Project Title: Belowground competition of American chestnut

Summary: Belowground dynamics of American chestnut have received little attention. A 13-year-old plantation experiment of American chestnut, northern red oak, and black cherry planted as monocultures and species mixtures at varying densities provide a unique opportunity to explore the long-term performance of American chestnut. In this project, we add measurements of belowground productivity to ongoing studies of aboveground productivity and chemical traits. Preliminary results suggest that planting density and species identity, rather than diversity itself, are driving belowground productivity in our experiment. Our final results will increase knowledge of American chestnut development in co-occurrence with other species and inform land managers how to best incorporate American chestnut into afforestation strategies.

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Project Duration: January – December 2019

Funding: $9,951 (see statement of matching funds below)

Short-term Project Goals:
1. Characterize belowground root production under varying plantation density and species mixtures.
2. Identify relative effects of competitor species on the root system productivity of American chestnut.
3. Investigate belowground root chemistry to complement ongoing analyses of aboveground foliar chemistry in these mixed species plantation stands.

Long-term Project Goals:
1. Determine optimal planting densities and species mixtures of American chestnut in both pure and mixed species plantations.
2. Help ensure useful silvicultural guidelines prior to reintroduction, through increased knowledge of the ecology of American chestnut.
3. Seek a mechanistic understanding of the causes of the positive correlation between productivity – diversity to increase profitability of forest plantations.

Project Narrative:

Introduction

Prior to the introduction of the chestnut blight, American chestnut was an important tree species throughout the eastern US deciduous forest (Braun 1950; Keever 1953). The loss of this species influenced myriad associated ecosystem services (Keever 1953; McCormick and Platt 1980; Diamond et al. 2000; Pierson et al. 2007; Jacobs et al. 2013). This included landscape-wide reductions in photosynthesis, productivity, and carbon sequestration, as well as increased leaching of nutrients and alterations of microhabitats (Lovett et al. 2006). Forest structure and composition were altered, with co-occurring species shifting into the dominant and co-dominant canopy positions due to the release caused by the decline of American chestnut (Smith 2009).

Considerable efforts have been directed at American chestnut restoration. During the last decades, significant progress has been made toward the goal of developing a blight-resistant hybrid chestnut through crosses with Chinese chestnut (*Castanea mollissima* Blume) (Hebard 2006). Here, phenotypic characteristics of American chestnut are regained through a series of backcrosses to American parents, reducing the proportion of Chinese alleles. The third-generation backcross (BC_3) retains American chestnut morphological characteristics through juvenile stages, with testing ongoing (Diskin et al. 2006; Steiner et al. 2017).

Blight resistant chestnut may become an important tree species for forest restoration (Jacobs et al. 2013). Contemporary research suggests that American chestnut is adapted to a wide range of site conditions and light environments, and is reported to be a fast-growing species with desirable timber (Jacobs and Severeid 2004; McEwan et al. 2006; Jacobs et al. 2009). Thus, chestnut should be an attractive tree species for many private landowners in eastern North America. While knowledge of chestnut's silvical characteristics in field settings has improved (Jacobs 2007; Jacobs et al. 2013; Wang et al. 2013), **its competitiveness in mixed species stands has been the focus of very few studies**. Mixed plantations are an important tool for forest restoration because they serve a wide variety of social, economic, and environmental objectives compared to monocultures (Paquette and Messier 2010).

Rationale and Objectives

Blight-resistant hybrid chestnut seedlings will become available for future reforestation efforts. Further insight into the silvical and ecological characteristics of American chestnut is thus needed to establish guidelines to aid restoration efforts. The most common silvicultural manipulation of forest stands and plantations is change in density (spacing), which determines the level of competition for resources. Further understanding of the long-term performance of American chestnut at various spacings is needed. An additional benefit of diverse plantations is that differences in functional traits between species can reduce competition for resources in mixtures compared to competition in monocultures (Tilman et al. 2001; Liang et al. 2016). Successful mixed plantations take advantage of complimentary characteristics of the assemblage of species, such as varying shade tolerance that facilitates a stratified canopy, or by combining species with different strategies for scavenging nutrients and water (Kelty 1992; Nichols et al. 2006). Therefore, a factorial design that crosses spacing and species diversity may yield important new insights into the long-term performance of American chestnut. Understanding how American chestnut responds to competition will allow forest managers to make more informed decisions in their efforts to reintroduce the species across the landscape.

The objective of this study is to gain further knowledge regarding factors that influence the growth and competitiveness of American chestnut grown alone and in combination with associated hardwood species. While recent studies have improved our understanding of above-ground competition of American chestnut, belowground dynamics have received relatively little attention. This knowledge is important because aboveground growth and productivity depend on belowground processes. Furthermore, root growth and root-soil interactions have important implications in carbon cycling, interactions with mycorrhizal communities, nutrient and water competition, and allelopathy. We assembled a diverse research team with expertise in modern analytical techniques to provide insights into American chestnut belowground development. Thus, **our specific objective is to evaluate root system productivity and root-soil chemistry interactions of American chestnut under varying spacings and species mixtures.**

Methodology

Study Site: This study was carried out at a previously established competition trial planted by PI-Jacobs and colleagues in 2007 at Martell Forest, Purdue University's primary research forest located in West Lafayette, Indiana. We planted stands of American chestnut (*Castanea dentata* (Marsh.) Borkh.), northern red oak (*Quercus rubra* L.) and black cherry (*Prunus serotina* Ehrh.) as monocultures, two species mixtures and all three species together, at three different densities (1m, 2m or 3m spacing between trees). Early growth and physiological data after five years were published previously (Gauthier et al. 2013). This 14-year-old experiment is now a closed canopy forest, and provides a unique opportunity to explore productivity-diversity relationships in an experimentally manipulated plantation forest.

Experimental Design: The experimental design was inspired by traditional competition experiments (Radosevich et al. 1997) and more recent studies and reviews on mixed plantings (Kerr 2004; Vanclay 2006). The split-split plot design consists of three different species (sub-sub plot) randomized within seven different mixtures (sub-plot). In turn, mixtures are randomized within three different spacings (main plot). Spacings were randomized within each block. Three blocks were installed in the spring of 2007, taking up approximately 2.4 ha. The seven mixtures were as follows: 1) 100% black cherry (B), 2) 100% American chestnut (C), 3) 100% northern red oak (N), 4) 50% cherry and 50% chestnut (BC), 5) 50% cherry and 50% oak (BN), 6) 50% oak and 50% chestnut (NC), 7) one-third of each species (NBC) (Fig 1a). All plots are 8 trees by 7 trees square, but differ in the spacing between trees, with a buffer of 1 tree row around the perimeter to minimize edge effects (Fig 1b). Spacings used for this study are 1 m (10000 stems ha^{-1}), 2 m (2500 stems ha^{-1}), and 3 m (1111 stems ha^{-1}). The experimental unit (EU) is the average of each species in each mixture and spacing combination, excluding the buffer row (n=108). Thus, all EUs were composed of 30 seedlings, providing at least 10 seedlings per species in each EU. For plots with two or more species, each species was planted alternately in each row, similar to a checkerboard pattern. A total of 1800 bareroot seedlings (1+0) of each species were purchased from Cascade Forest Nursery in Cascade, Iowa, USA. Seedlings of all species were grown on the same site and subjected to the same fertilization, irrigation, and root culture regimes under standard nursery conditions. Northern red oak and black cherry were from seed sources local to the nursery. Pure American chestnut seeds were collected from a stand of trees > 100 years of age near Galesville, Wisconsin, USA. The experimental design is illustrated in Figure 1.

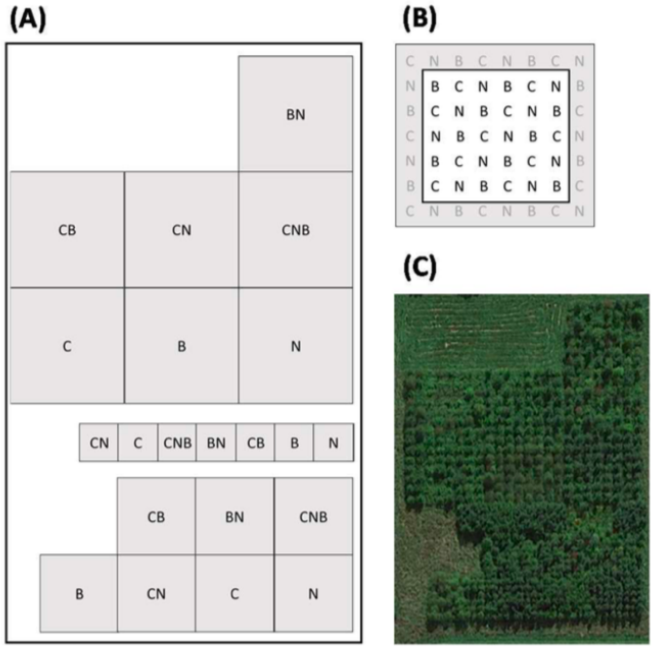

FIGURE 1: (A) *Layout of treatments within one of the three replicate blocks,* ***(B)*** *layout of planted trees within a plot, and* ***(C)*** *a satellite photo of one block. Three species were planted either as monocultures (C, N, or B), 2-species mixtures (CN, CB, or BN) or as 3-species mixtures (CNB).*

We are evaluating belowground productivity using in-growth cores to estimate root system growth (Stevens and Jones 2006). A problem with studying root production in forests is that one cannot assess productivity (biomass produced per year) by measuring standing root biomass because standing roots represent an unknown mixture of growth across many years. In-growth cores solve this issue by isolating root production from a set time period (Fig. 2). The in-growth core method involves 5 steps: (1) extract a cylindrical core of soil 7.5 cm across and 50 cm deep using a soil corer; (2) remove the original roots from the soil sample; (3) place the polypropylene mesh ingrowth core into the hole and fill it with the same (root-free) soil that was extracted from that location; (4) allow one full year of root growth; (5) retrieve the ingrowth containing roots produced in exactly one year. Measurements can then be performed on roots produced during exactly one growing season. Roots from the original coring (step 1) were also weighed so that correlations between new growth and previous root mass can be evaluated (Oliviera et al. 2000).

The different tree spacing treatments vary in plot size (Fig 1A), and thus we deployed one ingrowth core in each 1m spaced subplot, two ingrowth cores in each 2m spaced plot, and three ingrowth cores in each 3m spaced subplot. Ingrowth cores were randomly located within each subplot, but equidistant from trees. In-growth cores were 5 cm in diameter, and 0.5 m deep to capture the surficial fine roots. Soil and roots were extracted in sections from 0-10 cm, 10-30 cm, and 30-50 cm so that we can evaluate root system stratification by depth. 112 ingrowth cores were installed in October-December 2018, and the cores were retrieved at the same time in 2019 (Fig. 2). Upon retrieval, soil was washed from roots on a 0.5 mm mesh. Roots were dried using silica gel, weighed to determine total annual productivity, and ground with liquid nitrogen. We are currently in the process of extracting genomic DNA using Qiagen DNeasy Plant Pro kits. Our next step is to quantify the proportion of roots from each species in each soil core layer using quantitative real-time polymerase chain reaction (qPCR) (Mommer et al. 2008).

FIGURE 2. *Left: Polypropylene mesh ingrowth cores. Middle: Ingrowth cores incubated in the field for one year. Right: roots and mycorrhizae extracted from ingrowth cores.*

Unlike aboveground parts of plants which can be visually identified to species, the roots of most plants are visually indistinguishable. To identify the relative abundance of each species in our mixed root samples, we will use a species identification method that is capable of generating species abundance data from root samples (Mommer et al. 2008). Briefly, genomic DNA will be extracted using Qiagen DNeasy Plant Pro DNA extraction kits that include a phenolic separation solution step because roots contain a high concentration of phenolics that inhibit downstream reactions (McNickle et al. 2008). First, we will identify species-specific DNA fragments by performing intersimple sequence repeat (ISSR) analyses on genomic DNA of the roots of the three species. Next, species-specific sequences will be used to develop a qPCR protocol for each individual species. (Mommer et al. 2008). Control samples with a known proportion of roots from each species (by weight) will serve as positive controls.

Analysis of variance (ANOVA) is used to examine significant ($p<0.05$) differences in root biomass as a function of spacing and proportion of each species. The average root production of each species per plot will be used as the experimental unit, providing three replicates per spacing and species combination ($n=63$). All analyses are carried out using R software.

Complementary measurements: We have an ongoing series of funded experiments in this mixed species plantation experiment to assess productivity-diversity relationships aboveground by measuring physiological, morphological, chemical, and structural functional traits. Litter traps are deployed under the canopy to collect falling leaves, and wood growth is estimated by measuring the diameter at breast height of all trees in the experiment. Soil nutrient availability is estimated using ion-exchange resin membrane methods. Soil moisture and the understory light environment are estimated using automated data loggers. Canopy structure is characterized using ground-based portable canopy lidar and high-resolution hemispherical photography. Foliar primary and secondary metabolites are quantified using standard analytical approaches.

Finally, we are monitoring nonstructural carbon dynamics in the chestnut trees in our competition experiment. Non-structural carbohydrate (NSC) reserves are stored sugars that a tree draws from to fuel normal metabolic functions and energy-intensive processes like reproduction, defence against pests, and regrowth following disturbance. NSC reserves represent the balance between carbon supply (from photosynthesis) and demand; they indicate a plant's capacity to respond to and recover from damaging agents and environmental change. NSC dynamics in mature *C. dentata* have yet to be studied, though carbohydrate reserves could be especially vital for the chestnuts as they have a strong capacity to resprout following disease and disturbance. We are tracking NSC concentrations throughout the woody plant body (leaves, branches, bole, and roots) to characterize seasonal NSC dynamics. Field sampling started in Spring 2019 and is ongoing (Fig. 3). Sugar and starch concentrations will be determined following the protocol of Landhäusser et al (2018). In summer 2019, we excavated and weighed the above and below-ground biomass of eight 13-year-old chestnut trees to build an allometric model that will be used to convert NSC concentration to total pool size (Fig 3). Our experimental design allows us to explore the degree to which competition mediates the relationship between productivity and NSC reserve accumulation.

Thus, financial support from TACF allowed us to add the crucial belowground component to our ongoing measurements. With this addition, we now have comprehensive data and knowledge to quantify total productivity, nutrient cycling, and non-structural carbon dynamics in these stands. Together, these data hold powerful insights into chestnut's growth and competitiveness under varying competition regimes.

FIGURE 3. *Left: Undergraduate technician Esther Mussmann excavating a chestnut stump (middle) for allometric model building. Right: MS student Madeline Montague collecting leaf and twig samples for nonstructural carbon (NSC) analysis.*

Preliminary results

Planting density and tree species identity significantly affected total annual root productivity in our plantation experiment ($p < 0.05$, ANOVA). Species differed in their allocation to root growth at varying soil depths (Fig. 3). Annual root production was roughly a tenth of the previous standing root biomass at ingrowth core locations (Fig. 4). Interestingly, diversity (number of tree species) was not significantly related to total annual root productivity. This suggests that species selection may have a stronger effect on ecosystem functioning than diversity itself in this system. Our interpretation of these results will benefit greatly with the forthcoming addition of species-specific productivity estimates for our diversity and density treatments. Species-specific productivity estimates will enable us to detect whether our trees alter their rooting habits in combination with other species. These estimates will further improve the quality of our data by allowing us to filter out belowground biomass from various non-target understory species.

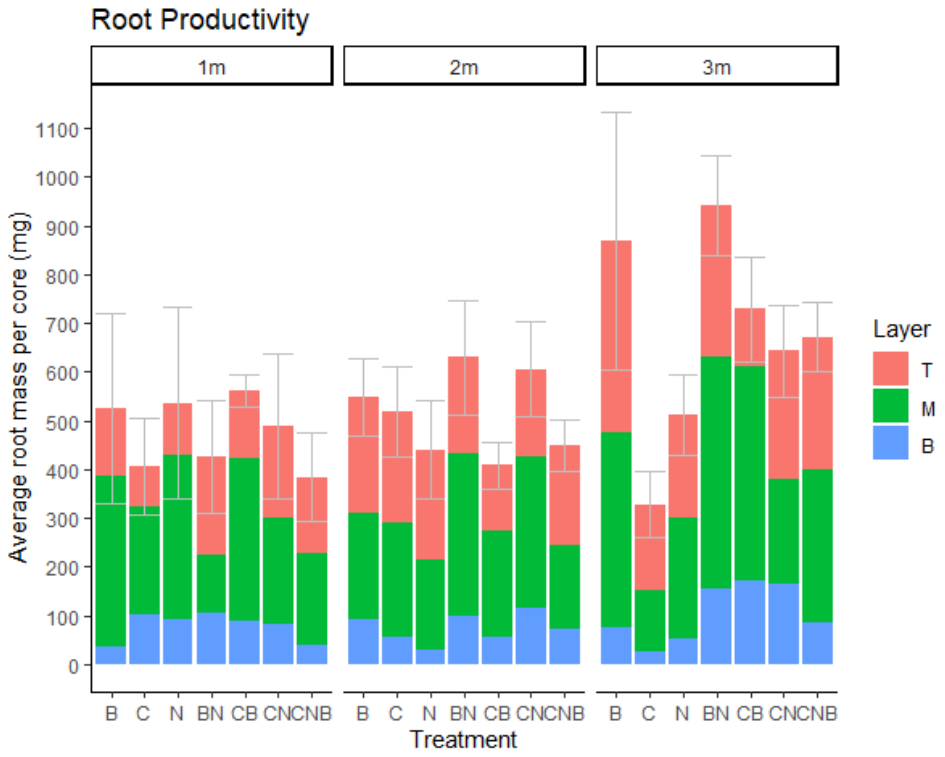

FIGURE 3. *Annual root productivity at varying density (1m, 2m, or 3m between trees) and diversity treatments. Root ingrowth cores were split into top (T, 0-10 cm below the litter layer), middle (M, 10-30 cm), and bottom (B, 30-50 cm) layers to evaluate vertical root stratification. Diversity treatments consist of chestnut (C), black cherry (B), and northern red oak (N) monocultures, as well as 2-species and 3-species combinations. Error bars represent ± SE from the average total root mass per ingrowth core.*

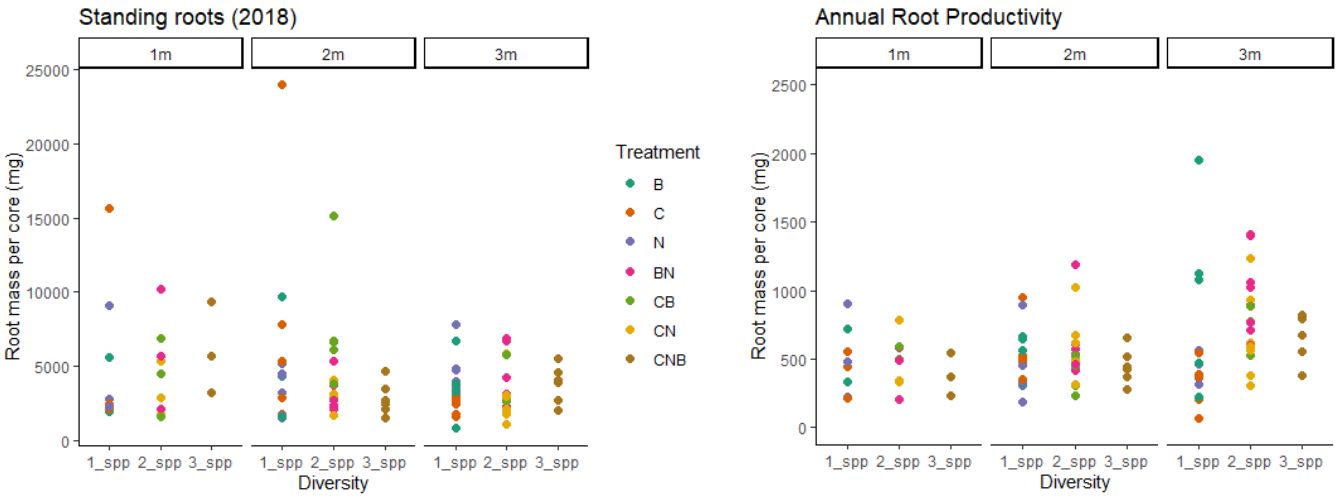

FIGURE 4. *Left: Standing root biomass in our 13-year old plantation experiment, measured at the location of ingrowth core installation. Diversity treatments consist of chestnut (C), black cherry (B), and northern red oak (N) monocultures, as well as 2-species and 3-species combinations. Planting density varies from 1m, 2m, and 3m between trees.*
Right: Annual productivity in our root ingrowth cores. Note the ten-fold difference in scale.

Reporting of results: Our group has benefitted from positive and constructive feedback at several scientific meetings. Preliminary results from this work have been included in presentations to the Society of American Foresters (SAF) in Louisville, KY, and at the International Union of Forest Research Organizations (IUFRO) at the 2019 World Congress in Curitiba, Brazil. Belowground productivity data from this experiment is the main theme of our upcoming presentation to the IUFRO Mixed Forest Working Group in Lund, Sweden in March 2020. The support of TACF for this research has been acknowledged at these events.

These data constitute the core of Madeline Montague's Master's Thesis research with an anticipated completion date in November 2020. Furthermore, a comprehensive manuscript will be authored and submitted to refereed journals such as *Plant and Soil* or *Forest Ecology and Management* upon completion of genetic analyses. The publications will be shared with TACF when available.

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