

American Chestnut Restoration in New England – Cold Damage as an Added Challenge

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The American chestnut (*Castanea dentata*) was once an ecological and economic keystone species in the eastern United States, and once comprised up to 50% of the basal area in portions of the Appalachian hardwood forest (Braun 1950). Its stature was impressive (some over 120 feet tall) and it grew remarkably fast (up to an inch in diameter per year) (Buttrick 1925, Kuhlman 1978). Its wood was straight grained and extremely rot resistant, which made it valuable for a wide-range of uses (e.g., construction, woodworking, furniture, railroad ties, telephone poles, musical instruments, and mine timbers) (Ronderos 2000). In addition, tannins from wood and bark were integral to a large leather tanning industry (Saucier 1973), and its large, sweet and nutritious nuts were an important source of food for wildlife, livestock and rural human communities (Rice et al. 1980).

About 100 years ago, American chestnut was removed as an overstory species in eastern forests following the accidental introduction of chestnut blight, caused by the fungal pathogen *Cryphonectria parasitica* (Griffin 2000). The blight produces stem cankers that eventually girdle and kill the trunk, but do not harm the root system. As a result of root collar sprouts from stems killed by the blight, scattered American chestnut persist in many portions of its former range, mainly in the forest under-story and with considerably reduced size and reproductive success. Sprouts may reach heights of 50 feet or more before they too are killed by the blight and turn into new root collar sprouts (Paillet 2002).

Because American chestnut played such a vital role in eastern deciduous forests, much effort has been applied to its restoration. The American Chestnut Foundation (TACF) has undertaken various avenues to either increase the blight resistance of American chestnut or reduce the virulence of the blight pathogen. Prominent among TACF's efforts has been the production of blight-resistant chestnut through hybridization with Chinese chestnut (*Castanea mollissima* – to provide the genes for blight resistance) followed by repeated backcrosses with American chestnut (to provide the genes for the stature, form and local adaptation inherent to native chestnuts) to produce B3F3 stock that contains about 94% American chestnut genes but has enhanced blight resistance (Hebard 2012). Up until recently, TACF's breeding efforts were concentrated in the central region of American chestnut's historical range. However, in order to fully restore the species, efforts have been extended to include genes from disparate locations and to evaluate B3F3 stock performance in many varied environments, including historical range limits that provide additional challenges. For example, in the hot and humid South, the health and productivity of American chestnuts are not only threatened by chestnut blight, but also a pathogenic root rot (*Phytophthora cinnamoni*) (Wang et al. 2013). In contrast, in the North, American chestnut appears limited by the species' marginal tolerance to the cold.

Although American chestnut's range extends into northern Vermont and New Hampshire and central Maine, its distribution in these locales is primarily limited to lower elevations near large bodies of water (e.g., the Champlain and Connecticut River valleys and the Atlantic coast; Wang et al. 2013), where winter temperature lows are more moderate and buffered from regional extremes. This range limitation to the warmest microsites suggests that a vulnerability to low temperature damage may be an important selection pressure at American chestnut's northern limit. In 2006 the USDA Forest Service Northern Research Station initiated a partnership with the University of Vermont and TACF to evaluate if marginal cold tolerance constrains chestnut restoration in the North, and if so, to then evaluate genetic selection and silvicultural options for mitigating this constraint.

Our initial research on this topic verified that American chestnut has only marginal cold tolerance in winter relative to two native competitors: northern red oak (*Quercus rubra*) and sugar maple (*Acer saccharum*) (Gurney et al. 2011). Indeed, American chestnut shoots were almost 10°F less cold hardy in mid-winter than the shoots of red oak and sugar maple. Importantly, this difference in hardiness translated into greater winter shoot injury in the field (Figure 1). American chestnut sources experienced terminal shoot mortality rates of between 30 to over 60% depending on the genetic source, whereas oak and maple showed no signs of injury (Gurney et al. 2011). Loss of terminal shoots on the chestnuts released lateral buds and resulted in growing stock with a shrub-like habit not typical of the species (Figure 2).

In addition to shoots, American chestnut nuts are also vulnerable to freeze-induced winter mortality that could reduce the reproductive capacity of the species in the North. Saielli et al. (2012) noted that Chinese chestnut nuts were less cold tolerant than American chestnut nuts and red oak acorns, and that American chestnut sources from a colder



Figure 1. Terminal shoot mortality of an American chestnut sapling in Vermont resulting from winter freezing injury.
Photo credit: Kendra Collins.

hardiness zone were more hardy than nut sources from warm and moderate hardiness zones. This suggested that crosses with Chinese chestnut to improve blight resistance could also result in a greater vulnerability of nuts to winter mortality. In contrast, nut cold hardiness might be bolstered in breeding programs by inclusion of genetic sources from cold locations.

Due to growing evidence that American chestnut restoration in the North may be constrained by freezing injury, in 2009 we established a replicated experiment on the Green Mountain National Forest to evaluate the influence of genetics and silvicultural treatment on American chestnut growth and shoot winter injury (Schaberg et al. 2013, Saielli et al. 2014). We assessed height and diameter growth and shoot winter injury of 13 genetic sources of American chestnut and two sources each of Chinese chestnut and red oak under three silvicultural treatments (open, partial and closed canopy overstories). Early results from this study indicated that seedlings grown under open canopies that provided greater access to light exhibited greater growth than seedlings grown under partial and closed canopies. However, open canopies also resulted in lower winter temperatures that

increased winter injury. Chinese chestnut seedlings had significantly greater growth but experienced greater winter injury than American chestnuts, whereas red oaks generally grew the least and experienced intermediate levels of winter injury. There were also differences in growth and winter injury among American chestnut sources: seedlings from warm and moderate temperature hardiness zones grew more in height and diameter, but experienced greater winter injury than seedlings from a colder zone. Results from this study highlight an apparent tradeoff between growth and cold tolerance at three levels: 1) among species (Chinese versus American chestnut and red oak), 2) among American chestnut sources (hardiness zones), and 3) with differences in the environment (open versus partial and closed canopy silvicultural treatments). In all cases, species, genetic sources within species, and silvicultural treatments associated with greater growth also experienced greater winter shoot mortality. As such, this may provide another example of the broader ecological tradeoff for plants between diverting energy and resources toward growth versus the formation of protective compounds (Harms and Mattson 1992) such as sugars and other cryoprotective substances used to avert freezing injury (Strimbeck et al. 2015).



Figure 2. The shrub-like form of saplings after the winter injury of terminal shoots than then release lateral buds.
Photo credit: Kendra Collins.

Longer-term (seven-year) data from the Green Mountain National Forest study has verified that American chestnut grown in the open exhibit growth that far exceeds that in intermediate or closed canopies (Schaberg et al. unpublished data). However, levels of winter shoot injury among silvicultural treatments over time have been less consistent - with greatest injury in the open treatment in only half of the years assessed. Freezing injury in the field probably reflects interactions among many factors, including the depth and duration of protective snowpack, yearly fluctuations in temperature lows, and the number and intensity of damaging freeze-thaw cycles. Despite consistent losses of shoots to winter injury, after seven years in the field American chestnut in the open treatment have experienced superlative height growth – almost four

(Article continues on next page)

(Chestnut article continued from previous page)



Figure 3. Spring frost injury to American chestnut trees on the Green Mountain National Forest grown in the open.
Photo credit: Paula Murakami

times greater than trees in the partial canopy treatment and over 13 times greater than trees in the closed treatment. Indeed, due to a combination of very low growth and repeated winter shoot injury, trees in the closed canopy treatment have experienced about twice the level of mortality of trees in other treatments (Schaberg et al. unpublished data).

Although the Green Mountain National Forest study was established to examine American chestnut growth and winter shoot injury, it also revealed another vulnerability of American chestnut to the cold – spring frost injury to expanding leaves (Figure 3). In every year since we started assessing frost injury in 2012, we have detected spring frost injury to leaves. The level of injury varies considerably from year to year – from a low of about 5% in 2014 to a high near 100% damage in 2015 (Schaberg et al. unpublished data). Although still under investigation, the level of damage seems dependent on the degree of leaf expansion relative to the timing of frost exposure. In 2015 and other years of severe frost injury, leaf damage was followed by a second flush of leaves – a process that allows for continued photosynthesis during the growing season but which likely depletes reserves of non-structural carbohydrates that otherwise could fuel woody growth.

Although cold damage to leaves, shoots and nuts is currently an added challenge to American chestnut restoration in New England, this limitation may decrease if the climate continues to warm as projected (Kunkel et al. 2013). In the North, the oak-hickory forest type, which once included chestnut, is projected to expand, particularly under high CO₂ emission climate scenarios (Iverson et al. 2008). The North may therefore be one of the most prominent locations for American chestnut restoration because it would allow for species range extension as southern habitats become less hospitable.

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