



Original research article

Evaluation of phenotypic traits and blight-resistance in an American chestnut backcross orchard in Georgia



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ABSTRACT

American chestnut (*Castanea dentata*) was once a cultural, ecological, and economic staple of hardwood forests of the Eastern United States; however, chestnut blight caused by *Cryphonectria parasitica* has severely threatened its significance. The American Chestnut Foundation (TACF) is a non-profit organization that has focused on backcross breeding as a means of restoring *C. dentata* to the wild. A major goal of this breeding program has been to introduce blight resistance from Chinese chestnut [*Castanea mollissima*] while recovering “American chestnut” morphology by backcrossing with *C. dentata*. The Berry College backcross orchard, in northwest Georgia, was the first such orchard established by TACF with the goal of producing advanced hybrids derived from crosses with wild *C. dentata* from Georgia (part of TACF’s state chapter program). In 2008, three lines of third backcross (BC3) hybrids were planted at the orchard along with F1, *C. mollissima*, and *C. dentata* controls. The theoretical model for the backcross breeding program predicts intermediate blight resistance, at best, in BC3 trees, along with an otherwise American chestnut morphology. This paper focuses on the degree to which this combination of desired traits has been found among the first lines of BC3 trees generated in Georgia. Trees were inoculated with blight in May 2013 (at age 4–5 yrs), and blight resistance was evaluated in October 2013 and March 2014 and used to calculate an average blight-susceptibility index (BSI). In September 2013, branch samples were collected and used to evaluate 20 leaf, stem, and bud traits known to differ consistently between *C. mollissima* and *C. dentata*. The average of standardized scores for morphological traits was used as an index of species identity (ISI) for each tree. On average, BC3 lines showed significant morphological differences when compared with Chinese chestnut lines, nesting morphologically with American chestnuts. Each BC3 line contained some trees with both intermediate blight resistance and morphological traits similar to *C. dentata*, supporting the prediction that both sets of traits have been advanced using the backcross methodology. These results are discussed in relationship to currently evolving understanding of the genetics of blight resistance and with respect to other traits needed for successful restoration in the southern United States.

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1. Introduction

American chestnut, *Castanea dentata* (Marsh.) Borkh. (Fagaceae; hereafter AM chestnut) flourished across eastern North America and provided rural residents with timber and a cash crop, at the same time being a valuable food resource for wild animals due to a consistent and abundant production of nuts (Anagnostakis, 1987). Chestnut blight, caused by *Cryphonectria parasitica* (Murrill) Barr; Cryphonectriaceae), was introduced to AM chestnuts in or before 1905, apparently having been imported on Japanese chestnut (*C. crenata* Siebold & Zucc.) and/or Chinese chestnut (*Castanea mollissima* Blume [hereafter CH chestnut] trees (Milgroom and Cortesi, 2004). After entering the bark via air-borne spores, cankers spread quickly in susceptible trees, and eventually girdle and kill the stem. The portion of the stem below the canker often remains alive and basal sprouting may be induced following infection (Griffin, 2000). Because of the lack of resistance in AM chestnut, by 1950 the disease had spread throughout its native range, top-killing approximately four billion trees (Jacobs et al., 2013). Currently, 431 +/- 30.2 million AM chestnut stems remain, but the vast majority (360 +/- 22 million) are very small (<2.5 cm in diameter; Dalgleish et al., 2015). These sprouts, along with far lower numbers of large long-term surviving AM chestnut trees, provide germplasm resources for projects designed to restore AM chestnut as a functional component of eastern US forests.

Many strategies to develop resistance to the chestnut blight have been advanced, including biocontrol using hypovirulent fungal strains (Milgroom and Cortesi, 2004), cross-breeding selected surviving AM chestnut trees (Griffin et al., 1983), genetic modification of AM chestnut (Zhang et al., 2013), and hybridization with resistant Asian chestnuts such as CH chestnut (Hebard, 2005). The American Chestnut Foundation (TACF) has focused considerable effort since its founding in 1983 on a backcross breeding approach to produce blight-resistant hybrids that retain the morphological features of AM chestnut (Hebard, 2012). In recent years, state chapters of TACF have begun their own backcross breeding programs with the intent of generating regionally adapted lines of backcross hybrids for restoration in their own or neighboring states (Fitzsimmons et al., 2012).

In the TACF backcross-breeding program, blight resistance is introduced to AM chestnut via an initial cross with a CH chestnut tree (Burnham et al., 1986). Following the production of such F1 hybrids, AM chestnut characteristics are recovered through a series of backcrosses with AM chestnuts. After each backcross, trees are selected to advance to the next generation based upon assessments of blight-resistance and morphological traits. In third generation backcross trees (BC3s), the American complement of the genome should on average be 94% (15/16th AM chestnut and 1/16th CH chestnut). The theoretical model (based upon at least two independently segregating but incompletely dominant genes) that has formed the basis for the TACF backcross breeding program holds that approximately 12% of backcross trees should harbor intermediate levels of blight resistance (Burnham et al., 1986). Theoretically, full resistance is to be recovered by intercrossing BC3 trees to produce BC3F2 trees, a small percentage of which may be genetically fixed for blight resistance. Selected BC3F2 trees are intended to be used to produce BC3F3 offspring for restoration to natural sites. The theoretical model underpinning this approach is being assessed via developing molecular and classical genetic analyses (Georgi et al., 2015).

It remains important to test the basic hypothesis that both intermediate blight resistance and otherwise AM chestnut morphological and physiological traits can be found in backcross trees originating in this program, particularly in trees emanating from state chapter programs that rely principally upon citizen scientists. Recent analyses have, in fact, failed to reveal the expected level of blight resistance in advanced backcross trees at TACF's main research orchard (Steiner et al., 2016). In this study, we assess BC3 trees originating in the Georgia TACF chapter for blight resistance as well as their retention of AM chestnut morphological characteristics. Using a set of 20 morphological traits, Diskin et al. (2006) demonstrated recovery of AM chestnut traits in a set of advanced backcross trees derived from the TACF breeding program. Our study represents a follow-up to this paper, but one focusing on backcross trees bred using wild AM chestnut trees from Georgia and including blight-resistance as an additional trait. Using indices of blight resistance and species identity derived from morphological traits, we predicted that: (1) AM and CH chestnut lines could be clearly distinguished via a morphological index of species identity, (2) BC3 lines would, on average, tend to show morphology similar to AM chestnuts, and (3) BC3 trees with intermediate blight resistance could be identified that showed an otherwise AM chestnut morphology.

2. Materials and methods

A TACF backcross breeding orchard was established in 2008 at Berry College, Floyd County, GA. This was the first backcross orchard established in Georgia as part of the TACF state chapter program. Third backcross trees were bred in 2007 and 2008 using second backcross (BC2) Graves-source trees (GL56, JN141, and BE50) at TACF's Meadowview, VA research farm as female parents (Table 1). These orchard trees were hand-pollinated using pollen collected from wild AM chestnut trees in Georgia (GAFA1 and GAFA2 from Fannin County, Georgia, and GAHA12 from Harris County). During controlled pollination, burs were bagged to prevent pollen contamination and approximately 10% of the bags were left as unpollinated controls. In the three cross-pollinations, control bags had 0.03 nuts per bur whereas pollinated bags had 0.4 nuts per bur, indicating little pollen contamination (GL56 X GAFA1 line [hereafter BC3-1] = 77 bags/167 nuts, 9 bags/3 nuts, JN141 X GAFA2 line [hereafter BC3-2] = 100 pollinated bags/68 nuts, 10 control bags/0 nuts, and BE50 X GAHA12 line [hereafter BC3-3] = 102 bags/96 nuts, 12 control bags/0 nuts). Control AM (AM-1, AM-2, AM-3) and CH (CH-1, CH-2) chestnut seeds were obtained from J. Hill Craddock (University of Tennessee – Chattanooga, Chattanooga, TN) and Paul Sisco (The American Chestnut Foundation, Asheville, NC), and the F1 line was derived from a wild AM chestnut in Walker County, Georgia (GAWA1) crossed with a CH chestnut (Lindstrom 67; Table 1).

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