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FROM THE EDITOR

It's spring at last! For those of us who experienced a long, cold, harsh winter, it is most welcome. For The American Chestnut Foundation, nearing the production of our first blight resistant seed is like the slow change to warmer temperatures. It marks the beginning of a longer cycle, putting the American chestnut back into the forest. There are still many questions that need to be addressed and much work to be done before we reach our goal, the restoration of the American chestnut to its natural habitat.

TACF's Vice President of Science, Hugh Irwin, begins this issue of *The Journal* with perhaps one of the most fundamental questions we facewhat constitutes successful species recovery1 He notes that our work will be to capture the highest level of genetic diversity. In their wide-ranging study of22 distinct American chestnut populations, Drs. Thomas Kubisiak and James Roberds begin to look at just that-how many breeding locations might be needed to capture the highest possible genetic variation. Drs. Thomas Kubisiak and Steven Patch, with Amelia Nutter, also provide important information about planting small American chestnut seedlings in the forest. They find that chestnut seedlings can be established in a forest environment with minimum care and follow-up.

For those of us who enjoy the warmer weather with a hike in the forest, Gregory Weaver provides a guide to hunting large chestnut trunks, remnants of the tree's former glory, in the Southern Appalachian forests. John Alger's discussion of the development of chestnut logging looks at the various uses of chestnut wood and what the forest itself can tell us about the logging industry.

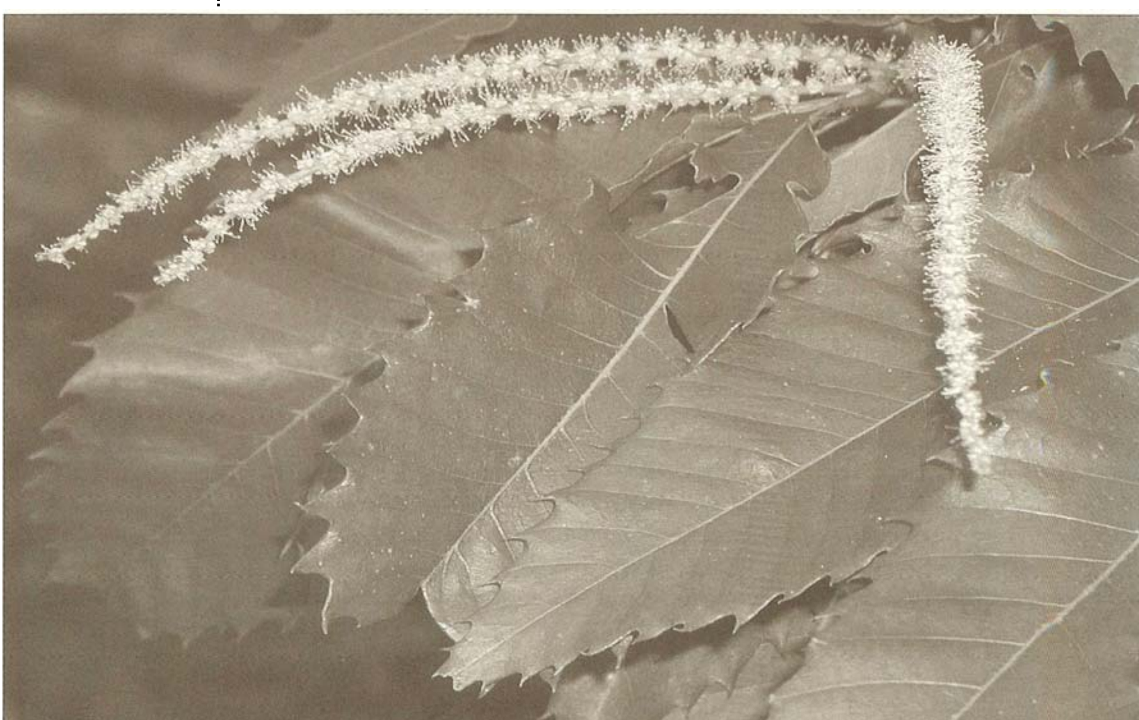
This issue of *The Journal* also presents two personal histories. TACF Staff Pathologist, Dr. Fred Hebard, provides us with a glimpse of Meadowview, VA in 1935 through the photos and memories of his neighbor, Havard Shortt. In addition, Henry Henkel Rhyne, Sr. provides us with his poignant memory about learning how to collect chestnuts the right way, something that future generations will again, hopefully, learn to do.

THE ROAD TO AMERICAN CHESTNUT RESTORATION

Hugh Irwin, TACF Vice President for Science

American chestnut still blooms naturally in areas of the eastern forest. This tree in Nantahala National Forest in North Carolina had prolific blooms

The American Chestnut Foundation has taken on the goal of "restoring the American chestnut to eastern forests through a scientific breeding program and cooperative research." This is an ambitious mission. Breeding a good chestnut timber tree or a chestnut with nuts like the American chestnut would be laudable goals in themselves. However, TACF has gone beyond these limited aspirations to focus on nothing less than the restoration of a species to its natural range. This mission has implications that may not be immediately obvious, and it raises questions that



need to be seriously engaged if the mission is to be carried out successfully. TACF's Science Cabinet is currently grappling with some of these difficult issues in order to design testing and deployment strategies for the future.

BIOLOGICAL AND ECOLOGICAL IMPLICATIONS OF SPECIES RESTORATION

American chestnut is in a somewhat unique situation among candidates for species restoration. It is difficult to deny that the tree species is in need of restoration, but there are vast numbers of individuals still alive. This causes a dilemma in how we view and approach restoration of American chestnut because it presents issues that both affirm and challenge the existing models.

Most species in need of restoration have a very limited number of individuals or populations remaining. In fact, a common method of assessing the threat to species viability is global ranking which measures the number of remaining individuals and populations. The Nature Conservancy and State Natural Heritage Programs developed one system that ranks species from G-1 "critically imperiled" to G-5 "demonstrably secure," based fundamentally on the assumption that as individuals and populations decrease a species' vulnerability to extinction increases. Species federally listed as endangered or threatened are generally considered critically imperiled and fall within the G-1 ranking in this system. (Elzinga, Salser, and Willoughby 1998).

American chestnut, is ranked G-4 "widespread, abundant, and apparently secure globally." It fits easily within the requirements of 10,000+ individuals and 101+ occurrences for G-4. There are probably millions of sprouts still remaining within the original range of American chestnut. It receives a G-4 rather than a G-5 because obviously "some cause for long-term concern exists."

TACF's backcross breeding program incorporates "mother trees" that are found flowering in the wild. Unless and until means are found to recruit the large population of American chestnut sprouts into the breeding program, these mother trees become the founding population of the restoration effort, and their small numbers, measured currently at about 375 and anticipated to approach 500 as the regional adaptability breeding programs mature (Hebard 2002), could create a bottleneck for the species.

The diversity of the resistance incorporated into restoration trees is also a relevant concern. Dr. Albert Ellingboe (2001), plant pathologist and Science Director for TACF, points out that *Cryphonectria parasitica,* the fungus responsible for chestnut blight is likely to evolve to overcome resistance unless resistance itself has sufficient variability. Incorporating more sources of resistance is important in order to assimilate variability of resistance genes.

American chestnut is also unique in its adaptations to survive as an understory plant. Dr. Frederick Paillet makes an excellent case that American chestnut is supremely adapted to survive in the shade of the forest waiting for an opportunity to take advantage of light gaps (Paillet 2002). American chestnut is also well known as a prolific sprouter. As long as it receives a minimum amount of light, it can frequently continue to survive in the understory, sprouting a new stem when the blight: kills its main stem. This remarkable biology has implications for species recovery of American chestnut. First, we can anticipate the species remaining in the wild for a long period of time. As humans we may want the recovery to happen quickly and, ecologically, the recovery may be highly desirable for the benefits to other species; however, species recovery may not be an urgently required task. Since the species is surviving in the wild, we have the time and the obligation to make sure the restoration is done carefully and well. This is in contrast to many imperiled species where recovery is an emergency operation. Species recovery would dictate that in addition to developing a resistant American chestnut, that the wild reserve of American chestnut trees be monitored and conserved. Conserving these trees could also help uncover more American chestnut trees with low levels of blight resistance and could lead to development of hypo virulence in the blight fungus. It is a backup in our restoration efforts, a genetic reservoir that can be drawn on in the future as the breeding and restoration effort continues.

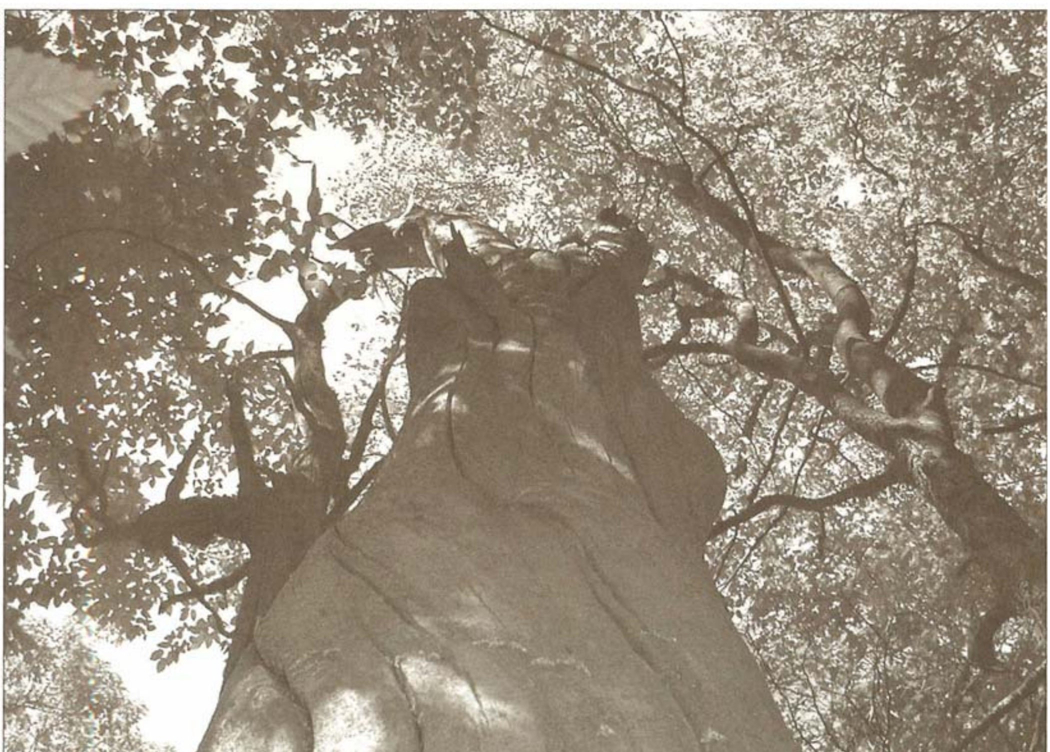
WHAT WOULD SPECIES RECOVERY MEAN

The biology of the species also poses questions that need to be answered in the course of TACF's efforts. Since we are involved in species recovery, but the main TACF breeding effort involves backcross breeding with Asiatic species, what constitutes sufficient American backcross to be considered "species" recovery as opposed to a successful hybrid? There is no clear precedent to answer this question. Our society at large has a stake in this species restoration and will undoubtedly weigh in on the question when deployment is near. TACF's third backcross, third intercross trees (BC3F3) will have approximately 90 percent American chestnut genes. These trees likely will exhibit many American characteristics, but also are likely to retain some Asiatic characteristics. While this may satisfy the requirements of restoration for some, for a large number of scientists and the public, it may not satisfy their idea of species restoration.

Another way to approach this issue is to test trees for their phenotype. TACF will be testing trees for both blight resistance and American characteristics. However, this is inherently a long-term project. American chestnut is not like a grain crop whose phenotype is expressed in one growing season. It will take perhaps a century to tell if trees truly exhibit

Blight usually kills american chestnut trees before they reach maturity. This American Chestnut tree in the mountains of North carolina survived to a larger size than most.

HUGH IRWIN 2001



American chestnut characteristics (Hebard 2002). Arnold (1995) points out another consideration for breeding efforts - the dangers of unconscious and incidental selection in captive populations that can shift the characteristics of the captive population. "Hereditary wildness," an ensemble of characteristics, that may be difficult to control or predict short of reintroduction in the wild, may also be difficult to maintain in breeding populations. Inbreeding depression is also expected in breeding situations, particularly small populations. Minimizing these negative effects while maximizing the contribution of genetic variability from wild American chestnut individuals will be an ongoing challenge for TACF's breeding program.

Fidelity of American characteristics that are sufficient to claim species recovery is likely to require checks of numerous and somewhat subtle biological and ecological characteristics. For instance, do restoration trees exhibit the American chestnut's ability to survive for long periods as an understory tree? Determining whether these types of characteristics are maintained in restoration trees will require a careful and long-term testing program. Arnold (1995) advocates an approach to monitoring traits for genetic variation in captive populations tailored to the systematics and ecology of the species, which may be useful in establishing the conformity of American chestnut characteristics in TACF's breeding program. Ultimately, a "restoration" tree must come out of a testing program that thoroughly establishes the fidelity of the breeding program in capturing what scientists and the interested public agree is American chestnut.

HOW MUCH OF THE GENETIC RESERVE SHOULD BE CAPTURED

The remaining American chestnut trees represent a tremendous genetic reserve that embodies a large part of the original genetic diversity of the species. With an original range stretching from Alabama to Maine, an elevation range from less than 1,000 feet to over 5,000 feet, a habitat adaptation from moist coves to dry ridges - this represents a tremendous ecological range and a great genetic diversity. Capturing the diversity and occurrence of rare genes represented in the remaining chestnut trees should be one of the criteria for species restoration.

TACF's regional breeding program seeks to satisfy this requirement through regionally oriented programs that bring local trees and local adaptation into the backcross breeding program. Several regional breeding programs are already in existence. But where do the needs of incorporating rare genes and maximum genetic variability and local adaptation intersect with feasibility? Again, it would be ideal to breed a recovery tree for a local area, for example a particular elevation range on a particular mountain, and incorporate all the remaining trees in the area in a breeding program tor the area. From a logistical standpoint, this would be impractical. Relying on a few dozen trees that are found naturally blooming in the wild, on the other hand, could represent a bottleneck for species recovery. This bottleneck can have two effects: (1) eliminating rare genes that may be important for future disease and survival challenges, and (2) reducing the amount of variability for specific characteristics (Frankel and Soule 1981). The second effect is more easily solved by effective breeding strategy than recovery of rare genes. Rare genes have a high probability of being lost during bottlenecks. Species with high interpopulation divergence, which is the case for American chestnut, require an extensive population sampling to capture the genetic variation for breeding programs (Godt and Hamrick 2001). There are methods to estimate the sample size needed to capture rare genes, but we do not know at this stage what rare genes could be important, the rate at which they occur, and how well the present programs capture these genes.

Another consideration is maintaining "adaptive complexes" of genes. If trees are crossed from too large a range, we could see outcrossing depression, in which adaptive complexes of genes are disrupted. This may be a critical consideration that has not yet been adequately addressed in our regional breeding programs.

Soule (1987) proposes that the ultimate goal of conservation strategies should be the survival and recovery of populations large enough to allow evolution through natural selection to occur. An intermediate goal is to recover larger population sizes that retain as much of the genetic variation of the species as possible and so maximize options for the future (Foose 1991). It is not yet clear what minimum founding population size is desirable tor chestnut restoration. It is also important to realize that minimum populations should be recognized as minimums. "More is always better and safer" (Foose, Boer, Seal, and Lande 1995).

Balancing the recovery of genetic diversity tor the species with the practicalities of a breeding program is a necessary charge of species restoration. Several possible solutions suggest themselves. If wild chestnut trees remain in our forests for the long-term, incorporating local diversity into the restoration tree can be spread out over decades or centuries. For some areas incorporating local diversity may take on higher importance. Restoration in natural areas, for example national parks and other areas of our public lands, may justify a more intense breeding effort to incorporate local diversity. Landowners or local communities may want to incorporate their local diversity into the restoration tree they use on their lands. Advances in genetic mapping could also make the selection of founder trees to maximize genetic diversity more accurate. All of these efforts would serve to broaden the base of the genetic restoration of the species.

Tools that would greatly aid recovery of the species would include advances in hypovirulence knowledge and techniques and in other biological controls of chestnut blight. In addition, forest management techniques have been found effective in bringing chestnut to reproductive age on mesic and intermediate sites (Griffin 2000). If wild trees can be enabled through a combination of these techniques to survive to flowering and reproductive age, new recovery strategies would be opened up. More native trees could be incorporated into the breeding program and natural introgression of resistance into native populations could occur. In addition achieving perfect blight resistance might become less of an imperative. There are significant barriers to implementing these strategies. However, if American chestnut restoration is seen as the long-term project it must be, these barriers will likely be addressed by advancing knowledge.

LOOKING TOWARD RESTORATION

By almost any realistic human time frame, complete restoration of American chestnut is a grand and long-range goal. Testing alone will take decades to be performed adequately. Realizing a restoration tree or trees is likely even further away. Deployment throughout the historical range is a complex task that faces scientific, social, and logistical hurtles. The length of time needed should not be discouraging. Within the time frame of the species, which has been in existence for millions of years, this period will be a brief interval.

Restoration of the species deserves the care and deliberate action that will take not only skill and knowledge but also time. The road to restoration will be marked by milestones that should be celebrated as significant markers on the way toward the ultimate goal. Many of these milestones can be anticipated and should form the goals of The American Chestnut Foundation's work plan for the future. Only by assessing the full scope of our endeavor and establishing a framework for addressing the issues and questions that need to be addressed can we move steadily toward our ultimate goal of restoring American chestnut throughout its range.

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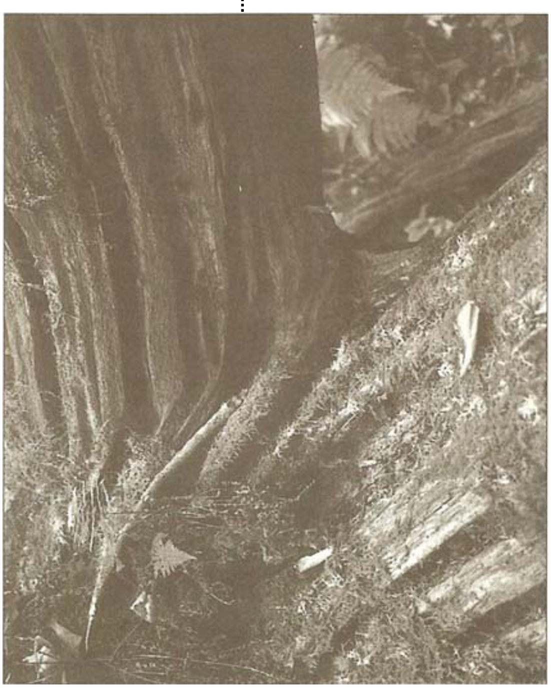
CHESTNUT GHOSTS:

Remnants of the Primeval American Chestnut Forest of the Southern Appalachians

Gregory R. Weaver

Today, many species of trees reach record size in the Southern Appalachian Mountains. Growing conditions are nearly ideal with abundant rainfall, a moderate climate, and fertile soil. The American chestnut was an important part of the Southern Appalachian ecosystem until its demise in the last century. Because of the rot resistance of chestnut wood and the prior sheer abundance of the tree, there are many remaining stumps, standing trunks and logs that help us understand how magnificent the chestnut forest was and how devastating is the loss of this tree. Knowledge of where chestnut formerly thrived is important to plan for restoration of the tree and to direct efforts where they are most likely to be successful.

Long, deep longitudinal furrows in the reddish wood identify this log as American Chestnut



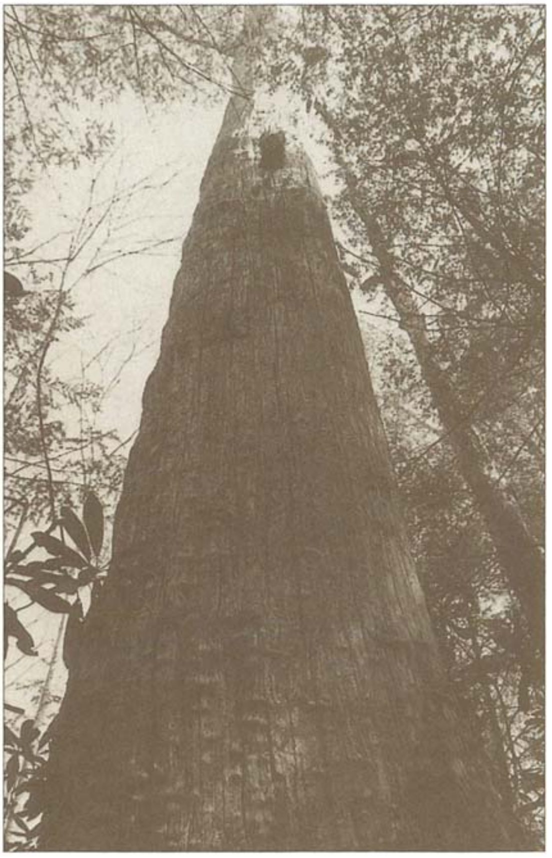
Ashe's 1911 *Chestnut in Tennessee* says that American chestnut was most plentiful in the Unaka and Smoky Mountains of eastern Tennessee, but also common on the Cumberland Plateau and the Highland Rim. Preferred sites were elevated benches of north and west slopes and crests of northern spurs from 1800 - 3500 feet in elevation. American chestnut grew in pure stands of 100 acres. Chestnut was less important in the central basin around Nashville and in the western part of the state.

The American chestnut tree grew to immense size. Bolgiano refers to 33 toot circumference American chestnut trees in

Tennessee and North Carolina. An article in the Scottsville, Kentucky *Argus* in 1876 told of a 9 foot diameter, 230 year old chestnut tree that was split into 700 rails. On its membership brochure, The American Chestnut Foundation displays a photograph of massive American chestnuts taken in western North Carolina about 100 years ago.

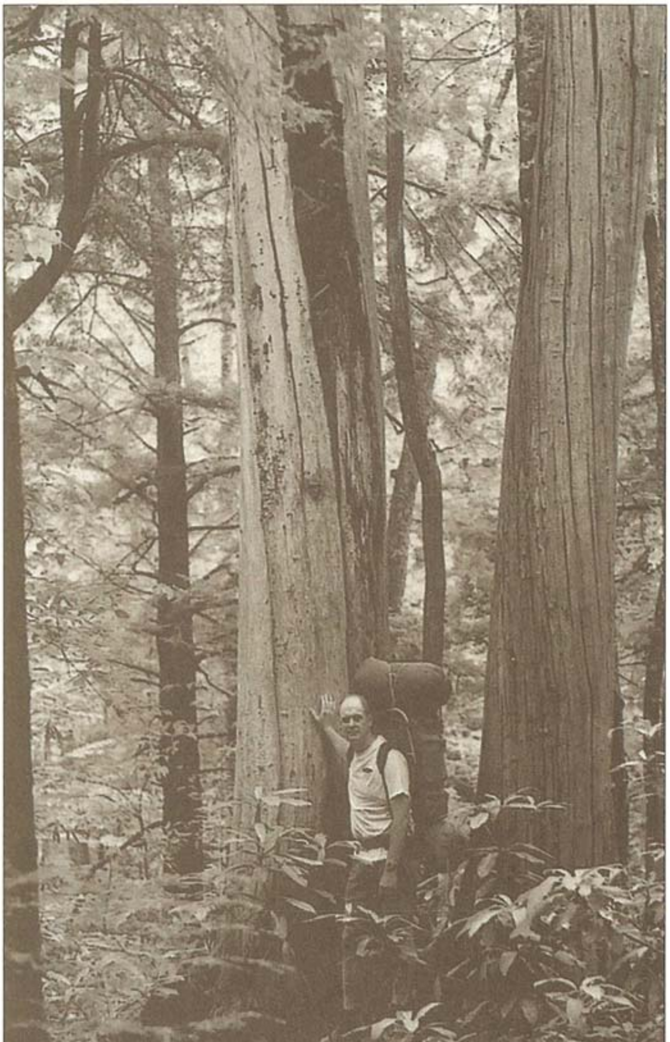
Tree cover has increased in Tennessee over the latter part of the twentieth century. Many of these second growth forests are visually attractive and have a great diversity of flora and fauna. However, to find the best remnants of the chestnut forest, it is necessary to go to remaining old growth forests (Table 1). Most of the old growth forests in Tennessee are accessible to the public. An unfortunate exception is Savage Gulf State Natural Area whose reportedly magnificent mixed mesophytic forest is closed to visitation.

The largest old growth forest in Tennessee is in the Great Smoky Mountains National Parle. The park's 540,000 acres straddle the Tennessee-North Carolina border. Estimates of the amount of old growth forest range between twenty and sixty percent of the park's acreage, with most recent estimates closer to the lower figure.



Large chestnut ghost. Gregory Bald Trail, Great Smoky Mountains National Park

The Great Smoky Mountains Natural History Association has published a map showing the areas of old growth forest in the park. Look for the chestnut logs and stumps in these forests at mid elevations. Large chestnut logs and stumps are plentiful along the Ramsay Cascades, Porters Creek, Gabes Mountain, and Gregory Bald trails. Look for straight trunks with a reddish color. If protected from the weather (e.g. upright trunks) the surface may be smooth. Logs that have been exposed to decay develop long longitudinal furrows. In the Smokies, these logs are usually covered with moss but the reddish color can still be seen. In areas of less



Two chestnut trunks- Gabes Mountain trail

rainfall, such as Middle Tennessee, gray lichens grow abundantly on the logs, sometimes hiding the reddish color. Chestnut heartwood often rots first, leaving many of the logs hollow.

Differentiate chestnut from red oak and hemlock. Red oak has a typical oak grain pattern. If oak bark can be seen on the log, that is an obvious clue. The bark is long gone from chestnut. The sapwood of hemlock is lighter and small branches are more common, even on larger trees. Neither red oak or hemlock logs develop the long, deep longitudinal furrows typical of chestnut.

The Park Service and Civilian Conservation Corps cut down many of the dead chestnut trees near the trails for safety reasons years ago. However, many large trunks are still standing several feet away from the trails. These are more easily found in the winter when the understory plants have lost their leaves.

Stump sprouts are living American chestnut trees that sprout from old root systems. They rarely attain substantial size before the trunk is killed by chestnut blight. Stump sprouts are common in some areas of the park Look for them along the first 11/2 miles of the Ramsay Cascades trail, at mid-elevation on the Gregory Bald trail, and along the crest of Sugarlands Mountain. Interestingly, many of the areas where the old chestnut logs are the largest and most plentiful (implying good chestnut habitat) do not have many stump sprouts. Perhaps the growing conditions for other species of trees are good there too and the stump sprouts have lost out to competition.

The Grotto Falls trail passes through an old growth forest dominated by hemlock. There are a few impressive chestnut stumps along the way, but overall, chestnut logs are not as coml11on as along the Ramsay Cascades trail. Ellison says that historically, chestnut and hemlock did not commonly coexist.

Study of the chestnut forests of the past will help us as we work toward restoring this magnificent tree.

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OLD GROWTH FORESTS IN TENNESSEE

Great Smoky Mountains National Park *(shared with North Carolina)*

Cherokee National Forest:

Holtzen Mountain—Pig Oak Branch
Joyce Kilmer—Slickrock and Citico Wilderness Areas (shared with North Carolina)
Falls Branch Scenic Area (Monroe County)
Big Frog Mountain (Polk County)
Roan High Bluff (on Roan Mountain)

Fall Creek Falls State Park

Piney Falls State Natural Area

Savage Gulf State Natural Area

Frozen Head State Natural Area:

Cherry Log Gap/Squire Knob
Sugar Tree Hollow/Beech Fork

University of the South (Dick Cave)

Hatchie River National Wildlife Refuge

Overton Park (Memphis)

memories

THOUGHTS OF LONG AGO

by Henry Henkel Rhyne, Sr.

Once upon a time, many years ago when I was a boy, my family had a summer home in the mountains of North Carolina, near Blowing Rock. This was a wonderful time for me. Other members of my family were there also, grandparents, aunts, uncles, and cousins.

Henry Henkle Ryne, Sr

It was different then from what it is today. From our back porch, the view included the John's River Gorge with an open view of the Gorge all the way to the famous Brown Mountain, where we could frequently see the Brown Mountain light. Slightly to the right was a clear view of Grandfather Mountain. The entire view, as far as we could see, was covered in forest. Most of the trees were chestnut.

With so much of the land covered in forest, the climate was much different from what it is now. We had to have a fire in the living room fireplace every day throughout the summer to help dispel the humidity in the air. The salt shakers had to be filled with a mixture of salt and rice and kept on the back of the wood burning stove so the salt would not clump together. The bed linens would often get damp and the pillows musty. We set them outside in the sun to air.

The streams, which ran freely and where I caught native brook trout, have now dried up or only flow after a long period of rain. The woods were damp and produced quantities of mushrooms which we spent much time hunting. There were not many mushroom hunters in those days, so we had them all to ourselves. We gathered the *Lactarius volemus* and *L. corrugatlts.*

The chestnut trees were tasseling over the summer and when the tassels fell off and turned brown, we put three tassels together and rolled paper around them and smoked them like "rabbit" tobacco. It was terribly strong. We didn't do this often. The chestnuts would then make burs. It took a long time for them to mature and begin to fall off the trees. At the end of August, we packed up and returned to the low lands so I could be put into school for another year. What a shameful thing! Later in the fall, we would go back up to the mountains to see the beautiful fall colors and to gather chestnuts.

One trip I remember especially. I was alone that day, picking up chestnuts off the damp forest floor, amid the fallen logs and decaying vegetation. As was my custom, I was using an old pillow case for the chestnuts I found. Something caught my attention, a slight movement, but when I looked up, I saw nothing. Then again my focus was interrupted and as I turned I saw a small, tow-headed boy of about 10 or 12, peering at me from behind a tree.

He was watching me intently, and seemed both hesitant and eager to speak. I asked him what he was doing and who he was and what he wanted. Edging out from behind the tree, the boy approached mc, and his answer startled me. "You ain't doing it right," he said. "Here, let mc show you." He then led me down a slope, to a fallen log, which had created a "dam" with a wealth of chestnuts caught there as they slid down the hill after falling from the trees. He took my pillow case, straddled the chestnuts, then using his hands as a scooper, proceeded to rake a pile of chestnuts into my make-shift sack. I was amazed, and thanked him as he turned and handed me the sack. I was about to ask him again who he was, where did he come from, what was his name, which just as quickly as he'd appeared, he disappeared into the forest.

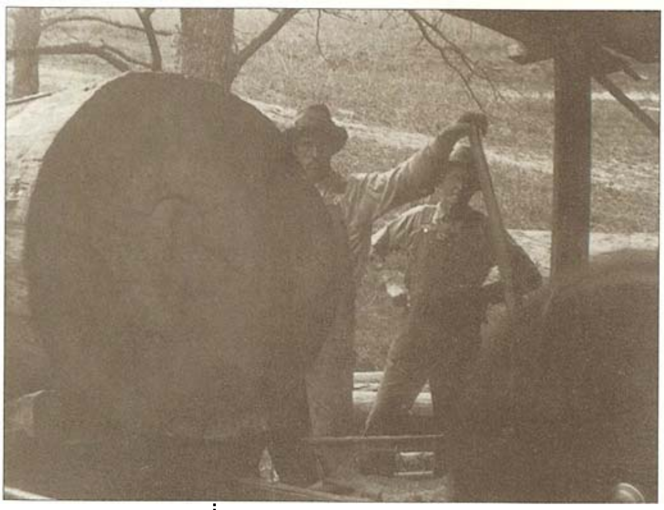
Henry H. Rhyne has been an outdoorsman and a businessman most of his life. As a youth, his family spent many summers in the mountains of N01'th Carolina, which helped him develop his love of the outdoors: his memories include many happy times spent near Grandfather Mountain. He graduated from Davidson College in North Carolina in 1934 *and flew for American Airlines during World War II. Also, he was an active and expert fly fisherman, hunter, trapper, mushroom collector, and photographer.*

Mr. Rhyne has had a life-long commitment to conservation and preservation of wilderness areas and has been a member of The American Chestnut Foundation since 1998. *In November of2002, Mr. Rhyne celebrated his 90th birthday.*

MEEADOWVIEW IN 1935: MEMORIES FROM HARVARD SHORTT

By: Fred Hebard, TACF Staff Pathologist

Havard Shortt, who is a neighbor of mine, stopped by with some pictures ofa chestnut tree he helped his father cut down in 1935~ when he was 14 years old. The picture of the two men at the sawmill shows one of the four 6'-long logs they cut from the upper part of the tree (Image 1). Havard's father, George, is the man with his hands on his hips. The man to the left is Charlie Smith, who owned the mill. Charlie is also shown with his back to the camera in the other photo (Image 2), which shows three of the 6'-long logs. The log from the bottom 10' of the tree was hollow. It was necessary to remove the handle from one end of a 6' cross-cut saw to cut the tree down. It took most of a Saturday to cut through the base of the trec. Havard's father then waited until Monday morning to fell the tree; Havard watched it fall as he turned a wagon down the lane to the tree.



Courtesy Harvard Scott

Havard and his father split the bottom log into six sections to drag it to the mill, which was only a few hundred yards downhill from the tree. They rolled the other logs there, using peevees and horses to turn and get them rolling. They cut them into 6' sections because they were going to make a chicken coop with the wood. The bottom log was straight grained, but the top logs had a twisted grain. A total of 2,198 board feet of lumber were milled from those logs. Some of the boards were 24" or 36" wide.

Havard's family had lived near the tree until he was about 12 or 13. He remembers gathering chestnuts from it before they moved. The tree was located about 1/4 mile north of Rich Valley Rd, down from the Earl

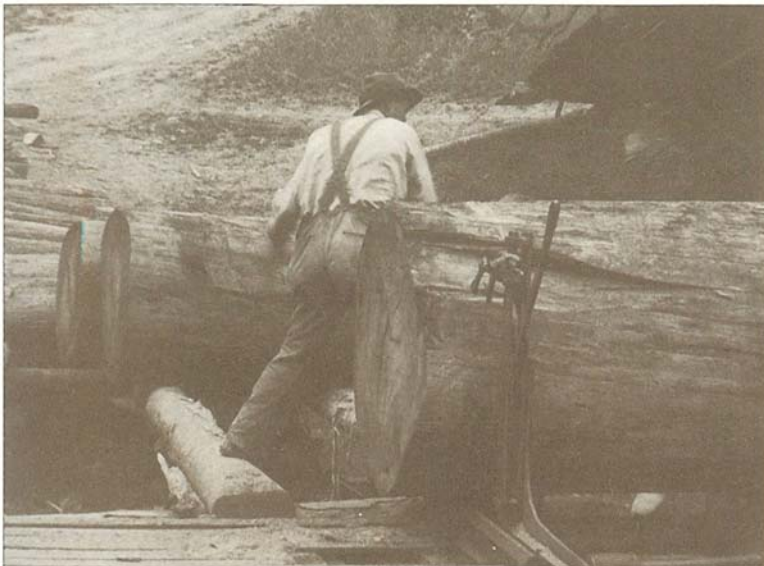


Image 2

Fogelman dairy farm. This is less than a mile ham where Glenn C. Price grew up. (One of the Meadowview Research Farms properties is named in honor of Glenn C. Price.) The third picture (Image 3) is of Bert Hayter's store, which was at the northeast comer of the intersection of Toole's Creek Rd and Rich Valley Rd. Glenn Price's father had purchased the land and the store from the Hayter's when the photo was taken.

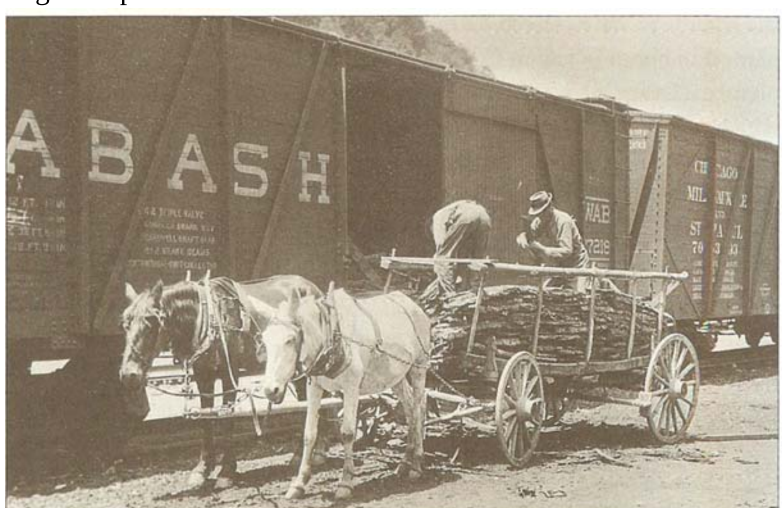
THE CHESTNUT LOGGERS

By John Alger, Buckdancer Consultants

The woods of the East have an eerie ghost. Its old bones lie scattered round the forest f1oor. Once in life it towered, dominating the slopes, sometimes suffering a few other sorts nearby but, mostly, only keeping kin near its spreading reach.

This was the American chestnut. Go to the cool, northing slopes of the Southern Appalachians. Walk up the coves to where the soil thins, becomes stony, more xeric. Look on the little ridge noses that spread like the fingers of a hand. There, the bones of a giant are to be seen. They are old bones now but their grandeur fades only slowly. The woods today are not as they were, but perhaps they will be again.

Though the giants of the slopes and ridge noses were the most dramatic representatives of the American chestnut, they were by no means the most numerous. A review of the witness and corner trees of the historic land grants and surveys of the region shows both the dominance of the species and a sense of type and location on the broken terrain. Chestnut clumps seem more common on lower slopes and ridges facing river planes. Trees of mod-



Loading chestnut bark at Marshal,NC.

erate (by comparison) size tended to pure stands or to heavily dominate stands on open slopes. The giants-those that have left stumps sixty to eighty inches in diameter-were largely confined to the thin soiled ridge noses and brows. This range of type and size would later become important to the commercial usage of the species. Who logged this species and to what uses did they put it? The human usage of the American chestnut was a mirror of the changing human society in its presence.

In the large sense, the usage of the chestnut mirrored the agricultural and industrial evolution of the region. That evolution began in the aboriginal forest where the fruit of the species gave a nutritional base for the game animals the American Indian depended on. It may also have provided a more significant food source for those cultures. (I am indebted to Dr. Fred Paillet for his suggestion that chestnut meal may have offered a corn substitute to the American Indian.) After the agricultural development ofthe coastal plains, chestnut became valued as forage for hogs that had cash value when driven to the lowland cotton plantations. The displacement of the Indian population by settlers continued that usage and provided the capital that led to the usage of the tree stem itself.

The properties and characteristics of the American chestnut made it attractive for different usages at different points in this country's agricultural and industrial development. Some of these characteristics are:

1) A higher sheer strength
2) Ease of splitting
3) A high tannic acid content in wood and bark
4) A strong resistance to ground rots
5) A long fiber length
6) A hard surface when sawn and finished
7) An attractive, straight grain structure
8) Good response to finish and stains
9) A tendency to throw a clear primary log of exceptional length
10) Ease of working when green
11) The tendency to clump from a root collar to a common diameter of stems

Of these, the sheer strength of the wood, its wase of splitting and riving and its resitance to decay drew the first loggers to the species, for the first

LeConte Hardwood Company tan bark yard along Pigeon Froge -Galinburg Road at Banner. 1920

loggers were farmers. The agricultural fortunes of the Mountain South were tied to the ability to enclose pasture, and field chestnut rail fences-"Snake fences"-were a standard into the 20th century. Even after barbwire, chestnut posts, charred at the tip in an open fire, were preferred to all others. Many timber deeds of the period find the landowner reserving the chestnut growth for his own use. As wintering over larger herds of stock became popular, so did the need for larger barns; barns in excess of the log crib structures. The beams for these were commonly chestnut, hewn out with broad ax and foot adz to lengths of upwards of40 feet. Finally, the shakes and shingles made 6:om the species would last far beyond the life of white oak. The original buildings of the Bent Creek Experimental Station (USDA Department of Agriculture, Forest Service) were covered with chestnut shingles at their construction in 1922. The shingles are still there and still sound today.

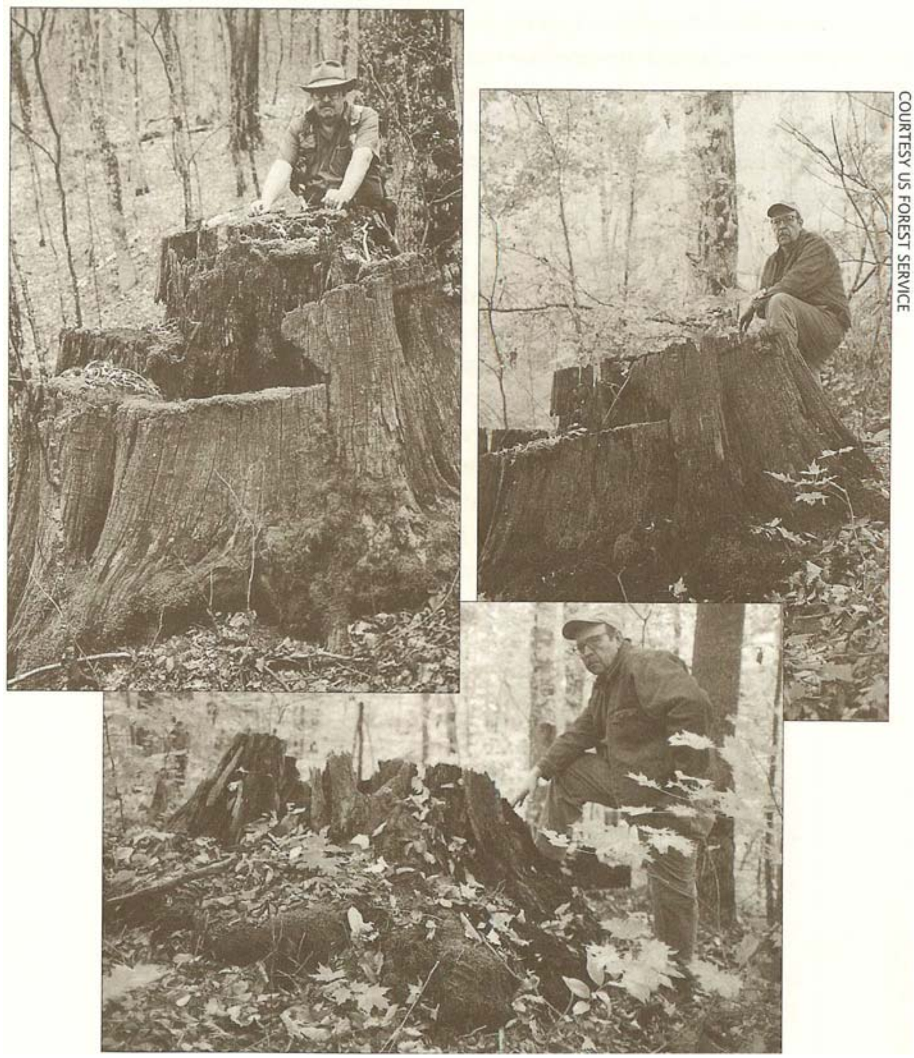
The growth of factories in the region created a new commercial demand for the species. Manufacturing, particularly of textiles, required a large amount of clear t100r space with minimal interruption by support columns. The t100rs of the old Asheville cotton mill were supported by chestnut beams 20 to 40 feet in length and 18 inches square. These beams were pit sawn, there were many such factories and today their beams provide the primary source of lumber.

Though the split ability of the species enhanced its use by farmers, it also restricted its wide use in construction. The cut nails of the nineteenth century would cause the 4/4 and 6/4 lumber to split as well. Large scale sawmilling of the species awaited the development and wider usage of the wire nail in the late 1800's before large acceptance came in the building and architectural marketplace. This was not a limitation for other uses. The chestnut clumps became an ideal source of telephone and power poles. Smaller single stems and the top wood of larger ones were hewn in the woods into crossties for the growing railroads. This practice was as likely to be done by small farmers on their own land; the ties then sold at rail side to a local broker. The bark of the species had been long recognized by the tanning industry; large logging companies and small farmers both would "ring out" three foot bark plates from logs before skidding.

The methods and tools of logging changed little over the time of commercial use. The faller's ax and crosscut saw were used at the stump. Judging from the relic stumps in the woods today, the falling technique was modified for the largest trees. In these, the directional notch was taken from the stump instead of the butt log. In some, a full "Humboldt" notch was made with parallel saw cuts and the wood between them knocked out with an ax. The leading edge of each log was then slightly rounded (again

The Curtis Creek flume – McDowell County, NC.

FALLING TECHNIQUES



(Top left) Undercut chestnut stump showing a saw cut notch
(Top right) Undercut chestnut stump in Walker Cove Reasearch Natural Area
(Bottom) Smaller chestnut had the falling notch taken from the log

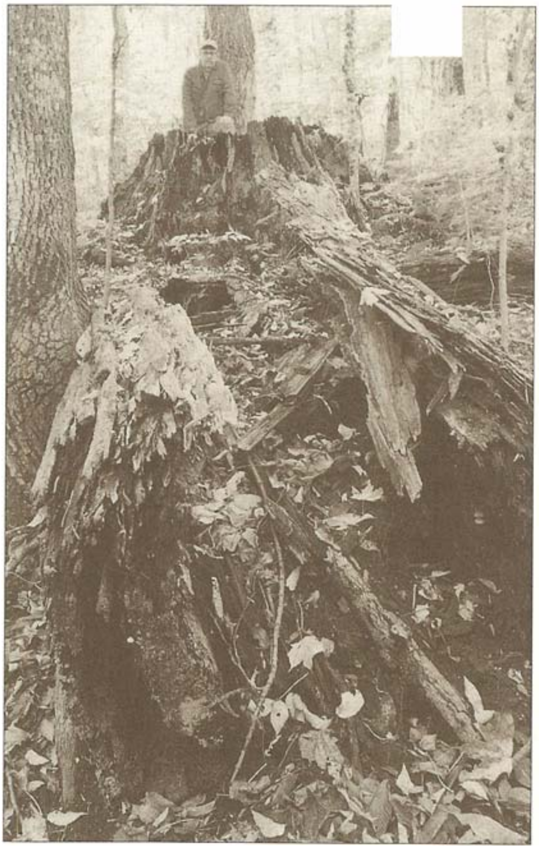
with an ax) and oxen, horses or mules then dragged the logs off the slopes on skidways. At the beginning of the 20th century, the larger concerns began to use small railroads to bring the logs to the mill ponds and also to construct flumes to carry out the small diameter "acid wood" to a rail siding where it could be further carried to tanneries and paper mills.

Today in Haywood County, NC on the banks of the Big East Fork of the Pigeon River, there lie piles of stone. Around and between them lie other far larger piles. These are of sawdust, chestnut sawdust. In the early 1900's, this was the site of the Denning and Powell mill and a small, un-named town. They logged the Big East Fork up to the spruce line under agreement with the Champion/Suncrest Lumber Company. Suncrest logged the spruce above. They logged the hardwoods below. It was a circular mill; not one of the big band "head rigs" like Champion used in its mill at Sunburst. Still, it was an enterprise of some complexity. A narrow gauge railway with a "Black Satchel" Climax locomotive snaked its way upstream and up the tributaries. Its way included stretches that today seem impossible but then carried long trains of logs to the mill. Small camps of loggers dotted the rail side. Portable mills-"Donkey Mills"-clung high up on the smaller streams to send out lumber where logs could not be carried. A flume reached high up the mountain slopes to bring out the short "acid wood" tor sale to the Champion Fiber Company at Canton.

About 50% of the mill's throughput was American chestnut and much more than that, counting the acid wood, harvested long ago. Today, it's an eerie place. There is only the sound of the river, but your mind may still hear the shriek of the head rig biting into a log. Still, all that is left are the stones and the dust of the chestnut.
The woods of today are not as they were but perhaps they will be again.

READING AND REFERENCE

1. The usage of nut crops by pre-European native Americans is noted in various publications and reports to the royal governors by traders and explorers. It is also mentioned by William Bartram in his journal of travels through the Carolinas and by Mary Chiltoski in her Cherokee Pharmacopia. The cormmercial trade in chestnut ted hogs is noted by James Mooney in his "Report Of The American Bureau Of Ethnology," Washington, 1888.



The bones of a giant. A large butt log that shattered on falling—Walker Cove Research Natural Area

2. Distribution and diameters of the species was developed by the author in a survey of witness and corner trees in the central Nantahala area, Macon County NC. This survey exists as a part of the White Oak and Wine Springs ecosystem demonstration conducted by the USDA Forest Service, National Forests in North Carolina. Surveys and studies from this project have not been published. It is also the product of observation in the Walker Cove Research Natural Area; Appalachian Ranger District, Buncombe County NC.

3. Characteristics of the species may be found in Gen. Tech. Rep. FPL-GTR-1l3, "Wood as an Engineering Material." US Government Printing Office.

4. Pre-mechanized logging practice IS described in, *Sound Wormy - The Memoir of Andrew Gennett Lumberman,* University of Georgia Press. Edited by Nicole Hailer, forward by John Alger (2002).

5. The description of the Denning and Powell operation is found in a survey by the author in the Shining Rock Wilderness Area, Haywood County NC. This is an unpublished survey for the USDA Forest Service and includes interview with James Powell who was born in his father's mill town there.

Science and natural history

EARLY RESULTS FROM A PILOT TEST OF PLANTING SMALL AMERICAN CHESTNUT SEEDLINGS UNDER A FOREST CANOPY

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Steven Patch, Professor, Mathematics Department, University of North Carolina-Asheville
A.Amelia Nutter, Mathematics Department, University of North Carolina-Asheville

INTRODUCTION

Successful development of American chestnut (*Castanea dentata)* hybrids that are resistant to chestnut blight *(Cryphonectria parasitica)* will require information about methods for effective and economical reintroduction

Figure 1. Natural understory vegetation on plots with the full canopy treatment consisted of scattered tree seedlings and sprouts that averaged 3 to 4 feet tall. The observer's left hand indicates height of a planted American chestnut seedling that has attained about half the height of a nearby red maple sprout (right hand) in four years. Heights of chestnut seedlings receiving the tree shelter treatment, in the adjacent row, were about the same as seedlings without shelters.

of this species in forests of the southern Appalachian Mountains (Boucher 2000)-American chestnut regenerates naturally from seedlings that become established and gradually accumulate beneath a closed tree canopy (Paillet and Rutter 1989, Billo 1998). Chestnut seedlings on a partially shaded forest floor gradually develop well-established root systems through successive sprouting and dieback episodes, and eventually will initiate rapid growth upon receiving additional light resulting from disturbance in the overstory canopy (Billo 1998, Paillet 2002).

Planted seedlings can be an effective and inexpensive method of establishing blight resistant American chestnut seedlings on forested sites (Klinger 2002). Little information is available, however, on establishing seedlings on a forested site and particularly survival and growth of seedlings that receive no follow-up maintenance. To obtain such information we designed a study to determine survival and growth of planted American chestnut seedlings in relation to overs tory canopy density. Our secondary objective was to determine if seedling survival and growth are influenced by cultural treatments applied at time of planting. Our's was a pilot study that will help us to plan and conduct a larger, more intensive study.

METHODS

This study was made in the Bent Creek Experimental Forest, located in the Pisgah National Forest, about 10 miles southwest of Asheville, NC. We followed methods outlined by Rutter (1992) to produce seedlings from nuts of American chestnut. Briefly, we obtained about 200 nuts in March 1998 and stratified them in damp peat moss for 2 months at 46°F. The nuts, which sprouted during stratification, were sown about 1 inch deep in raised nursery beds; germination was about 95 percent. Except for rainfall, the seedlings were seldom watered. Estimated nursery seedling mortality was $<$ 5 percent. Total height of the 1-year-old nursery seedlings averaged 7 $\pm$ 2 in and ranged between 3 in and 12 in. For field planting we excavated the seedlings in December using a shovel. The root system of most seedlings was characterized by few lateral roots and a taproot that slightly exceeded length of the aboveground stem.

We planted the seedlings in a large intermountain basin with hilly terrain and deep (>40 in), well-drained soils characterized by clay accumulation in the B horizon. The site sloped slightly (5 percent) to the south. The sites overstory primarily is composed of xeric to subxeric species of oak *(Quercus)*, including white *(alba)*, scarlet *(coccinea)*, and black *(velutina)*. Chestnut oak *(Q prinus)*, a typical associate of American chestnut in the southern Appalachians, is rare on the study site, but is common on nearby, more steeply sloping mountainsides. The midstory canopy includes widely scattered red maple *(Acer rubrum)*, sourwood (*Oxydendron arboreum)*, and dogwood (*Cornus florida)*. Basal area of the overstory and midstory averaged 110ft^2 and 20 ft^2/ac, respectively. At the time of planting the sparse shrub layer was mostly tree seedlings and saplings (Fig. 1), although mountain laurel *(Kalmia latifolia)* occasionally was present. A portion of this forested site was clearcut in 1997 to salvage windthrown trees in a down burst area resulting from the remnants of Hurricane Opal on October 5, 1995; the stand on an adjacent part of the site was relatively undisturbed.

Two blocks, each consisting of three plots, were established in the study site. One plot of each block was situated in the clearcut portion of the stand, one in the undamaged stand, and one between the clearcut and undamaged areas. Each plot measured 12 ft: x IS ft: and was planted with 20 seedlings (5 each in 4 rows) spaced 3 ft: apart. In late December 1998, we manually planted the seedlings using a planting bar with a foot-long blade. One person planted all seedlings during a light rain, when air temperature was 40°F. Each seedling was planted in less than a minute, because the primary root was short «10 in) and had few laterals. Seedlings with top lengths < 5 in were discarded. The small number of available seedlings allowed us to replicate the study in only two blocks, for a total of 120 seedlings.

We studied seedling survival and height growth in response to three canopy densities and four cultural treatments. The three canopy densities were: none (plots established in the clearcut), partial (plots placed at the edge between the clearcut and uncut areas), and full (plots located in the uncut stand). Each row of five seedlings received one of four randomly assigned cultural treatments: (1) fertilizer, (2) tree shelter, (3) fertilizer and shelter, or (4) no treatment (the control). The fertilization treatment consisted of a commercially produced soil amendment (Gromax™, forestry dry site formulation 17-3-5 with super-absorbent gel, minor elements, and biostimulants) contained in a premeasured 0.25ounce packet. We applied the fertilizer treatment in early March 1999, using an S-inch deep hole made with a planting bar about 4 in from each seedling. The opaque, corrugated white plastic tree shelters measured 3 in x 3 in x 24 in tall and were positioned to rest on the ground. We made no follow-up cultural treatment after planting, except to replace disturbed tree shelters.

Seedlings were examined for survival and measured for total height immediately after planting, 6 months after planting, and annually each early October. Because conventional wisdom suggests that survival should be lower among small, runty seedlings compared to large robust seedlings, we used a t-test to evaluate the hypothesis that first year survival was not associated with seedling size, as quantified by total height. At five points within each plot we measured mean photosynthetically active radiation expressed as percent of full sunlight-once using a portable light meter positioned about two ft above ground level.

We used a split-plot design. The whole plots were a randomized complete-block design with two blocks containing each of the three canopy treatments. Four combinations of fertilizer and shelter were assigned to each of the six split plots. Twenty of the trees were planted in soil that later was found to be somewhat compacted by an old roadbed. Because the survival of those trees was much lower than that of other trees in the study (P=0.002 by chi-square test of independence) we dropped them from our analysis.

To analyze the effects of survival after five years, we applied a mixed model methodology using a binomial error distribution. The model was fitted with Statistical Analysis System (SASTM) using the GLIMMIX macro to adapt: to binomial response variable in a mixed model with the restricted maximum likelihood estimation method and the Satterthwaite approximation for degrees of freedom. Whole-plot error was used to test significance of canopy and within-plot error was used to test significance of shelter, fertilizer and any interactions. Because none of the interactions was significant, the reduced model with only main effects was then fit.

RESULTS

Overall seedling survival declined sharply during the first year, from 100 percent immediately after planting to 66 percent in October (Fig. 2). First year survival was not associated (P=0.53) with initial seedling height; both live and dead seedlings averaged about 7.8 in. Survival declined little during the next 2 years and averaged about 58 percent at seedling age five.

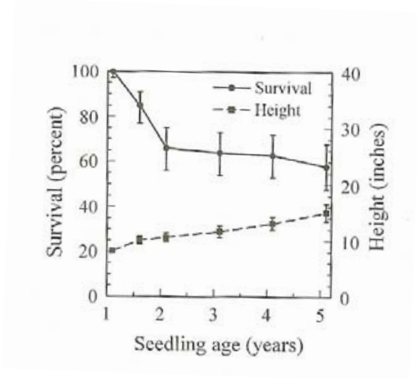

Figure 2. Mean (± 95 percent confidence intervals) survival and height of American chestnut seedlings at planting, when one-year of age, and periodically thereafter in Bent Creek Experimental Forest.

Total height of all surviving seedlings has almost doubled, from about 8 in at planting to 14.8 in after 4 years of field growth. We took light measurements on May 30, 2001; they averaged 97 percent, 45 percent, and 10 percent under canopy treatments of none, partial, and full, respectively.

At age 5, mean seedling survival ranged from 28 to 82 percent among canopy treatments (Table 1), but the means were not significantly different (P= 0.40). Confidence intervals for the three mean survival rates were large - ranging from almost 0 to 100 percent - and relatively consistent, indicating a high amount of variability. Among cultural treatments, survival was significantly lower (P=0.010) for seedlings receiving fertilizer (42 percent) than for those not fertilized (75 percent). However, survival was significantly higher (P=O .025) for seedlings receiving the shelter treatment (74 percent) than for those not receiving shelter (44 percent).

Overall seedling height averaged 15.7 in at age 5 and did not differ significantly (P=0.40) among any of the canopy or cultural treatments. In an unplanned investigation of the cause of slow height growth and high mortality of seedlings in some treatments, we excavated a small (10.6 inch) seedling in a full canopy, shelter and fertilizer treatment that had apparently died during the late summer of 2002 (Fig. 3). Examination of the seedling revealed that only the top was dead, the root system was alive, and it had top-died and root-sprouted at least twice since planting and likely would have sprouted again, in spring 2003. Using a diagnostic test, we found no evidence that this seedling was infected with *Phytophthora cinnamomi*. We observed little damage to seedlings from rodent girdling, rabbit clipping, or deer browsing.

DISCUSSION

Results of our study suggest that small American chestnut seedlings can be successfully established in a forested environment with minimal investment of time, equipment, and no follow-up atten-
tion after planting. Although not statistically different,
average survival of seedlings planted under the full canopy (82 percent) tended to be greater than survival of seedlings under tl1e partial canopy (65 percent) or no canopy (28 percent) conditions. We speculate that increased replication of field plots would have allowed detection of a significant difference in survival among canopy treatments. Height growth of the seedlings was slow in all of the canopy treatments.

A likely contributing factor to the high level of mortality during the first growing season following planting was low soil moisture; precipitation was about half of normal from August through October. An introduced disease, Phytophthora root rot, can cause high mortality in American chestnut (Crandall et aI1945), however, we neither observed symptoms of this disease in our study plots nor detected sporangia on the roots of a small excavated seedling. We noted no mortality from chestnut blight, probably because the short seedling stems presented small target areas for infection (Paillet 2002). The only explanation we offer for the lower survival associated with the fertilization treatment is root desiccation caused by increased
soil salt content during the dry summer after planting; we suggest additional study on this topic. Unlike other areas of the eastern U.S. where herbivory is a problem and must be dealt with (Griffin et a11991, Klinger 1992), we observed little damage from deer and none that contributed to mortality. Although tree shelters increased overall survival and could

Table 1. Estimated percent survival (lower-upper 95 percent confidence limits) for the canopy, fertilizer, and shelter treatments 4 years after field planting of 1-yr-old AmericanChestnut seedinlings in Bent Creek

Treatment	Survival[a]
No Canopy	27.7a (0.4 - 97.1)
Partial Canopy	65.0a (2.5 – 99.3)
Full Canopy	82.5a (5.5 – 99.7)
No fertilizer	74.8a (45.0 – 91.6)
Fertilized	42.8b (17.6 – 72.5)
No shelter	44.5a (17.9 – 74.6)
Sheltered	73.7b (44.0 – 90.8)

[a]Means in each of the three similar treatment gorups followed by the same letter do not differ significantly at the 0.05 level of probablility

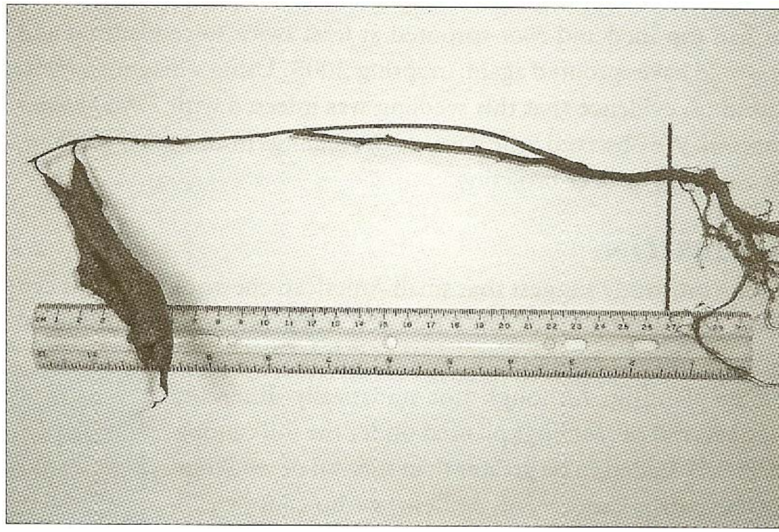

Figure 3. The above-ground portion of this 5-year old American chestnut seedling was dead in October 2002, but not the roots, which had resprouted at least twice since planting four years earlier. Now 10.6 inches tall, the seedling had doubled in size following planting in the full canopy treatment. (The vertical line at the seedling's root collar indicates ground level).

offer protection from deer, we observed little benefit in the full-canopy treatment and maintenance required considerable effort.

The co-occurrence of American chestnut and mountain laurel (Griffin et a11991, Paillet 1996, personal communication Fred Hebard), or other ericaceous species (Griffin 1992) has been noted elsewhere. In our study, we observed that mountain laurel occurred on only one plot, which also had the highest survival of chestnut seedlings (100 percent). This coincidence is probably more interesting than important, but suggests that much remains to be learned about the ecology of American chestnut. For example, Vandermast et al (2002) found an allelopathic relationship with American chestnut for selected co-occurring species, particularly rose bay rhododendron *(Rhododendron maximum).*

Planting stock used in our study was small, I-year old seedlings with equally small root systems. We did not design the study to investigate the effects of chestnut seedling size or vigor on survival and growth, although we found that seedling size apparently did not affect early survival. Competition from sprouting stumps of other vegetation has been intense in the no-canopy study plots; height of the largely hardwood-sprout stand averages about 6 ft compared to about 1.5 ft for the chestnut seedlings. Planting a larger chestnut seedling with a more vigorous root system would have likely allowed more successful competition, but would have required greater effort and possibly increased the likelihood of infection from root disease (Crandall et aI1945).

We know of no other study results with which to compare our findings. However, evidence suggests that American chestnut stands can "store" small resprouting seedlings for many years beneath an overstory until they are released by increased light resulting from disturbance in the canopy (Paillet and Rutter 1989, Paillet 1994, Billa 1998). The seedling we excavated had been among the smallest planted, only 5-in tall initially, but slowly was developing a root system in the limited light provided under the full forest canopy. Loftis (1990) proposed a shelterwood regeneration system for oak seedlings. By adjusting the mid- and over-story canopy density to stimulate continued development of understory seedlings, such a system could be adapted to chestnut. Although we did not design our study to determine if shaded American chestnut seedlings would respond to release, a rapid height growth response is likely (Griffin 1992, Paillet 1990, Paillet 1994, Paillet 1995).

CONCLUSION

Our study clearly demonstrates that American chestnut seedlings can be successfully and economically established by planting in a forested environment that simulates conditions favorable for natural regeneration. The l-year-old seedlings we used averaged only about 7 in tall. Based on current standards, seedlings of this size would likely be discarded as too small to justify planting. It is likely that seeds of blight resistant American chestnut will be initially limited in quantity and when well-watered and fertilized nursery seedlings are produced, some will be naturally small. We suggest that small American chestnut seedlings could be used in a program of planting beneath an oak canopy,
such as described in this study. We assume that hybrid American chest-
nut seedlings resistant to the blight will have survival and height growth characteristics similar to the seedlings we used. An essential part of this "pseudo-natural" regeneration system, however, would include monitoring development of seedlings and timely manipulation of the over-

story. We suggest there is a need for larger, operation-scale studies to confirm our results, particularly on mountainous sites better suited to American chestnut.

ACKNOWLEDGEMENTS

We thank Forrest MacGregor, former Development Director of The American Chestnut Foundation, and John Alger, President of Buck dancer Consultants, for facilitating our study by providing nuts from The American Chestnut Foundation. *Also*, Ronald Myers, North Carolina Division of Forest Resources, provided valuable insight into the early development and growth of American chestnut sprouts and information on Phytophthora root rot. Finally, Dr. Paul Sisco, Southern Appalachian Regional Science Coordinator with The American Chestnut Foundation, suggested writing this paper and provided helpful critical comments on an earlier draft.

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GENETIC VARIATION IN NATURAL POPULATIONS OF AMERICAN CHESTNUT

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Prior to the blight epidemic, American chestnut *(Castanea dentata* Borkh.) was one of the most important timber and nut-producing tree species in eastern North America (D *.S.* Census Bureau 1908). Its native range extended from southern Maine and Ontario in the north to Georgia, Alabama and Mississippi in the south (Sargent 1905). It now exists primarily as stump sprouts across its entire native range. After nearly a century of blight, numerous living stems of American chestnut still exist (Stephenson et al. 1991). Prolific stump sprouting and the fact that the blight fungus does not infect the root system have enabled American chestnut trees to persist. However, sexual reproduction is infrequent and its gene pool will likely face serious erosion when old root systems fail to produce sprouts and perish.

In an attempt to restore the American chestnut to its former status as a dominant canopy component in eastern forests, The American Chestnut Foundation (TACF) has developed a vigorous backcross breeding program designed to introduce the resistance of Chinese chestnut (C. *mollissima* Blume) into American chestnut (Hebard 1994). TACF's initial efforts have focused on American chestnut trees in southwest Virginia, but the goal is to restore the species throughout its entire native range. Hence, separate breeding programs have been started in a number of states. One question that is of primary interest to TACF and its State Chapters is how many breeding locations or separate programs will be needed across the entire range to capture most of the genetic variation still present in the species.

Previously, little was known about how genetic variability is distributed in American chestnut. In an exploratory examination of genetic variability, Huang et al. (1998) obtained results with allozyme and random amplified polymorphic DNA (RAPD) markers that suggest as many as four regional populations might exist. However, statistical tests were not performed to quantity the magnitude of this component and whether it was significant. Because the question of whether regional genetic structure occurs among populations had not been settled, nor patterns of genetic variability completely described, we felt compelled to embark on a more thorough examination of genetic variation using state-of the-art microsatellite DNA and RAPD markers.

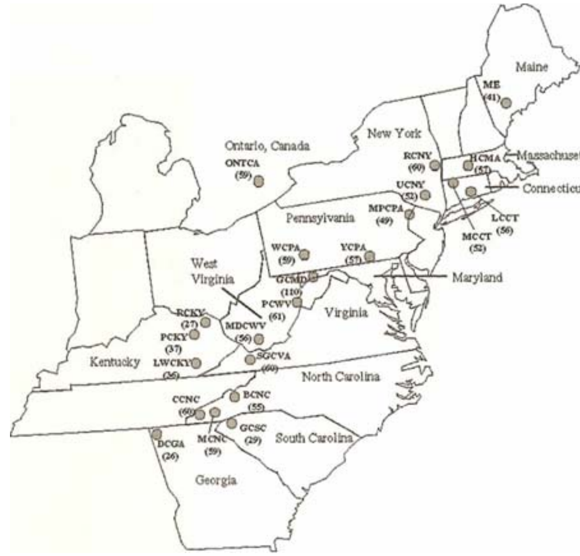


Figure 1. Map of the geographic origin of the 22 *Castanea dentata* Borkh. populations sampled in this investigation.

A number of people (many of whom are dedicated TACF members; Sandra Anagnostakis; Dave Armstrong, Glen Beaver, Robert Bernatzky; Mary Bunch, Peter Carson, Hill Craddock, Mark Double, Fred Hebard, Craig Hibben, E. Kenneth James, Michael Kluempke, Jeff Lewis, Paul Sisco, Bob Summersgill, Wayne Swank, Melissa Thomas-VanGundy, Wells Thurber, Cathy Townsend, Stan Webb and Eric Weisse; if I forgot anyone please forgive me!) helped to collect leaf or dormant bud samples of American chestnut. In total, samples were collected at 22 sites across the natural range (refer to Figure 1). Most samples were collected from sites in State or National Forests, but a few collection sites were located on Plivate land holdings. Each sample was assigned a unique ID and sent to the USDA Forcst Service's Soutl1ern Institute of Forcst Genctics in Saucier, Mississippi for DNA extraction and analysis.

Prior to conducting the study, one of our main concerns regarding this investigation was the inclusion of trees that were not pure American chestnut. Inappropliate trees include hybrids or pure species otl1cr tl1an American chestnut, especially the native relative known as chinkapin *(Castanea pztmila* Mill.). Inclusion of such "contaminants" could have iflated our estimates of genetic diversity, especially in those populations containing the nOI11-American chestnut samples, as well as potentially clouded any true patterns of genetic variability. Chloroplast DNA sequence variations have been widely used to investigate relationships among plant species (Palmer

Primera that amplified the spacer region between the *trn*T and *trn*L 5’ exon of the chloroplasts genome (Taberlet et al. 1991) could be used to uniquely identify American chestnut from all other Castanea spp.

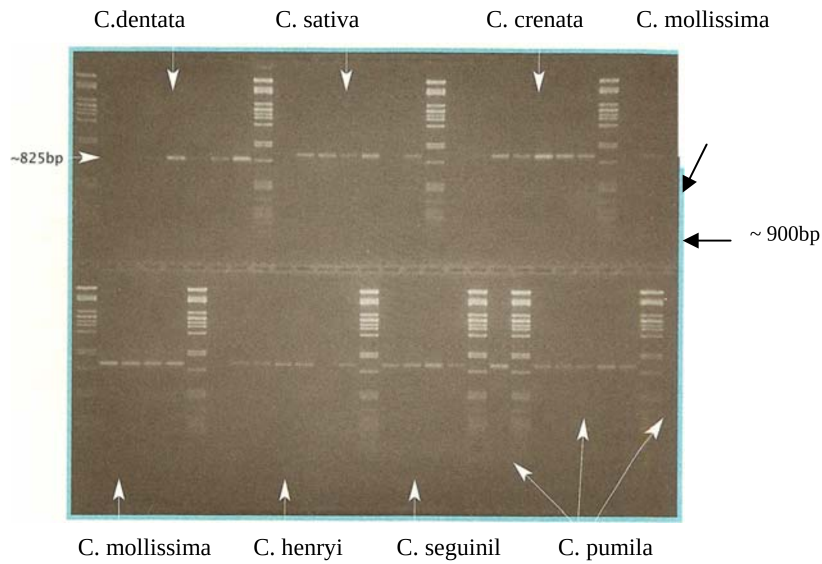


Figure 2. Chloroplast-specific marker amplified by primers a&b from Taberlet et al (1991)

et al. 1988, Clegg et al. 1991) because they evolve slowly. To our good fortune, we identified a chloroplast-specific marker (Taberlet et al. 1991) that uniquely differentiates American chestnut from all other chestnut and chinkapin species (for example refer to Figures 2 and 3).

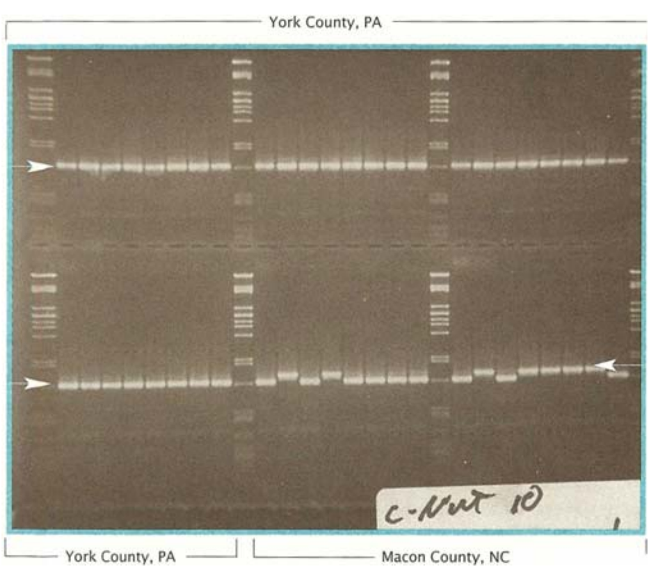
Unfortunately, chloroplasts are inherited only from the mother (maternally) hence this precluded our ability to distinguish hybrids of paternal origin. As a result, our sample set might still contain some hybrids, however, the number should have been small as most collections were made in either State Forests or National Forests where non-native chestnut and chinkapin species do not extensively occur. Of the 1158 trees sampled for this study, 165 trees (14.2%) from nine different sample sites were eliminated from further analysis as they were not pure American chestnut based on the size of the chloroplast marker (for example see Figure 3). In total as many as 993 trees were available for analysis of genetic variation.

The results of this study suggest that high levels of microsatellite and RAPD nriability exist in American chestnut, and that most of this variation occurs within local populations (95.2% and 94.5%, respectively). These results are comparable to observations made in other long-lived, outcrossing, woody plant species with similar life history characteristics (Hamrick and Godt 1990; Hamrick et al. 1992), where as a rule, greater than 90% of the variation occurs within populations. Our results are also consistent with previous observations of allozyme variability in European chestnut (C. *sativa* Mill.) and American chestnut where 90% of the diversity was reported to exist within populations (Pigliucci et al. 1990; Huang et al. 1998). These results suggest that extensive gene flow, probably via long distance pollen movement, was possible prior to the blight. Hence, most of the genetic variation of the species is contained within anyone population.

825bp= American chestnut
900bp= hybrid or species other than American chestnut

~ 825bp

~ 825bp



~ 900bp

Figure 3. Example of usefullness of chloroplast-specific marker in identifying hybrids or pure species opther than American chestnut

The results of this study also suggest that a cline in allele frequencies and number of rare alleles exists along the Appalachian axis. Clinal variation of allele frequencies along latitudinal and longitudinal gradients has been reported for a number of tree species (Lagercrantz and Ryman 1990; Zanetto and Kremer; Leonardi and Menozzi 1995, Tomaru et al. 1997), including European chestnut (Pigliucci et al. 1990; Villani et al. 1991; Villani et al. 1992; Villani et al. 1994). The main proposition set forth to explain this phenomenon is that geographical variation in allele frequencies resulted from post-glacial migration and founding events. Such processes are consistent with the patterns of variability we observed for American chestnut. The highest levels of gene diversity and the greatest numbers of rare alleles are found in the southwestern portion of its range. This suggests that its glacial refugium existed in the southern portions of its range, perhaps extending southward into the Gulf Coastal plain of present day Alabama and Mississippi.

Although most of the genetic variation found in American chestnut occurs within local populations, a statistically significant proportion exists among populations. Although our estimates of among population differentiation might be considered low (average 0.048), the values Obtained indicate that populations significantly differ in allele frequency. Moreover, population pairwise estimates of genetic distance were shown to be significantly associated with the geographic distance between populations, suggesting that populations in close geographic proximity are slightly more genetically similar than geographically distant populations. These findings lead us to conclude that although long distance gene flow was possible in the past, it was infrequent enough to allow some genetic differentiation to take place.

Unlike the results of Huang et al. (1998), the results of this study suggest that little, if any, geographic structure exists in American chestnut. In other words, when statistical techniques such as cluster analysis or principal component analysis were performed, populations did not group or cluster together based on their geographic origin. Trees from the far northerly extent of the species range such as in Maine or Ontario were just as likely to group or cluster with trees that were sampled from North Carolina or Virginia as they were to cluster with trees from more proximal populations such as New York or Massachusetts. Prior to introduction of the blight, genetic variability in American chestnut followed a pattern consistent with the hypothesis of a single large interbreeding 'meta'-population where genetic drift played a major evolutionary role.

Currently, roughly 95% of the neutral genetic variation of the species can be captured by sampling within anyone population of American chestnut. However, we caution that the results of this study are based on neutral genetic loci and do not necessarily reflect genetic differentiation at adaptive genes or gene complexes. Such genes or gene complexes might include those that influence such traits as bud break, flowering time, cold hardiness, drought tolerance, nutrient uptake, leaf senescence, etc. Therefore, in order to assure that most of the variation produced by these types of genes or gene complexes are also captured in conservation and breeding endeavors, sampling should focus on collecting a fairly large number of individuals (50 to 100 or more) from each of several geographic areas. As proposed in Huang et al. (1998), we also suggest that a MINIMUM of at least three regions, representing northern, central, and southern portions of the species range, be considered in conservation and breeding efforts.

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