Forest Ecology and Management 291 (2013) 289–299

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Inter- and intra-specific competitiveness of plantation-grown American chestnut (*Castanea dentata*)

Martin-Michel Gauthier[a,1], Kate E. Zellers[a], Magnus Löf[b], Douglass F. Jacobs[a,*]

[a] Hardwood Tree Improvement and Regeneration Center, Department of Forestry and Natural Resources, Purdue University, 715 W State Street, West Lafayette, IN 47907-2061, USA
[b] Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, PO Box 49, S-230 53 Alnarp, Sweden

ARTICLE INFO

Article history:
Received 29 June 2012
Received in revised form 31 October 2012
Accepted 10 November 2012
Available online 7 January 2013

Keywords:
Afforestation
American chestnut
Crown competition factor
Ecophysiology
Forest restoration
Stand density

ABSTRACT

The introduction of the fungal pathogen *Cryphonectria parasitica* (Murr.) Barr. decimated American chestnut (*Castanea dentata* (Marsh.) Borkh.) throughout its native range in North America. A blight-resistant backcross hybrid form of American chestnut has been developed, and these backcross trees are likely to be incorporated into restoration programs in the near future. To help guide future afforestation efforts, this study examined juvenile (five growing seasons) morphological and physiological competitive aspects of American chestnut grown in a plantation setting with northern red oak (*Quercus rubra* L.) and black cherry (*Prunus serotina* Ehrh.) in Indiana, USA. Species were grown in seven possible species combinations including both monospecific and polyspecific combinations at three densities (1 × 1 m, 2 × 2 m, and 3 × 3 m). Despite an initial advantage in height, American chestnut exhibited the lowest relative height growth in the 2 × 2 and 3 × 3 m spacings, resulting in less total height compared to the other two species 5 years after planting. Relative height growth, as well as final absolute heights, were comparable among species in the 1 × 1 m spacing. Black cherry exhibited 2–3 times greater relative ground-line diameter (GLD) growth compared to oak and chestnut at all spacings. Linear regressions showed that growth was generally proportional to net photosynthesis (*A*) for all species. Increases in *A* likely resulted from increases in leaf nitrogen concentration. Chestnut exhibited lower *A* than cherry and oak in years 2 and 3, but no differences occurred in year 4. Additionally, chestnut had significantly higher predawn leaf water potential (leaf Ψ_{pd}) in year 4, reflecting greater drought stress in cherry and oak. While black cherry grew most aggressively, northern red oak and American chestnut performed acceptably, with high survival rates and moderate growth, especially in the 1 × 1 m spacing. American chestnut had the poorest stem form overall, but fared better in the 1 × 1 m spacing where the crown competition factor (CCF) was highest. Hence, an intermediate spacing between 1 × 1 and 2 × 2 m could optimize chestnut's growth and stem form. Mixture effects may be attributed mainly to individual species growth characteristics rather than inter-specific interactions during this juvenile developmental stage.

1. Introduction

The anthropogenic importation of exotic pests and pathogens through international trade has become increasingly influential on ecosystems worldwide in the modern era. Some of these exotic pests have severely affected keystone forest tree species, and thereby influenced natural ecosystems. One important example from North America during the last century involves chestnut blight caused by the fungus *Cryphonectria parasitica* (Murr.) Barr. Chestnut blight, which causes a diffuse canker disease, spread rapidly throughout the natural range of American chestnut (*Castanea dentata* (Marsh.) Borkh.), and all but eliminated this once dominant tree species within the span of a few decades (Braun, 1950; Roane et al., 1986; Anagnostakis, 1987; Jacobs et al., 2013).

Prior to the introduction of the chestnut blight, American chestnut was a dominant tree species throughout the eastern deciduous forest of the United States, comprising up to 40–50% of the forest canopy (Braun, 1950; Keever, 1953), with a distribution of over 800,000 km^2 (Little, 1977; Russell, 1987). The loss of such an important tree 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). In addition, forest structure and tree species composition were altered, with co-occurring species shifting into dominant and co-dominant

* Corresponding author. Tel.: +1 765 494 3608; fax: +1 765 494 9461.
E-mail address: djacobs@purdue.edu (D.F. Jacobs).
[1] Present address: Direction de la recherche forestière, Ministère des Ressources naturelles du Québec, 2700 rue Einstein, Québec, QC, Canada G1P 3W8.

0378-1127/$ - see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2012.11.014

canopy positions due to the release caused by the decline of American chestnut (Smith et al., 2009).

In response to this economical and ecological catastrophe, 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) has been shown to retain American chestnut morphological characteristics through juvenile stages, with testing ongoing (Diskin et al., 2006). The reintroduction of blight-resistant chestnut is therefore expected to occur within the near future (Griffin, 2000; Steiner and Carlson, 2006).

Blight resistant chestnut has the potential to 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, for economical and ecological reasons it should be an attractive tree species for many private landowners in eastern North America. However, relatively little is known regarding the silvical and physiological characteristics of American chestnut in field settings (Jacobs, 2007; Jacobs et al., 2013). Although the body of literature regarding American chestnut has vastly increased in recent years, the competitiveness of American chestnut has been the focus of very few studies. Additionally, little is known about the response of American chestnut in mixed plantation settings, which has been identified as an important tool for forest restoration as these plantation designs may meet a wide variety of social, economical, and environmental objectives in comparison with monocultures (Paquette and Messier, 2010).

The role of plantations in both reforestation and afforestation efforts has become an increasingly important component of global forest cover and wood production (Kelty, 2006). Historically, plantations were established mainly as monocultures, which allows for simplified management practices and harvesting operations; but public pressure to meet multiple objectives beyond economic returns has spurred interest in mixed species plantations (Lamb et al., 2005). While mixed plantations may help meet a broader range of objectives, the greater complexity that results from inter-specific interactions requires greater insight for effective management. Typically, 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 nitrogen-fixing species with other non-nitrogen-fixing species (Kelty, 1992; Nichols et al., 2006).

The most common silvicultural manipulation of forest stands and plantations is change in density (spacing). It therefore stands to reason that further understanding of how American chestnut performs at various spacings is needed. At higher densities, competition for above- and below-ground resources can be limiting, eventually leading to mortality of less competitive individuals. Competition for light is largely determined by growing space occupancy, as trees with larger crowns have greater ability to intercept more sunlight. A simple metric of this competition is the crown competition factor (CCF), the ratio of the sum of potential crown areas of all trees within a planting to the actual ground area of the planting (Schlesinger, 1997). Density dependent competition for both above- and below-ground resources can lead to a reduction in physiological activity and subsequent growth. Understanding how American chestnut responds to density-induced stress will allow forest managers to make more informed decisions in their efforts to reintroduce the species across the landscape.

The aim of this study was to gain further knowledge regarding factors that influence the growth and competitiveness of American chestnut grown with associated fine hardwood species, such as northern red oak (*Quercus rubra* L.) and black cherry (*Prunus serotina* Ehrh.), in an effort to ensure successful outplanting of chestnut in the future. Specific objectives include (i) evaluating the relative competitiveness and early growth characteristics of American chestnut under varying spacings and species mixtures; and (ii) examining ecophysiological responses of American chestnut seedlings under varying spacings and species mixtures.

2. Materials and methods

2.1. Study site

The study site was established at Purdue University's Martell Forest, located in West Lafayette, Indiana, USA (40°26′42″N, 87°01′47″W). The area of Martell Forest used for this research was part of a 16 ha agricultural field, with the main soil type comprised of Rockfield silt loam (USDA NRCS, 2011). It is a moderately well drained, productive site. Mean annual (1981–2010) precipitation in West Lafayette is 970 mm, and mean annual temperature is 10.4 °C (National Climatic Data Center, 2012).

2.2. Experimental design and plantation establishment

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). Spacings used for this study are 1×1 m (10,000 stems ha^{-1}), 2×2 m (2500 stems ha^{-1}), and 3×3 m (1111 stems ha^{-1}). The experimental unit (EU) is the average of each species in each mixture and spacing combination ($n = 108$). All EUs were composed of 30 seedlings, providing at least 10 seedlings per species in each EU. One guard row was planted around each sub-plot. The planting pattern of the guard row was the same as inside 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 seeds 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. Although the original seed source is unknown, another stand of pure American chestnut 30 km away near West Salem, Wisconsin was established around the same time period with seed thought to be of Pennsylvania origin (Paillet and Rutter, 1989). Seed from these two stands was used previously in a trial examining American chestnut plantation competitiveness (Jacobs and Severeid, 2004). Because the genetic composition of blight-resistant, back crossed chestnut to be used for restoration is approximately 94% American chestnut (Burnham, 1981; Hebard, 2006) and has been selected for American chestnut phenotype (Hebard, 2006; Diskin et al., 2006), silvicultural studies