Project Title: Radial growth analysis of 13 sources of *Castanea dentata* growing in common garden on the Green Mountain National Forest, VT.

Summary: Spring phenology, foliar frost damage, and shoot winter injury were assessed on trees representing 13 American chestnut sources growing at the species' northern range limit in a provenance study on the Green Mountain National Forest (VT). For this grant we conducted annual growth ring analyses to determine the impact of early springs, frost events, winter shoot damage, and local climate on growth of American chestnut sources. American chestnut sources with fast growth and limited winter injury and spring frost damage should be considered in restoration efforts in the northern part of the species' range.

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Duration of project: 12 months

Total amount requested: $3715 to support a dendrochronology technician, supplies and travel-related expenses to collect increment cores from 107 American chestnut trees representing 13 American chestnut sources at our existing provenance study. In addition to collecting cores, the technician will measure annual growth rings, crossdate all cores for accuracy and conduct statistical analyses relating radial growth to phenology, spring leaf frost injury and shoot winter injury, and correlations with temperature and moisture data.

Short and long-term goals:

Our short-term goals were to better understand the direct impact of spring phenology (budbreak and leaf-out), spring frost events, shoot winter injury and local climate drivers on annual growth of American chestnut sources in a provenance study at the northern limit of the species' historical range. Collection of tree increment cores will allow us to fully quantify annual growth (basal area increment, earlywood and latewood area) for the period of our previous data collections (2012-2016) and determine the impact of spring frost events and shoot winter injury on growth. Our long-term goals are to determine which sources are best adapted to local climate/weather events and make recommendations to TACF to help better inform their breeding program decisions and current restoration efforts. Further, with deregulation of a transgenic American chestnut on the horizon, the need to better understand the existing genetic diversity within American chestnut populations is of timely importance. For landscape-scale restoration, a transgenic tree will need to be crossed with American chestnuts with sufficient genetic diversity to overcome inbreeding depression, and an understanding of the trade-offs of utilizing multiple American chestnut genetic sources will better inform that effort.

Narrative:

Introduction:

An important consideration for American chestnut restoration is the careful selection and inclusion of chestnut sources that are appropriately adapted to the broad range of climate regimes experienced throughout the species' native range. This is particularly pertinent at the northern limit of American chestnut's range where warming of annual temperatures has been well-documented. In Vermont, average temperatures have increased 1.5°C since 1941 (Galford et al. 2014). In the northeastern U.S. average annual and winter temperatures have risen by 1.1°C and 2.2°C, respectfully, since 1970 (Hayhoe et al. 2007, USGCRP 2009). Over the last century, surface air temperatures have warmed by 0.08°C/decade with even greater warming occurring over the last three decades of 0.25°C/decade in the northeastern US (Hayhoe et al. 2007). Winter temperatures have shown the greatest increase (0.7°C/decade) compared to summer temperatures (0.12°C/decade) since about 1970 and climate models predict that annual average surface temperatures in northeastern North America will increase 2.9-5.3°C by 2070-2099 (Hayhoe et al. 2007). Indeed, there seems to be no end in sight to rising temperatures in the northeast. For example, summer of 2018 in Burlington, VT broke several temperature records including warmest July (mean temp = 24.4°C, max temp = 30.7°C), the greatest number of days > 29.4°C (21 days), and all-time highest minimum temp (26.7°C) (NWS Burlington). Concurrent with rising temperatures is the occurrence of extreme weather events such as the "polar vortex" during the winter of 2013-2014 that saw an extended period of below average winter temperatures in the northeast (Galford et al. 2014).

In addition to an overall warming climate in the northeast, the arrival of spring is occurring earlier. In Vermont, spring arrival is occurring earlier at a rate of 2-3 days/decade, thus extending the growing season by 3.7 days/decade (Galford et al. 2014). Temperature records from 1916-2003 indicate the advancement of first leaf-out by 0.4 days/decade and between 1970 and 2000, this rate increased to 2.2 days/decade (Hayhoe et al. 2007). Polgar et al. (2014) compared leaf-out phenology data of 43 temperate woody species growing in Concord, MA originally recorded by Henry David Thoreau during the 1850s to current leaf-out observations (2009-2013) in the same area and found that 23 temperate woody species leafed out as much as 18 days earlier than in Thoreau's time. This trend in advancing leaf-out is expected to continue and some models predict that by the end of the century tree leaf-out may occur almost three weeks earlier than present day leaf-out (Hayhoe et al. 2007).

Although early leaf-out may extend the typical growing season, thereby allowing for greater photosynthetic gain, it may also increase the risk of foliar injury and loss of sensitive new foliage when exposed to spring frost events (Augspurger 2009). In 2007, an above-average warm March that caused plants to break dormancy early was followed by a significant frost event in the eastern U.S. (Gu et al. 2008). Temperatures during the freeze event reached as low as -7°C causing significant necrosis to new foliage, shoots and flowers across temperate forests and crops throughout the eastern U.S. (Gu et al. 2008). Similarly, in 2010, the northeastern U.S. experienced an unusually warm spring causing leaf-out to occur 10-14 days earlier than normal. This was followed by a freezing event (May 9-11) that resulted in widespread foliar damage, particularly at higher elevations throughout the region (Hufkens et al. 2012). The occurrence of future spring warming trends and freeze events like those that occurred in 2007 and 2010 are uncertain though predictions suggest they may occur with greater frequency (Inouye 2000, Polgar and Primack 2011).

Considering these changes in climate (early arrival of spring, warmer winter and annual temperatures) it seems prudent that efforts to restore American chestnut should consider the influence of a changing climate when choosing sources best suited for survival, particularly at the northern edge of chestnut's former range. It has been established that American chestnut seed from warmer regions is less cold tolerant than those from colder regions (Saielli et al. 2012). Likewise, American chestnut shoots from warm temperature zones are more susceptible to shoot winter injury than sources from cold temperature zones (Saielli et al. 2014). Through a collaborative effort between the U.S. Forest Service, The American Chestnut Foundation, and The University of Vermont, a provenance study of American chestnut sources representing the species' historical range (NC, VA, MD, PA, NJ, NY, VT, ME) was established in 2009 on the Green Mountain National Forest in central Vermont where spring budbreak, leaf-out, susceptibility to spring foliar frost damage, and shoot winter injury were assessed from 2012-2016.

Previous data that supported study initiation:

Trees were assessed both individually and grouped by temperature zones (warm – KY, MD, NJ, moderate – PA, NY, cold – VT, ME). Over five years, average leaf-out occurred significantly earlier in saplings whose origins are from the warm zone compared to those from cold and moderate zones (P=0.002, Figure 1).

A significant frost event occurred in 2012, 2013 and 2015 which damaged sensitive new foliage (Figure 2). In 2012 an early frost event occurred from April 26 to April 30 with temperatures reaching as low as -4.5°C. Likewise, in 2013 a short-lived, but widespread frost event occurred from May 14-15 with temperatures reaching as low as -2.3°C. In both years, the warm temperature zone sources experienced the greatest amount of damage (2012, P<0.001; 2013, P=0.0174). In 2015, a particularly devastating frost event impacted the foliage of all trees on May 23 when low temperatures reached -3.9°C. Once again, sources from the warm temperature zone as well as the moderate temperature zone suffered the greatest amount of damage compared to cold temperature zone sources (P=0.0113). We propose that spring frosts may result in increased vulnerability of warm temperature zone sources to foliar frost damage.

Figure 1. Julian days (from January 1 to phenology ranking of 3.5 or greater; 2012-2016) to leaf-out among temperatures zones. Means (±1 SE) with different uppercase letters are significantly different.

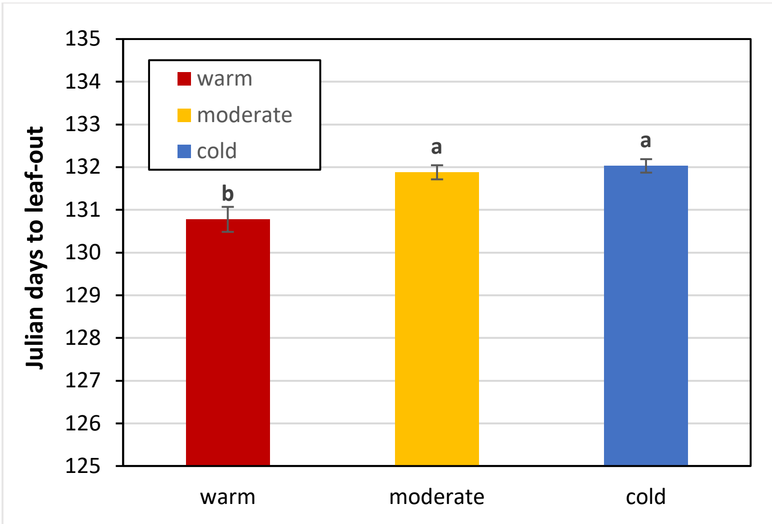
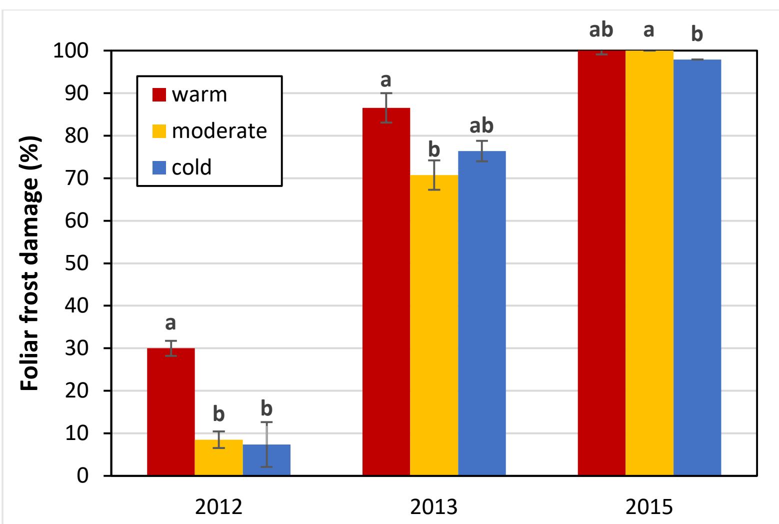
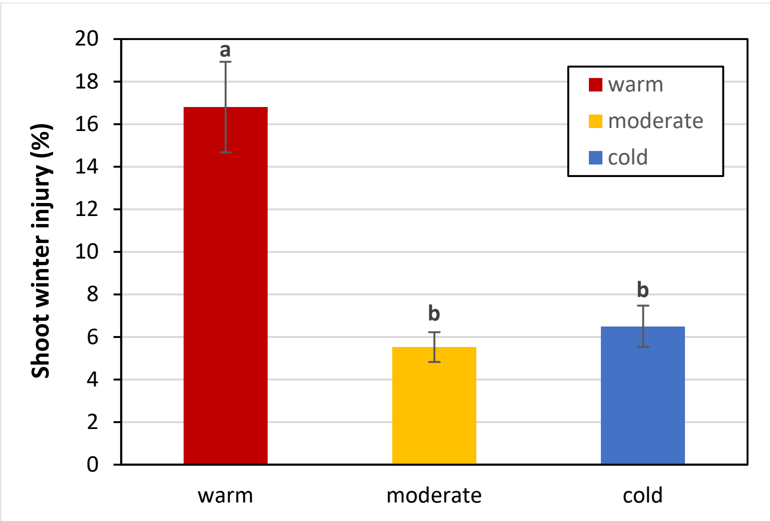


Figure 2. Percent foliar frost damage among temperatures zones in 2012, 2013 and 2015. Means (±1 SE) with different uppercase letters are significantly different. Photo depicts frost damage that occurred in 2015.



Shoot winter injury results were consistent with those determined previously by Saielli et al. (2014) using a subset of the same trees. Shoots from warm temperature zone sources sustained three times as much winter injury compared to moderate temperature zone sources and nearly two and half times more than cold temperature zone sources (*P*<0.001, Figure 3).

Figure 3. Percent shoot winter injury among temperatures zones (2012-2016). Means (±1 SE) with different uppercase letters are significantly different. Photo shows damaged tip of shoot caused by winter injury.



Study overview and methods:

Considering the visual and statistically significant impact of spring foliar frost damage and shoot winter injury among chestnut sources, we investigated the impact on annual tree growth to determine if these events and resulting tissue damage negatively impacted basal annual increment (BAI), earlywood and latewood growth among individual sources and temperature zone groupings. In addition, we compared local climate measures of temperature and precipitation with growth metrics.

Methods:

Trees were cored following standard dendrochronological techniques (Stokes and Smiley 1968). Two xylem increment cores (5 mm) were collected from each tree as low as possible on the trunk and 180° from each other. Following collection, cores were oven-dried, mounted, and sanded with progressively finer grit sandpaper (ranging from 220 to 800 grit, Figure 4). Annual whole-ring increments were visually crossdated using the list method (Yamaguchi 1991), and microscopically measured to 0.001 mm precision using a Velmex sliding stage unit (Velmex Inc., Bloomfield, NY) and MeasureJ2X software (VoorTech Consulting, Holderness, NH). In addition, we measured earlywood and latewood widths. The program COFECHA was utilized to statistically crossdate ring series for the detection and subsequent correction of locally absent and/or false rings (Holmes 1983, Grissino-Mayer 2001).

Figure 4. Increment cores showing growth rings from a single American chestnut tree in our provenance planting.

Statistical analyses:

Raw ring width measurements were averaged per tree followed by mean tree chronology standardization techniques to create ring-width index (RWI) chronologies. Basal area increment (BAI, converts diameter increments (cm/year) into basal area increments (cm^2/year) was calculated from RWI thereby removing age/size related growth trends (West 1980). BAI chronologies were then calculated per source to determine if differences exist using analyses of variance. Detrending methods using appropriate splines allowed us to compare annual total, earlywood and latewood growth to our measures of budbreak, leaf-out, spring foliar frost damage, and shoot winter injury as well as climate variables (monthly maximum temperature, minimum temperature, total precipitation, heating degree days and cooling degree days) obtained from the National Climate Data Center (NOAA National Climate Data Center 2018) during the period 2012-2016.

Results overview:

<u>Phenology</u>

- In three of the five years assessed, sources from the warm temperature zone broke bud earlier than sources from the other temperature zones.
- In four of the five years assessed, sources from the warm temperature zone leafed out earlier than sources from the other temperature zones.

Cold injury

- Spring frost injury to leaves occurred in three of the five years of the study.
- When injury was not severe, injury was greatest for warm temperature zone sources than either moderate and cold (2012) or moderate (2013) temperature zone sources.
- Shoot winter injury was evident every year of the study.
- In three of the five years, sources from the warm temperature zone experienced more shoot winter injury.

Radial growth

- Eight years of growth were recorded from increment cores.
- BAI showed a steady increase over time as trees matured.
- By 2018 (the last ring recorded) trees were growing at an annual rate of approximately 34 cm^2 – a level that far exceeds rates of growth for other hardwoods measured in Vermont.
- Although variable and intermittent, there was a tendency for trees from the moderate temperature zone to exhibit greater growth than trees from one or both of the other temperature zones.

Associations of growth with phenology and cold injury

- For all temperature zones combined, earlier leaf-out was associated with greater growth.
- In contrast, shoot winter injury was associated with reduced growth.

Associations of growth with climate data

- Radial growth was positively correlated with multiple moisture metrics for both the previous and current year of growth.
- In contrast, growth was negatively correlated with temperatures for only the previous December.

Implications for Practice

- Regardless of genetic source, American chestnut had some inherent vulnerability to both winter shoot freezing injury and spring leaf frost damage. The level of susceptibility varied among genetic sources, with sources from warm temperature zones generally having the greatest risk of damage.

- Genetic sources sometimes differed in growth, but differences were modest compared to the high overall growth potential of the species. Growth was generally higher with a lengthened growing season (earlier budbreak and leaf out), but was depressed following elevated shoot winter injury.

- Although considered a modestly drought tolerant species, correlations with climate factors highlight the positive influence on adequate moisture availability on American chestnut growth.
- In general, trees from the moderate temperature zone tended to have low foliar frost and shoot winter injury while also exhibiting exemplary growth. This combination may allow for improved competitive success - even in cold northerly environments like our planting site.

Note: A full description of this study including detailed results and discussion of findings is summarized in the following manuscript that is in internal review prior to submission to the journal *Forest Science*:

Schaberg, P.G., P.F. Murakami, K.M. Collins, C.F. Hansen, G.J. Hawley. Pre-submission Review. Phenology, cold injury and growth of American chestnut in a range-wide provenance test. Forest Science.

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