants.

Model B: The second and more liberal of these two models removed the CMN-related survivorship benefits found by Booth and Hoeksema (2010) from all age classes in size classes 1 and 2. Therefore, all size class 1 ages were attributed the -14.4% survival reduction and all size class 2 ages received the -26.6% survival reduction. This model contrasts the prior, more conservative model by assuming that CMN-related survival benefits are size specific, but not age specific. As stable size class distributions of these two models did not differ noticeably, I limit comparisons of stable size class distributions to Model B. However, for purposes of discussing the effects of CMN-related survivorship reductions on λ, we discuss both Models A and B.

The A and B models are the most conservative model estimates of the effect of CMN removal on forest demography, since they assume that CMNs only affect survival of either the one- and two-year olds or the first and second size classes. While Booth and Hoeksema (2010) ended their study after two years, it is possible that these reductions in mortality by CMNs could persist further into the life cycle of the trees. Therefore, I sought to understand the potential life-long influences of CMNs upon forest stable size class structure and population growth rates, λ. To do so, I developed an additional 15 models, each removing the second-year CMN mortality reduction of 26.6% from additional and progressively later size classes in the tree life cycle. The final two models, one removing the CMN survivorship reduction from all size classes but the last, and the other removing the CMN survivorship reduction from all size classes, will be hereafter referred to as X and Y, respectively.

Modified bootstrapping for 95% confidence intervals

For all datasets, real or altered, I modified the traditional bootstrapping technique so that randomized sampling with replacement of each size class, except the final size class, would continue until at least one instance of growth into the next size class was observed in the new bootstrapped dataset. Bootstrapping of the final size class did not use this contingency, but I ensured that at least one death was recorded. Without these modifications, the calculations of λ would not be possible for model iterations in which size classes $0 - 16$ did not have one member moving onto the next size class and would, similarly, fail to stabilize if death did not occur in the last size class. All bootstrapping to calculate 95% confidence intervals for the finite rate of increase, λ, were derived from

50000 iterations of the real or modified growth and mortality data, while size class

fecundity was held constant.

Software

PopTools version 3.2.3 was used to calculate the finite rate of increase, λ, as well

as stable size class structure for each model and elasticity analysis for the observed

demographic data (Hoeksema et al. 2010, Hood 2010). Similarly, PopTools was used to

calculate the MRT within each size class. R statistics was used to calculate λ and 95%

confidence intervals for all matrix models. Additionally, R statistics was used to

calculate intermediate size classes from the observed demographic data using the

Vandermeer-Moloney algorithm (Moloney 1986). The finite rate of increase, λ, was

calculated using both PopTools and R statistics but the two calculations did not differ

appreciably, so I report only the results from R statistics.

RESULTS

In total, I specified 17 size classes characterized by growth rates, mortality, and

reproduction (Table 2-1, Figure 2-2, Figure 2-3). Probability estimates of stasis, growth,

mortality, and contribution of recruits in the following year per individual of each size

class were calculated from demographic data collected on 492 and 341 trees, for size

classes 1–4 and size classes 5–17, respectively.

Modeling of observed forest data

Modeling of the observed forest data estimated a ~ 2% yearly reduction in population size (λ= 0.9822; Table 2-2) of the mixed-size class *Pinus radiata* populations in Cambria, California at KNRMR. This result assumes fixed vital and reproductive rates of the population. The projected stable size class structure resembled an inverse-J curve (Figure 2-4, Figure 2-5). In this stable size class projection, the large majority of plants (~82%) reside within the first size class; however, thereafter numbers of plants within size classes dramatically and progressively decline since the large majority of size class 1 individuals do not survive into higher size classes (Table 2-3, Figure 2-4, Figure 2-5). Additionally, a large proportion of recruits are maintained in the population due to reproduction by fecund mature size classes.   Using the 2009 demographic data to determine an estimated length of time before convergence upon the predicted stable size class structure yielded a 50-year time span.

Elasticity Analysis

Elasticity values for growth out of or stasis within the first and second size classes were appreciably lower than those of the following size classes, and orders of magnitude less than those of some later size classes. Elasticity analysis suggests that population growth rate is most influenced by the stasis of later size classes, even more so than reproduction within or growth out of these same later size classes, and of these later size classes, stasis within the final size class appears to be most influential of all. Changes to values of fecundity had little relative influence upon population growth; however, changes to later size class fecundity values had more influence than those associated with earlier size classes (Table 2-4).

Calculation of elasticities of unadjusted size class survivorship and the estimated adjusted annual survivorship revealed large relative differences within and between these categories. The unadjusted survivorship elasticities indicate a much greater potential for changes in survivorship to later size classes, specifically size classes 14 – 17, to influence population growth rates (2 – 20 times greater). In stark contrast, estimates of elasticity for adjusted annual survivorship of size classes suggest that survivorship is relatively important throughout most of the life cycle of this species (Size classes 3 – 17); however, seedling elasticities (Size classes 1 and 2) for estimated annual survivorship are still relatively low in comparison those later size classes (Table 2-4).

Modeling of the hypothetical, non-CMN forest: adjusted models

Model projections of reduced survivorship only for one and two year-old plants within either size class one or two (Model A), reflective of the findings by Booth and Hoeksema (2010), had no significant effect upon population growth rates of the population (Table 2-2, Figure 2-6). Similarly, the model projection of these survivorship reductions upon all age classes of the first and second size classes (Model B) was not significantly different from the observed population projections λ or Model A (Table 2-2, Figure 2-6). Additionally, the iterative application of the reduction in survivorship (-26.6) to models including higher size classes (up to size class 16) were not significantly different from the λ of the observed projection model. In contrast, I observed a dramatic and significant decrease in λ when this reduction in survivorship was applied to the entire life cycle of this species (Table 2-2, Figure 2-6).

Calculations of stable size class structure for the adjusted models showed a relatively small, though noticeable shift from that determined for the observed forest data. As the reduction of survivorship was incrementally attributed to higher size classes, a greater proportion of the population resides in size class one and in later size classes. These incremental increases continued with progressive reduction of survivorship within each size class until the survivorship reduction was attributed to the entire tree life cycle, whereby the proportion of the population represented by each size class returned to similar levels of those seen in the observed demographic data. As a result, the projected stable size class structure of the forest without any CMN effects on mortality was similar to the projected size class structure using observed demographic data (Figure 2-4).

DISCUSSION

The demographic work conducted in this study indicates that this stand of Monterey pine has a negative growth rate, and hence if this growth trend continues, the population will go extinct. Additionally, model comparisons indicate that EM fungal community succession and consequent development of late-stage CMNs that have been shown to positively influence seedling survivorship (Booth and Hoeksema 2010) may not significantly influence growth rates or stable size class structure of the Monterey pine population. If however, these CMN effects are not limited to seedlings, but instead continue to influence survivorship throughout the tree's life cycle, the successional development of these fungal networks may be extremely important for survival of Monterey pine and other forests where stands display higher levels of seedlings recruitment or survival (e.g. those that have been recently disturbed).

Finally, these results are derived from a deterministic model utilizing available demographic data. The differences between the projected stable size class structure and that observed in the actual forest suggest that this population experiences or has experienced a variable environment not captured in the demographic data collected since 2002. Continued monitoring of these stands may reveal the source of this environmental variability and lead to the subsequent development of a stochastic model that projects a population structure that more closely resembles that observed in 2009. Conversely, the frequency or magnitude of past environmental variation may not be as great as it has been historically, for instance through active suppression of the natural fire regime. Continued monitoring of these stands may help to confirm the results of this study by failing to observe great swings in forest demographics.

Demography of a native Monterey pine stand

There have been numerous studies conducted on the demography of Monterey pine; however, many of these are limited to exotic stands (Acuna et al. 2010, Mosquera-Losada et al. 2010), a large percentage of which are specific to plantations in Australia and New Zealand (e.g. Dzierzon and Mason 2006, Haywood 2009), with a growing number addressing the increasing incidence of invasion posed by Monterey pine in non-native habitat (Williams and Wardle 2007, Baker and Murray 2010, Gomez et al. 2011). In contrast, relatively few studies have been conducted within the native range of *Pinus radiata*, even fewer of which have investigated population structure or growth (but see White 1999, Stephens et al. 2004, Piirto and Valkonen 2005, O'brien et al. 2007). None,

to my knowledge, have tracked a native stand for consecutive years for longer-term demographic purposes.

Estimated population growth rates of the observed stand were significantly lower than one (λ= 0.9822; 95% CI = 0.9684, 0.9985), suggesting that if growth, mortality, and reproduction estimates remain constant, the population will eventually be extirpated. It is important to note that these coastal Monterey pine populations reside in environmentally variable habitats and that recruitment events post-fire may be significant. As indicated by the 2009 demographic data (Table 2-3, Figure 2-6), these stands are of mixed-size class structure, a feature common to forests experiencing low severity fire regimes (Agee 1998) that do not cause a massive release of the aerial, semi-closed cone seed-bank, or one in which the fire regime has been largely removed from the system. In lieu of its natural fire regime, Monterey pine is known to release some amount of its canopy stored seeds in response to dryer environmental conditions (Roy 1966); however, increasing forest floor detritus or increased canopy shading may limit the germination of these seeds and therefore, the number of seedlings may be insufficient to perpetuate the population (Stephens et al. 2004).

The size class distribution observed during the 2009 census differs noticeably from that of the projected estimates of stable size class distribution. A spike in the demographic distribution of size classes 4 and 6, versus the typical J-curve distribution common to mixed-age forests (Peng 2000) seen in the stable size class estimate (Table 2-3, Figure 2-6), suggests a degree of instability in the population, with a relatively strong cohort moving through the population. Estimates of the time to a stable size class structure of 50 years agree with this finding, indicating the relative degree to which the

size class structure of the 2009 population differs from that calculated from the deterministic model. This 50-year estimate may be partially explained by the presence of these strong cohorts within the 2009 data, and the time frame it will take for them to pass through the population. Contrastingly, this estimate may be an indication that the population is shifting from the historic natural fire-maintained size class structure to one in which fire has been removed from the system.

Common mycorrhizal network effects on forest demographics

My hypothesis that the large differences in seedling mortality (-56%) observed between seedlings with and without access to mycorrhizal networks in a field experiment (Booth and Hoeksema 2010) would translate to significant differences between model estimates of the finite rate of growth, λ, was not supported when considering only the first two size classes. The significant overlap between estimates of λ for the observed demographic data and models A and B suggests that the mortality reductions of Monterey pine seedlings caused by CMNs will not likely translate to long-term population level effects upon plant community dynamics or community structure (Table 2-2, Figure 2-6). In fact, out of the 17 hypothetical non-CMN models, no estimated λs were statistically different from that estimated for the observed demographic data, except, that of the final model, Y, which removed CMN survival benefits from the entire life cycle of the Monterey pine. This result is at least partly in agreement with the elasticity analysis of the observed demographic data, which suggests that changes in mortality for smaller size classes will have little repercussion for growth rates of the population. These findings are consistent with the comparative study of 45 herbaceous and 21 woody plant elasticity

values conducted by Silvertown et al. (1993) that found that growth and fecundity were significantly less important to the λ of woody plants than to herbaceous plant species and conversely, survival was of greater importance to woody species than herbaceous plants. Calculation of unadjusted survivorship agree with this study's findings; however, comparisons between elasticities of unadjusted survivorship and estimated annual survivorship for each size class indicate a much greater relative role of seedling survivorship in influencing population growth rates. Still, the estimated annual survivorship elasticities suggest that changes to survivorship of later size classes will be more influential to population growth rates than similar changes to the youngest size classes of trees.

The final model, Y, estimated a drastically and significantly lower λ than that of any other model, including the observed demographic data (Table 2-2, Figure 2-6). It is somewhat surprising that the models including survival reductions for other later size classes including 14, 15, and 16 did not exhibit a significant shift in population growth rate, λ. Elasticity values for these size classes, specifically for stasis, were appreciably higher than other lower size classes and additively, much greater than that of size class 17. It is possible then that this final size class, lacking high mortality rates and predisposed to high reproductive rates (Table 2-1), would maintain an adequate number of recruits in the population to supply, over time, additional mature, fecund individuals to perpetuate the population. Comparisons of stable size class distributions between the observed model, model X, and model Y lends support for this idea whereby greater proportions of those late size classes, especially the last, maintain a proportionally greater amount of recruits in the population (Figure 2-4).

Model fidelity

The results presented here are reflective of the demographic data collected in this stand since 2002. The deterministic modeling approach taken here has been argued to be more accurate when there are five or fewer consecutive years of data (Doak et al. 2005), while stochastic models are preferred when enough years of data have been collected. This preference for stochastic models is true even more so within environments characterized by large climatic fluctuations or for populations that experience frequent or semi-frequent disturbance. Monterey pine is a fire adapted species and so fire disturbance may result in greater seedling recruitment events that could drastically affect population growth rates. It should be noted that mortality estimates were excessive, with mortality of the first size class exceeding 80% (Table 2-1, Figure 2-2). Similarly, fecundity values were modest in comparison to those expected to be expected post-fire (Table 2-1, Figure 2-3). Roy (1966) observed increased recruitment and growth of Monterey pine in areas of bare, mineral soil and increased light, i.e. just those environmental characteristics one would expect to change following a minor or major forest fire (Stephens et al. 2004). Additionally, Fenton (1951) observed recruitment following a stand fire estimated at ~900,000 seedlings ha^{-1}. Although perhaps not entirely applicable due to its occurrence in a Monterey pine plantation, this observation highlights the importance for fire in recruitment of this species. Therefore, the calculation of elasticity values for a population experiencing periodic stimulation of seedling recruitment may differ dramatically from that observed in this study (Table 2-4). The reality however, is that fires are actively suppressed in the California stands of

Monterey pine due to encroaching human development. Introduction of fire into these habitats could greatly increase recruitment and survivorship of seedlings, at least in the short term, which may increase population growth rates significantly.

The differences between the stable size class distribution and the observed size class distributions in 2009 suggest that these populations reside in a variable environment; however, the demographic data of the past nine years do not reflect this variability (Figure 2-5). The model estimates presented above may then be a forecast of how these populations will respond in the long term with continued fire suppression or limited environmental variability. Additional demographic work within this, and other populations, could provide more accurate model estimates of population growth rates and validation or refutation of these results.

CONCLUSION

There is a growing body of literature suggesting that variation in plant growth and survivorship is strongly influenced by ectomycorrhizal fungal community composition (e.g. Parke et al. 1983, Booth 2004, Booth and Hoeksema 2010); however, these studies have (perhaps out of necessity) all focused on how these compositional changes affect young, immature woody-plants. The modeling approach that I have employed in this study suggests that while CMNs may strongly influence the mortality rates of Monterey pine seedlings (Booth and Hoeksema 2010), the long-lasting influence of these effects on populations of Monterey pines, at least measured by the metrics of population growth rate and stable size class structure, may be modest (Table 2-2, Figure 5-2, Figure 4). If this is true, the temporal variation of EM fungal communities observed during succession that

leads to the development of these CMNs may be of little consequence for forest populations. If, however, the observed benefit of CMNs for plant survivorship endures throughout the life cycle of Monterey pine, EM fungal succession could drastically influence plant population dynamics in the long term in these forests.   Importantly, relatively small differences in survivorship or growth for later size classes in the woody plants life cycle may strongly influence population growth rates (Table 2-4).

It is, perhaps, a cruel irony for the ectomycorrhizologist that those life cycle stages most strongly implicated in influencing woody plant population growth rates are the most difficult, logistically, to quantify in their response to variation in EM fungal community composition. This result, however, should not limit investigation into this realm as science has consistently bypassed obstacles that once seemed insurmountable. In order to understand the potential for variation in ectomycorrhizal communities to influence populations of woody, perennial plants, researchers must begin to construct studies that aim to uncover its effect upon the growth, survival, and fecundity at later stages of plant development. It may be necessary, in turn, to take a multifaceted approach to this problem by invoking a combination of methods including, but not limited to, long-term research sites and extrapolative modeling.
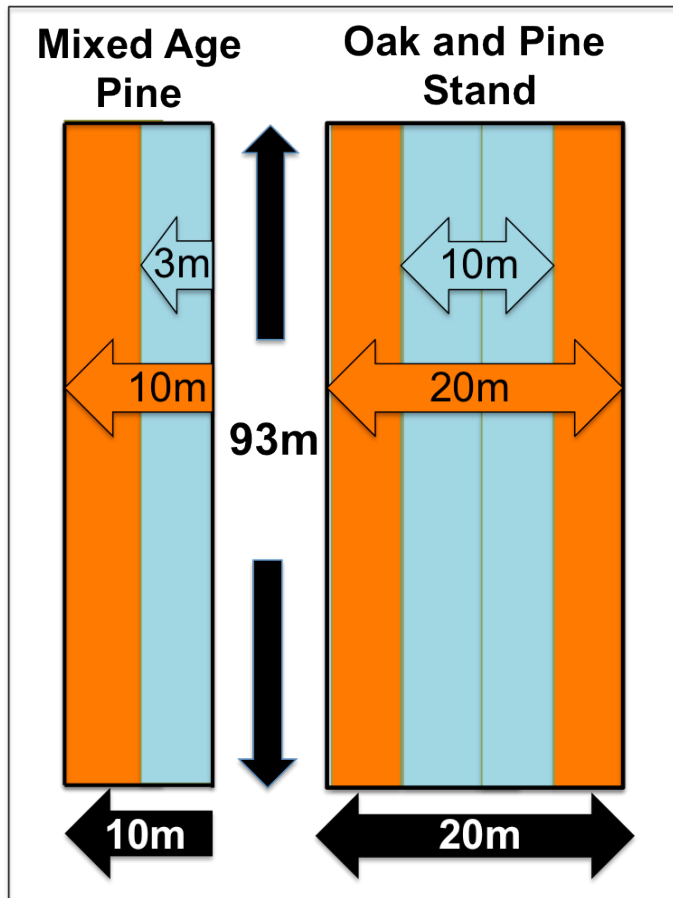
Figure 2-1: Diagram of forest plots in which data for the demographic matrix projections were collected. All data collected from the mixed age pine stand (MSC) was used for model estimates along with all data for trees 6.5 cm diameter at breast height or greater in the oak and pine stand (OP). Regions in blue represent those areas of the plots fully sampled for trees of all sizes. Regions in orange represent those areas of the plots where only trees ≥ 140 cm tall were sampled.
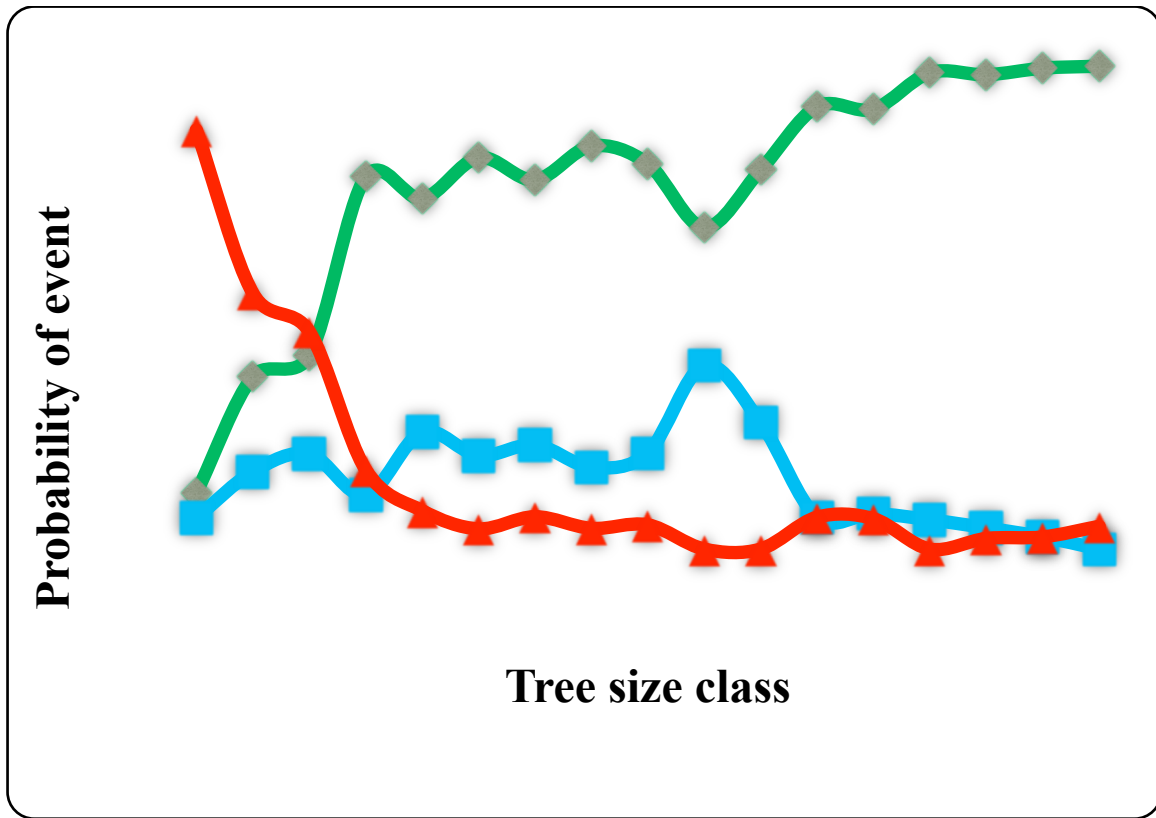
Figure 2-2: The average probability of a demographic event occurring for each size class for stasis (remaining in a stage into the next year, green), growth (growing into the next stage in the following year, blue), and mortality (dying in the present year, red).
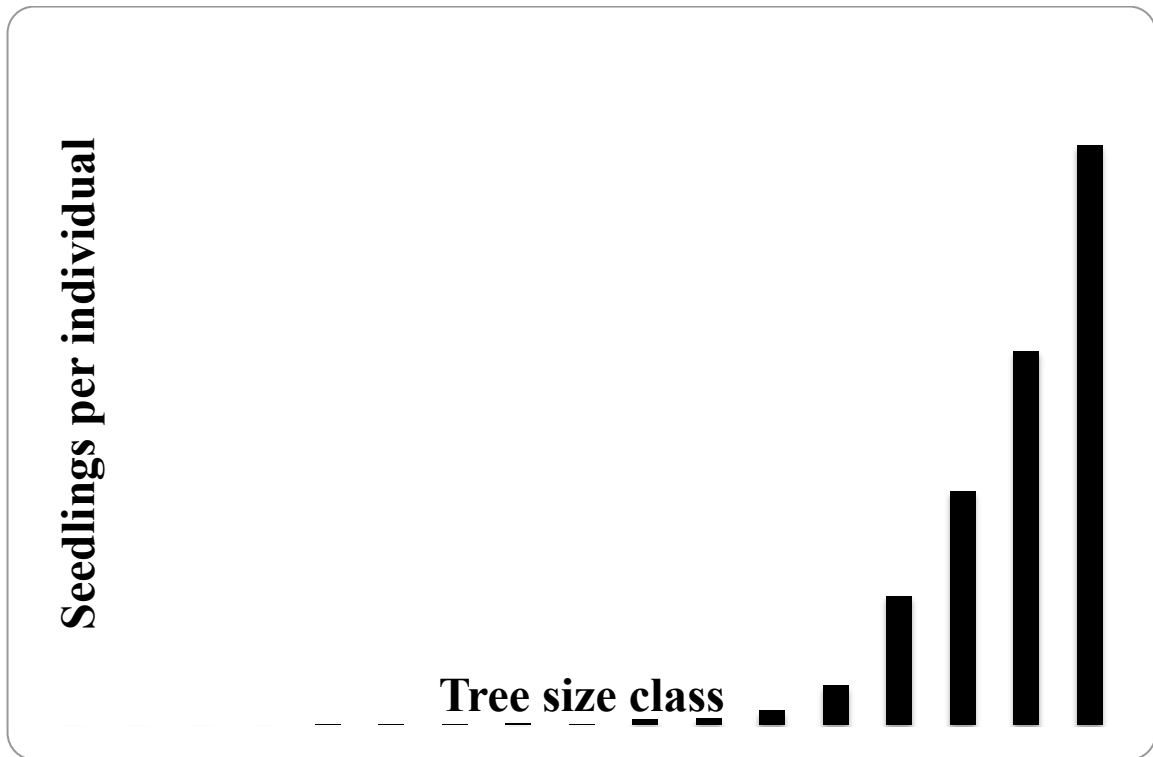
Figure 2-3: The average relative contribution of recruits per individual within each size class appearing in the following year.

Table 2-1: Parameter estimates for matrix model size classes: In all, 17 representative size classes were defined, with individuals ranging from 3 cm tall to > 300 cm tall and 98.1 cm diameter at breast height (DBH, 1.4 meters). 492 and 341 trees were used to estimate the life parameters of size classes 1-4 and 5 – 17, respectively. Columns 2 through 8 represent characteristics defining the decided upon size classes (St = stasis, G = growth, M = mortality, R = average contribution to recruits in next year per tree within size class). Column 9 represents the number of data points used to estimate the growth parameters of each size class; however it is important to note that due to the nature of the demographic data set an individual plant may be represented more than once in one or more size classes.

Size class	Height (cm)	DBH (cm)	St (%)	G (%)	M (%)	R (#)	Mean cones	N years of data
1	<15	N/A	0.111	0.061	0.828	0	0	198
2	15 - < 30	N/A	0.341	0.153	0.506	0	0	249
3	30 - < 47	N/A	0.383	0.188	0.430	0	0	128
4	47 – <140	N/A	0.736	0.107	0.157	0	0	121
5	≥ 140	0.4 – < 1.9	0.693	0.231	0.076	0.0032	0.01	515
6	≥ 140	1.9 - < 3.5	0.774	0.185	0.040	0.0217	0.07	372
7	≥ 140	3.5 – < 5.0	0.730	0.206	0.064	0.0407	0.14	141
8	≥ 140	5.0 - < 6.5	0.797	0.162	0.041	0.1050	0.35	74
9	≥ 140	6.5 - < 8.1	0.762	0.190	0.048	0.0636	0.21	36
10	≥ 140	8.1 - < 9.7	0.636	0.363	0.000	0.3302	1.1	23
11	≥ 140	9.7 - < 12.5	0.750	0.250	0.000	0.4166	1.4	46
12	≥ 140	12.5 - < 17	0.875	0.063	0.063	0.9253	3.1	57
13	≥ 140	17 - < 31.1	0.750	0.125	0.125	2.5916	8.7	42
14	≥ 140	31.1 - < 42	0.942	0.058	0.000	8.4888	28.5	68
15	≥ 140	42 - < 55.0	0.938	0.042	0.021	15.3560	51.6	54
16	≥ 140	55 - < 61.4	0.951	0.024	0.024	24.6004	82.7	48
17	≥ 140	61.4 <	0.955	0.000	0.045	38.1266	128.1	84

Table 2-2 – Finite growth rate, λ, for all 18 projected models including the upper and lower 95% confidence intervals (95% CI). The observed forest model estimate of λ was determined without any modifications to size class parameter estimates of mortality. Models A and B remove the common mycorrhizal network (CMN) benefit of 14.4% and 26.6% to increased survivorship from aged one and two individuals regardless of size or from size class one and two regardless of age, respectively. Each following model incrementally removes the Booth and Hoeksema (2010) estimated 2nd year survival reduction of 26.6% from a progressively higher size class, maintaining those modifications to survivorship made for model A and model B, until the entire tree life cycle has had the CMN removed.

Model	95% CI, lower bound of finite growth rate, λ	Finite growth rate, λ	95% CI, upper bound of finite growth rate, λ
Observed forest Data	0.9684	0.9822	0.9985
Non-CMN Ages 1 + 2 (Model A)	0.9662	0.9789	0.9963
Non-CMN Size class 1 + 2 (Model B)	0.9650	0.9778	0.9957
Non-CMN up to size class 3	0.9412	0.9750	0.9943
Non-CMN up to size class 4	0.9412	0.9707	0.9922
Non-CMN up to size class 5	0.9412	0.9679	0.9913
Non-CMN up to size class 6	0.9412	0.9657	0.9907
Non-CMN up to size class 7	0.9412	0.9648	0.9906
Non-CMN up to size class 8	0.9412	0.9643	0.9906
Non-CMN up to size class 9	0.9410	0.9641	0.9906
Non-CMN up to size class 10	0.9406	0.9641	0.9906
Non-CMN up to size class 11	0.9405	0.9640	0.9906
Non-CMN up to size class 12	0.9405	0.9640	0.9906
Non-CMN up to size class 13	0.9405	0.9640	0.9906
Non-CMN up to size class 14	0.9405	0.9640	0.9905
Non-CMN up to size class 15	0.9286	0.9640	0.9904
Non-CMN up to size class 16 (Model X)	0.9167	0.9640	0.9903
Non-CMN up to size class 17 (Model Y)	0.6944	0.7217	0.8333

Table 2-3 – Size class distribution of pines within the 2009 census compared to the estimated stable size class structure. * = rescaled estimates of pines <140 cm as determined by multiplying observed estimates by 10/3 to account for the adult skewed sampling scheme within the mixed size class plot (described in methods). DBH = diameter at breast height, 1.4 meters.

| Tree size class	2009 census (#)	2009 census (%)	Estimated proportional stable size class structure
0.0 – < 15 cm tall	36.67*	0.058*	0.8183
15 – < 30 cm tall	40*	0.063*	0.0775
30 – < 47 cm tall	56.67*	0.089*	0.0204
47 – < 140 cm tall	283.3*	0.445*	0.0155
0.4 - < 1.9 cm DBH	44	0.069	0.0058
1.9 - < 3.5 cm DBH	76	0.119	0.0064
3.5 - < 5.0 cm DBH	43	0.068	0.0047
5.0 - < 6.5 cm DBH	21	0.033	0.0052
6.5 - < 8.1 cm DBH	8	0.013	0.0032
8.1 - < 9.7 cm DBH	2	0.003	0.0017
9.7 - < 12.5 cm DBH	2	0.003	0.0030
12.5 - < 17.0 cm DBH	2	0.003	0.0052
17.0 - < 31.1 cm DBH	2	0.003	0.0042
31.1 - < 42.0 cm DBH	5	0.008	0.0053
42.0 - < 55.0 cm DBH	7	0.011	0.0082
55.0 - < 61.4 cm DBH	5	0.008	0.0047
> 61.4 cm DBH	3	0.005	0.0107
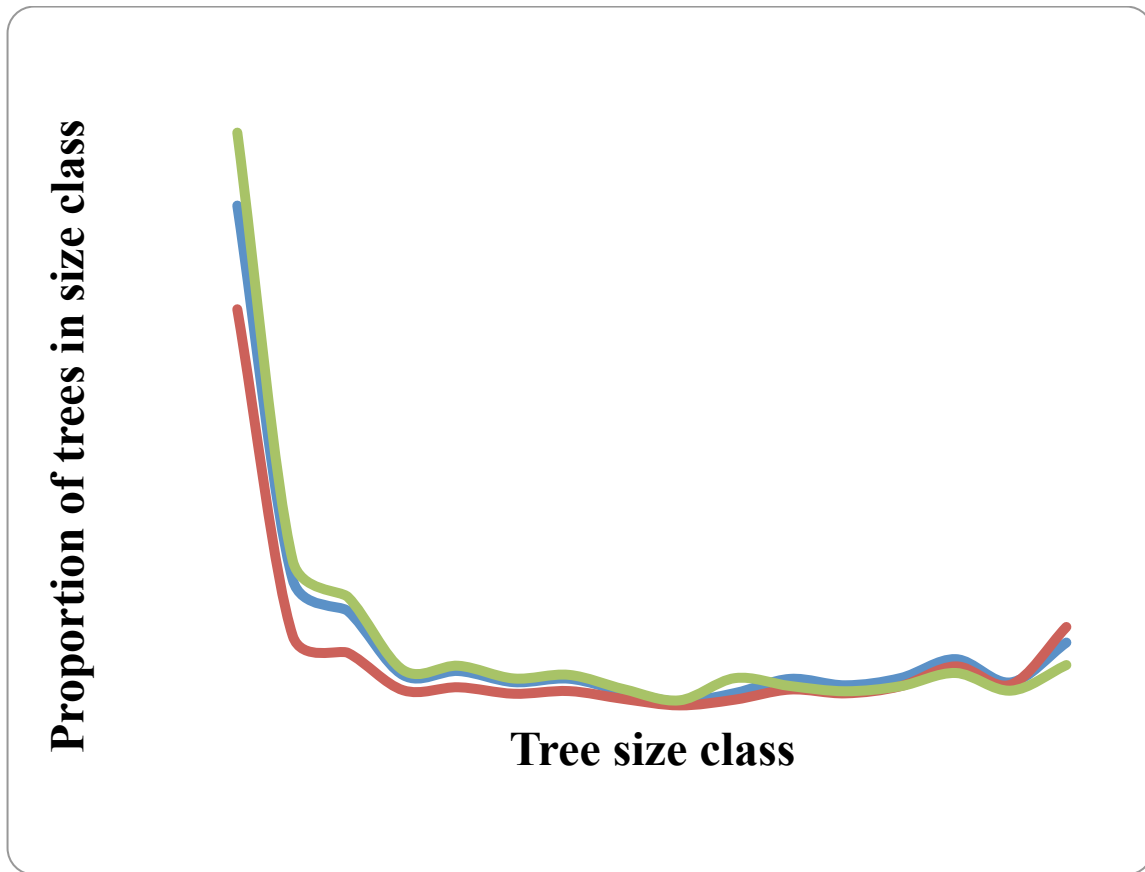
Figure 2-4: Proportional distribution of individuals within projected stable size class structure (Not depicted is size class 1, but see below for value). These three models were chosen as they represent the extremes observed for stable size class structures of all 18 models. Depicted are the observed forest data model (1st size class = .8183, blue line), the model removing the common mycorrhizal network benefit for all but the last size class (1st size class = .8986, model Y, red line), and the final model removing the common mycorrhizal network mortality reduction for all size classes (1st size class = .8067, model X, green line).
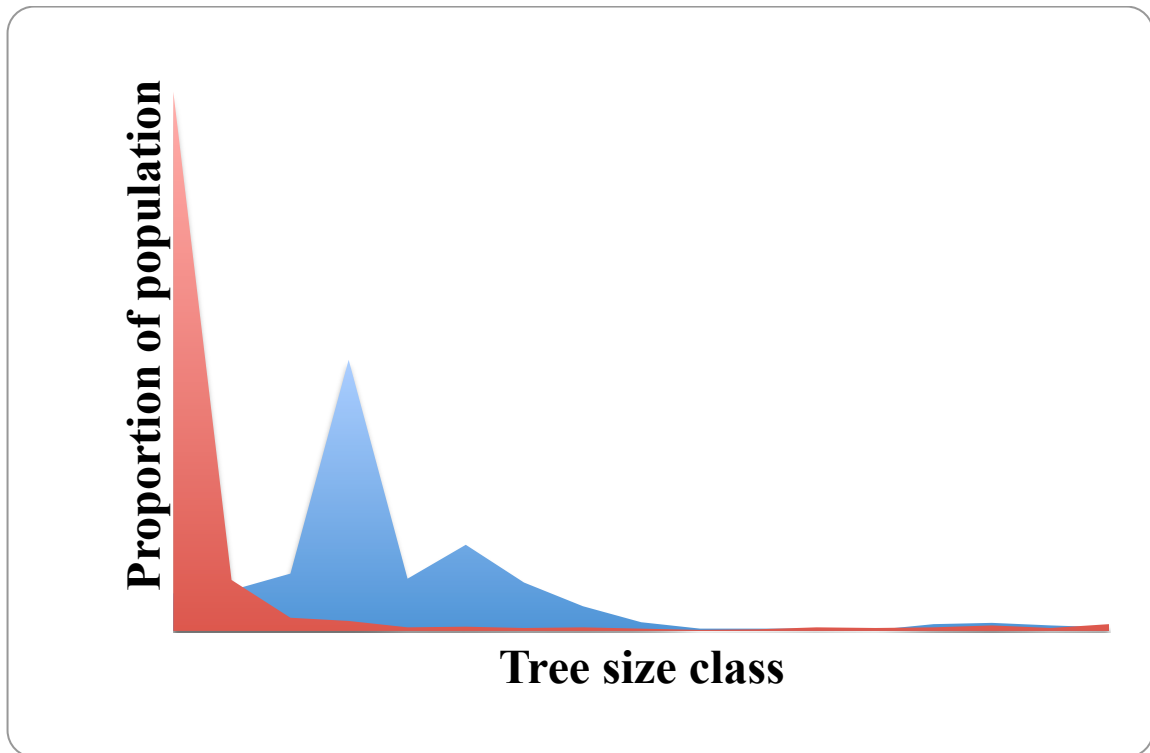
Figure 2-5 – Proportion of population within each size class for model estimated stable size class distributions for observed forest data (shaded red) versus the size class distribution for the last demographic census in 2009 (shaded blue).

Table 2-4: Elasticity analysis of observed demographic data reflecting the relative effect a small perturbation to the projection matrix affect the population growth rate. Elasticity values of fecundity (F), stasis (St), and growth (G) sum to a total of 1; however, in this table they may not due to rounding. Elasticity of survivorship is the sum of stasis and growth. Due to variation in the duration of time spent in a size class, values for survivorship may not be comparable between size classes. Therefore, unadjusted survivorship elasticities (St + G) have been divided by the maximum residence time (MRT) in each size class to give the adjusted elasticity for annual survivorship. * = Calculated by summing the estimated maximum number of years a seedlings is likely to remain in this size class

| Size class	F	St	G	Unadjusted Survivorship	MRT	Adj. annual survivorship
1	0.0000	0.0014	0.0078	0.0091	4.0*	0.0023
2	0.0000	0.0045	0.0078	0.0123	5.0*	0.0025
3	0.0000	0.0050	0.0078	0.0128	1.62	0.0079
4	0.0000	0.0232	0.0078	0.0310	3.79	0.0082
5	0.0000	0.0186	0.0078	0.0264	3.26	0.0081
6	0.0000	0.0289	0.0078	0.0367	4.42	0.0083
7	0.0000	0.0225	0.0078	0.0303	3.70	0.0082
8	0.0000	0.0334	0.0078	0.0412	4.93	0.0084
9	0.0000	0.0215	0.0078	0.0293	3.59	0.0082
10	0.0000	0.0105	0.0078	0.0183	2.30	0.0080
11	0.0000	0.0412	0.0078	0.0490	3.75	0.0131
12	0.0001	0.0410	0.0077	0.0487	5.78	0.0084
13	0.0001	0.0426	0.0076	0.0502	5.99	0.0084
14	0.0005	0.1218	0.0070	0.1288	13.51	0.0095
15	0.0014	0.1681	0.0056	0.1737	17.86	0.0097
16	0.0013	0.0771	0.0043	0.0814	12.05	0.0068
17	0.0043	0.2129	0.0000	0.2129	27.77	0.0077
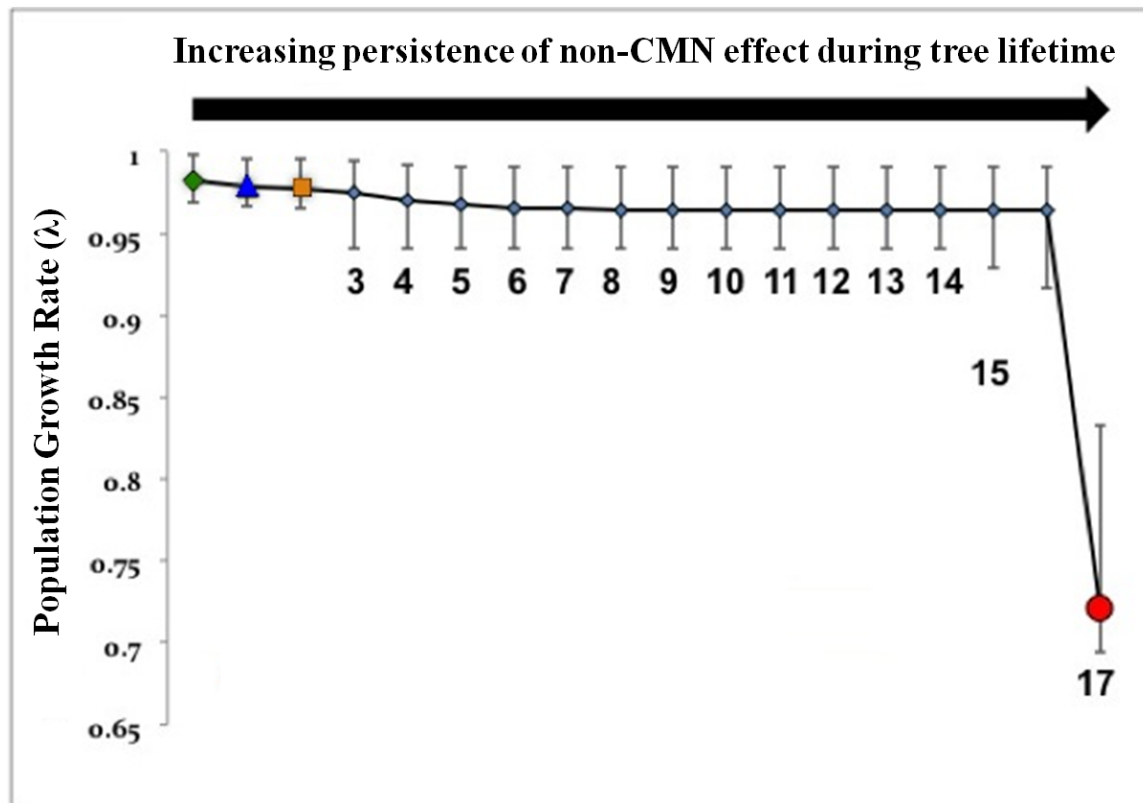
Figure 2-6: Projected population growth rates, λ, of the 18 projection matrices. From left to right include model estimates of λ for observed forest data (λ =0.982, 95% CI ± 0.998, 0.968, Green diamond), removal of common mycorrhizal network (CMN) benefit to survivorship (14.4%, 26.6%) from seedlings age one and two (λ =0.979, 95% CI ± 0.996, 0.966, Yellow triangle), removal of CMN benefit (14.4%, 26.6% of first and second size class (λ =0.978, 95% CI ± 0.995, 0.965, Orange square). Each following point with associated number represents the model estimate of λ with CMN benefit to survivorship (26.6%) removed up to that numbered size class except for first size class which had only a 14.4% benefit to seedling survivorship removed. The final point estimate of λ (λ=0.694, 95% CI ± 0.833, 0.721, Red circle) to the far right represents removal of the CMN benefit from the entire life cycle of the tree. Error bars are ± 95% confidence intervals.

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