Progeny Test:

ASSESSING THE INFLUENCE OF GENETICS AND THE ENVIRONMENT ON AMERICAN CHESTNUT AT ITS NORTHERN RANGE LIMIT

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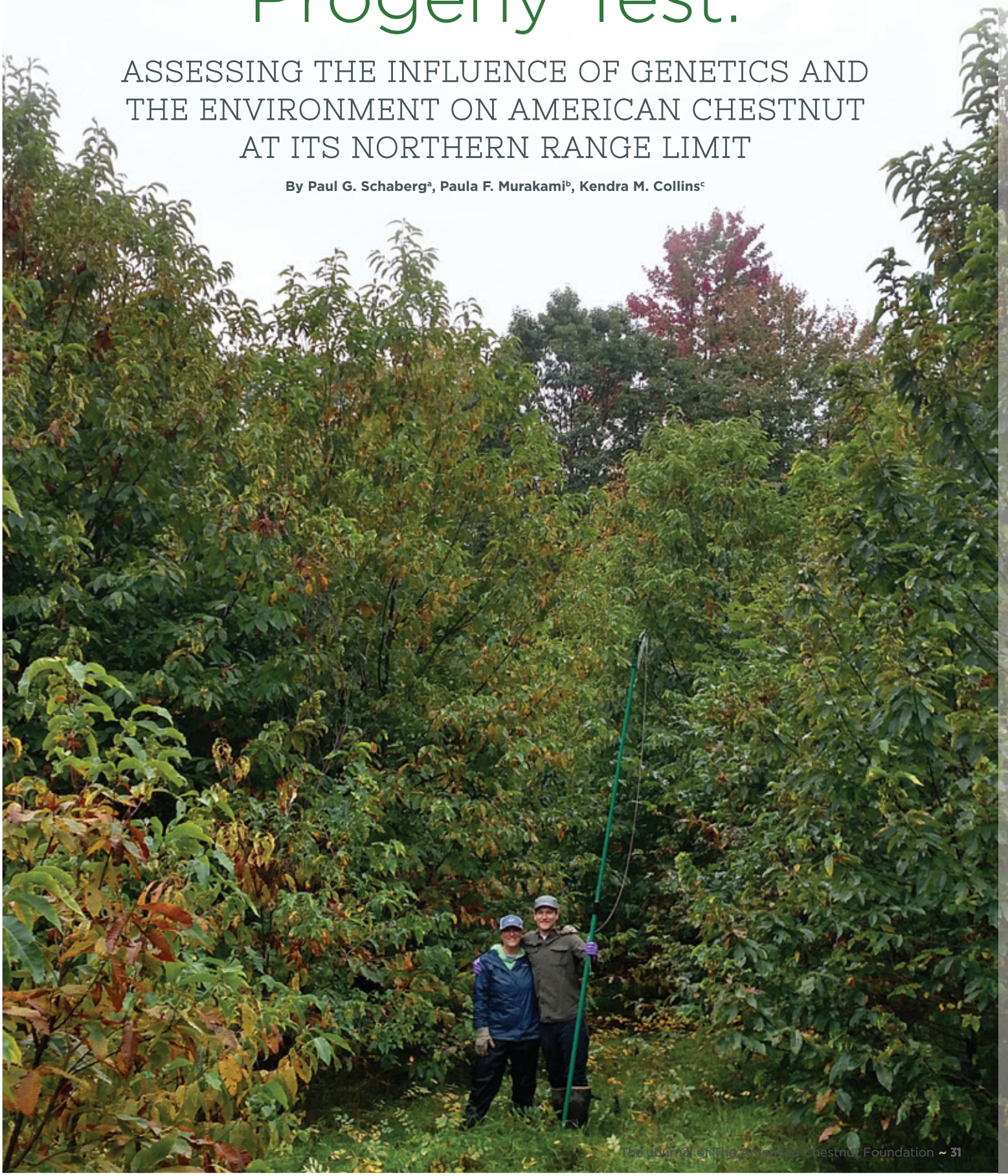
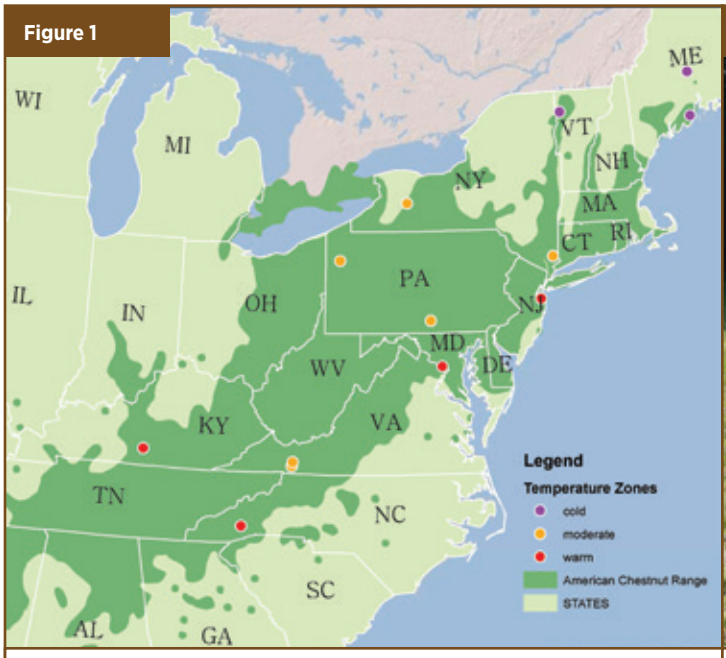


Chestnut blight is the primary factor that constrains American chestnut populations in North America. However, genetic and environmental factors unrelated to blight tolerance also influence chestnut health and productivity. Furthermore, these influences may be particularly important in novel environments, such as a species' range limit. One way to examine the influences of genetics and the environment on tree performance is to grow trees from across a species' range together in a common garden where environmental conditions are more uniform and differences among seed sources can be better attributed to tree genetics. This type of common garden planting is called a provenance test.

In 2009, a collaboration between the USDA Forest Service, TACF and the University of Vermont established what is likely the first and only range-wide provenance test of American chestnut seed sources. This planting, on the Green Mountain National Forest in Vermont, includes trees from 13 seed sources from across the species' range planted within American chestnut's northern limit (**Figures 1** and **2**). Plantation trees were started from nuts graciously provided by TACF chapter volunteers. Over the years, our collaborative group measured springtime bud and leaf phenology, spring leaf frost damage and shoot winter injury (**Figure 3**) – all factors that could influence tree performance and growth at a cold northern location. And in 2018 we used increment cores to remove pencil-thin cylinders of wood from stems to assess radial growth and relate that growth to temperature and moisture measurements over time (**Figures 4** and **5**). These analyses and results were recently compiled in a paper (Schaberg et al. 2022) that used seed source temperature zone as an indicator of broad genetic adaptations to the cold that

Figure 1



Locations and temperature zones of American chestnut sources planted in a provenance study on the Green Mountain National Forest in Vermont.

Figure 2

American chestnut provenance study on the Green Mountain National Forest, VT in 2012 (left, three years after initial planting) and 2019 (right).

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Figure 3

Emerging chestnut leaves (A), foliar frost damage (B) and winter shoot injury (C).

may influence performance in the chilly north. Temperature zones were established using data on the mean minimum winter temperatures over 10-30 years for weather stations nearest seed source locations; these averages were -5 °C and above for the warm temperature zone, -5 to -10 °C for the moderate temperature zone, and below -10 °C for the cold temperature zone.

Figure 4

Collecting a tree core using an increment borer.

Our analyses showed that the timing of bud break and leaf-out varied as much as 19 days across the five years assessed (2012 to 2016) and was earliest in years with warm springs. There were often differences in the timing of leaf development among seed source temperature zones. In general, seed sources from the warm temperature zone broke bud and leafed out earlier than moderate and cold temperature zones.

Frost injury to leaves was evident in three of the five years measured and ranged from moderate (33% of leaves damaged) to severe (100% of leaves injured). Differences in injury among temperature zones was only detected when damage was moderate and then varied depending on the timing of frost occurrence relative to the stage of leaf expansion (leaves were most vulnerable when partially expanded).

Shoot winter injury occurred every year and ranged from low (less than

Figure 5

Mounted and sanded tree cores for microscopic analysis.

5% of shoots) to high levels (about 40% of shoots). In three of the five years assessed, seed sources from the warm temperature zone had the most winter injury.

Although radial growth was low when trees were young, by the time the trees were ten years old, growth was robust. In fact, by the last year that we assessed, growth was greater than any tree species that we have measured in other studies throughout Vermont except one – the notoriously fast growing eastern white pine. However, growth of our American chestnuts showed no signs of plateauing when last measured, so we expect that these chestnuts could exceed white pine productivity over time. Differences in radial growth among the temperature zones were comparatively small, but growth tended to be greatest for warm and moderate zone sources and least for cold zone sources. In general, growth was greater with earlier leaf-out, and less with greater shoot winter injury. The climate factor best associated with growth was moisture – higher moisture availability in the summer, late fall and mid-winter were all associated with greater growth. Even though American chestnut is considered a moderately drought tolerant species, it clearly benefited from adequate moisture availability.

In summary, regardless of the genetic source, American chestnuts were sensitive to cold damage (spring leaf frost damage and shoot winter injury) when planted at its northern range limit. Levels of cold injury often varied amongst genetic sources, with sources from the warm zone generally showing the greatest vulnerability to cold damage. Genetic sources occasionally differed in growth, but these differences were modest compared to the high growth potential of the trees. Growth generally increased with a lengthened growing season (afforded by early leaf-out), but growth was depressed following winter shoot injury and loss. Higher moisture availability across multiple seasons was the climate parameter best associated with good growth. Warm temperature zone sources were most likely to leaf-out early and grow well but were the sources most likely to also experience winter shoot injury. Cold temperature zone sources experienced little shoot winter injury, but often experienced only modest growth. Moderate temperature zone sources tended to have low foliar frost and shoot winter injury while also experiencing high growth even at this northern site – a potentially winning combination for chestnut growing at the northern limit of its historical range.

REFERENCE

Schaberg, P.G., P.F. Murakami, K.M. Collins, C.F. Hansen, G.J. Hawley. 2022. Phenology, cold injury and growth of American chestnut in a range-wide provenance test. Forest Ecology and Management. 513:120178 https://doi.org/10.1016/j.foreco.2022.120178