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REGIONAL ADAPTATION IN AMERICAN CHESTNUT

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Abstract: Conservation of forest genetic resources, such as restoration of American chestnut, requires knowledge of genetic variation patterns in adaptive, non-neutral alleles. Almost no such information is available for American chestnut, but there is information available from other forest tree species including species that are sympatric with chestnut. Some of that information is summarized in this paper, and the adaptive significance of several growth and physiological characteristics is discussed. Most tree species exhibit "racial" patterns of genetic variation that parallel geographic gradients in climate. Wild populations that have survived in a locality for many generations have a genetic identity of place that reflects a history of natural selection and adaptation. Judging from genetic variation patterns in sympatric species, American chestnut populations are probably genetically distinct in important and somewhat predictable ways. American chestnut breeding and restoration projects should be guided by this knowledge.

Keywords: genetic / geographic / racial / variation / selection / adaptation / growth rate / cold tolerance / phenology

INTRODUCTION

With new technologies for controlling chestnut blight on the horizon, we are beginning to contemplate the restoration of American chestnut to something like its former importance in our forests. The creation of genetically resistant trees through breeding or genetic engineering is especially promising as a foundation for restoration efforts. However, blight-resistant alleles can be introduced to (or found in) only a tiny fraction of the chestnut trees that still survive, so any restoration program that employs blight-resistant trees will inevitably force the species through a genetic "bottleneck" with the danger that important alleles may inadvertently be lost. Like other plant species, especially those with large natural distributions, American chestnut undoubtedly contains a great deal of genetic variation. This diversity should be protected (Irwin 2003), and indeed it should be exploited if possible in the restoration process itself. But to do so will require an understanding of how genetic variation is structured within the species.

Information about range-wide genetic variation in American chestnut is limited to studies of allozymes and DNA markers of unknown and probably neutral adaptive significance (Huang et al. 1998, Kubisiak and Roberds 2003). These studies revealed that differences among populations account for only 5 to 10 percent of the total genetic variation measured, results that closely resemble the findings of other studies of neutral alleles in species that are similar to American chestnut in mating system, longevity, population size and density, and other characteristics that affect gene flow (Hamrick and Godt 1990). This is useful knowledge – for example, it tells us that gene flow among populations has been relatively strong within this species – but it tells us virtually nothing about the structure of genetic variation in alleles subjected to the pressures of natural selection. Patterns of variation in adaptively neutral genetic markers may bear little relationship to patterns of variation in adaptively relevant alleles, whose variation patterns may also differ from one another according to what kind of characteristics they control (Morgenstern 1996). Genetic variation in "fitness" characteristics (in the terminology of Darwinian theory), especially those responding to regional selection gradients such as climate, is highly relevant to conservation or restoration efforts undertaken at a regional or range-wide scale.

Unfortunately, we know almost nothing about genetic variation in fitness characteristics within American chestnut. There is, however, a fairly substantial body of such information from studies of other tree species, and this knowledge can be used to inform future decisions about American chestnut. This literature comes from replicated, "provenance" tests of progeny from natural populations grown in a common environment. Such experiments, if properly designed, permit the researcher to apply the methods of quantitative genetics to measure and test contributions of genetic variation to phenotypic variation, even without knowing the underlying DNA structure or mode of gene action. It is even possible to partition the relative contributions of among- versus within-population genetic variance just as population geneticists do when working directly with DNA markers. In this paper I provide some examples of such research on eastern forest tree species. Although we cannot know for certain, American chestnut would probably exhibit similar genetic variation over similar environmental gradients if it were studied in the same way.

EXAMPLES OF REGIONAL VARIATION IN ADAPTIVE CHARACTERISTICS

Bud-Burst Timing in Eastern American Species

Deciduous trees can take advantage of abundant moisture and shade-free conditions (in the case of plants growing below the forest canopy) by initiating growth early in the spring, but early growth initiation increases the risk of frost injury to young leaves. Thus, genetic control of bud-burst timing is probably under strong selective pressure for optimality in any given environment. It is typically the case in common garden tests that populations from colder (more northern or higher elevation) environments burst bud earlier in the spring. Bud burst in trees is usually cued by rising temperature, and populations from colder climates are adapted to grow (and begin growing) under cooler temperatures. When the geographic pattern of bud-burst timing is the opposite (*e.g.*, southern populations earlier in common gardens), as has been recorded in a few species, it is likely attributable to a different environmental cue for growth (photoperiod) rather than a fundamental difference in the way the plant has adapted to environmental gradients (Steiner 1979a). Of course, in nature, plants in warmer climates always begin growing before plants in colder climates. But if the onset of spring is heralded by the appearance of leaves on trees, spring would be even more delayed in the north if all populations of a species required equally warm temperatures for growth.

Steiner (1975 and 1979b) described geographic patterns of genetic variation in bud-burst timing in three species that are broadly sympatric with American chestnut: yellow birch, eastern white pine, and Virginia pine. The first two species are sympatric with chestnut throughout most of its Appalachian distribution, but they also occur widely in the Lake States and southeastern Canada. Virginia pine occurs naturally only from central Pennsylvania southward, but the whole of its distribution is very similar to the southern half of American chestnut's. All three species showed the typical north-early / south-late pattern of variation in bud-burst timing in common-garden tests. Also, all three exhibited genetic variation within their area of sympatry with chestnut, with clinal gradients statistically detectable over minimum distances of 100 to 300 km. A partial exception was yellow birch, which showed no clear latitudinal gradient in bud-burst timing in from Pennsylvania southward (roughly the southern half of the American chestnut range). Steiner (1975) also found that population variation in time of flowering (pollen release) generally corresponded with population variation in bud-burst timing. This may not be the case with the late-flowering American chestnut, whose habit of flowering in mid-summer may not be so closely linked in both a physiological and genetic sense with its phenology of vegetative growth.

Broad climatic gradients in genetic variation are almost always somewhat muddled by populations that do not fit the trend, and this was true in Steiner's studies. Elevations of origin differed greatly for the Appalachian populations of all three species, and it is reasonable to suppose that adaptation to elevation might have explained locally “anomalous” populations. However, there was no detectable relationship between elevation and bud-burst timing, at least after accounting for latitude (the more southern populations tended to occur at higher elevations). A better test of the effect of elevation of origin on genetic variation would be to deliberately sample a number of populations along an elevational transect up and down a single mountain. I am not aware of any such study in the Appalachians, but McGee (1974) studied four populations of northern red oak collected from different elevations “within 100 km of Asheville, North Carolina” and found a possible elevational effect on genetic differentiation in bud-burst timing in that species. From these studies we can predict that American chestnut seed that is moved to environments that are warmer or colder than the native environment will likely be somewhat “off” in the timing of new growth in the spring, growth cessation in late summer, and perhaps flowering.

Genetic Variation in Cold Tolerance in Two Species

The process of acclimation to cold in woody plants begins after the cessation of growth and is triggered by diminishing day length. Acclimation deepens as plants experience increasingly colder temperatures, reaching a maximum when temperatures are coldest, in January or February. This process has a metabolic cost, and plants that develop greater levels of cold tolerance presumably pay a price for that advantage. The benefit to a plant of adequate cold tolerance, and the cost of its absence, is clear and direct. Not surprisingly, geographic patterns of genetic variation in ability to acclimate to low temperature tend to look very much like January low-temperature isotherms on a map.

Williams (1984) described a nicely done study of genetic variation in cold tolerance within green ash. Green ash has a native range that extends far beyond the region in which American chestnut grows, but Williams’ study included seven populations of green ash from the area of overlap with our species of interest. These populations differed in the expected fashion: the rapidity of acclimation and depth of mid-winter cold tolerance were greatest in New York and Pennsylvania populations, intermediate in central Virginia populations, and least in eastern Tennessee populations. These represented nearly half of the total range of variation in mid-winter cold tolerance levels for all green ash populations studied (which included Manitoba and South Dakota provenances, but none more southern than Tennessee). Williams also found significant *within*-population genetic variation in cold tolerance – except in populations near the northern limit of the range, where the species is presumably at its limit of adaptation to cold.

The results described above were obtained under controlled, laboratory conditions using twigs taken from trees grown out-of-doors. Williams (1984) also measured actual winter injury over a three-year period in nine replicate plantings of a green ash provenance test in the upper Midwest and Northeast. As one would expect, trees that had originated from progressively warmer climates had progressively more severe winter injury. Put another way, the fraction of trees that escaped winter injury diminished as population origin went from north to south. Interestingly, Williams found that some trees escaped injury when growing in environments colder than where they originated, sometimes even much colder, but moving a population to colder environments was *always* accompanied by an increase in the risk of winter injury as measured by percentage of trees injured.

The mating systems, life history characteristics, and population structure of American chestnut and many other forest tree species tend to promote gene flow, which acts to minimize genetic differentiation between nearby populations (Loveless and Hamrick 1984). There are very few known instances of clearly adaptive genetic differentiation in temperate forest trees occurring over distances of a few kilometers or less. One example is that described by Berrang and Steiner (1986) and Steiner and Berrang (1990) for cold tolerance variation in pitch pine. Pitch pine and American chestnut have almost identical distributions and often co-occur on the same sites. Near State College, Pennsylvania, pitch pine is common within an area called the "Barrens," which often (and during any month of the year) has substantially lower nighttime temperatures than the surrounding countryside. Pitch pine also grows in areas near the Barrens that have locally normal temperatures. These authors compared the development of cold tolerance in dormant seedlings raised under controlled conditions but originating from Barrens and non-Barrens trees. Compared to the neighboring population on normal sites, Barrens seedlings acclimated more rapidly in the fall, achieved greater levels of cold tolerance in mid-winter, and de-acclimated more slowly in the spring. Evidently, differences in selection pressure over the distances separating these populations (about 8 km) have been strong enough to create genetically distinct populations.

Genetic Variation in Height Growth Rate in Northern Red Oak

Everyone knows that plant growth is greatly influenced by environmental conditions, but growth rate is always under genetic control, as well. Growth rate is fundamentally important to plant fitness, though rapid growth is not always (or even usually) the best strategy for ecological success. As Grime (1979) has pointed out, there is essentially a "zero-sum" relationship between plant investment in growth, reproduction, and defense or toleration of stress – the benefits vary according to circumstances, but the costs are always there, and a plant cannot afford to excel at everything. In range-wide provenance tests of species whose distributions span warm/cold or wet/dry climatic gradients, it is typically the case that populations from warmer or moister environments are genetically capable of faster growth than is found in their poor relations living at the limits of hospitable conditions (Wright 1976). This pattern probably arises because competition is a stronger selective force in the milder climates (favoring rapid growth), and stress is a stronger force in the harsher environments, where investment in cold tolerance or drought tolerance or avoidance (always at some metabolic cost) is more advantageous than producing more foliage.

However, this generalization applies most particularly to species that inhabit a truly wide range of environments. Through the smaller and more homogenous region occupied by American chestnut, patterns of genetic variation in growth rate have typically had a strongly "random" character in provenance tests, usually defying simple geographic description. The occurrence of apparently random variation does not necessarily mean that the controlling alleles are selectively neutral, but it may mean that the forces that favor or disfavor rapid growth are more local than regional in occurrence.

Northern red oak occupies the same region as American chestnut plus a little more, occurring from the Gulf Coastal Plain (but not Florida) to eastern Kansas and southern Ontario. Several genetic tests of this species (summarized and reanalyzed by Steiner 1998) were designed to permit the partitioning of genetic variation into "local" and "regional" components. In tests that included populations no more than a few hundred kilometers apart, virtually all of the genetic variation in growth rate occurred *within* populations (populations differed little or not at all). However, even in a "range-wide" test (with distances between populations of up to 2000 km), within-population genetic variance still accounted for 64 percent of total genetic variance in growth rate. Furthermore, variation *among* northern red oak populations in growth rate, when it occurs, does not show a clear and straightforward geographic pattern (Steiner 1998). Steiner argued that selective forces acting on growth rate in northern red oak may plausibly operate on a very local, "microsite" scale in stands of this species. (Forest soils are typically very heterogeneous *vis-à-vis* growth potential in northern red oak.) If American chestnut has a similar pattern of genetic variation, then a typical population may contain most of the genetic variation that occurs within the species in alleles controlling growth rate. However, the possibility of important, inter-population variation should not be ignored.

CONCLUSIONS

We know almost nothing about genetic variation in characteristics of American chestnut that play a role in adaptation to the environment. However, most tree species exhibit “racial” patterns of genetic variation that parallel geographic gradients in climate. Wild populations that have survived in a locality for many generations have a genetic identity of place that reflects a history of natural selection and adaptation. When environmental differences are large enough, natural selection may favor genetic differentiation even on a rather local scale. Studies of other species have consistently revealed genetic variation – within the species’ region of sympatry with American chestnut – in adaptively important characteristics such as growth rate, phenology, and cold tolerance. Disrupting these variation patterns by careless human meddling can result in trees that are unsuited to their environments in subtle but perhaps important ways, particularly considering that trees with normal lifespans must survive many decades of environmental vicissitude. In the absence of evidence to the contrary, we should expect that American chestnut populations also differ genetically from one another in similar ways. This knowledge should guide breeding and restoration projects in American chestnut. Restoration projects should seek to preserve as much natural genetic variation as possible within American chestnut, and blight-resistant trees used to restore wild populations should be derived from locally or regionally native American chestnut trees.

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