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Editor's Notes - Journal Fall/Winter 1994-95

How many times have you heard people say, "It's all a matter of context"? If someone has been misunderstood, he's likely to exclaim, "You're taking me out of context!" What he is saying is that his actions or words take on greater impact, show subtle shades of meaning or are more easily communicated within a larger framework. These broad fabrics, these philosophies we ascribe to, the organizations we support, the families we nurture, the landscapes we preserve, these all return something to us as we support them. We gain a sense of meaning.

For decades, environmental conservation has been a strong force. Many people contribute their talents, their hearts and minds, their resources and their time to protect species and lands. For their effort they feel they have done something worthwhile. As we know, the environmental conservation movement would not exist without the support of every individual who contributes.

Each person has a job to do that he and he alone can do well. In pursuing his interest, he spins a thread, a trail, that can then link up with someone else's work. Woven together, these different efforts take shape. With perseverance, a brilliant tapestry may grow.

Every ACF member makes a contribution; and this grand effort upon which we have embarked will succeed only with your commitment, your perseverance and curiosity. This new Journal format is an effort to draw you all in, to stimulate your interest and commitment to our goal: the restoration of the American chestnut. And we invite you to write. Ask questions, make comments, ask questions of the authors of the pieces published here and we'll have them answer you.

This issue of The Journal is intended to show you how, quietly in some cases for decades, many of our supporters have been spinning their individual threads for the greater good. You'll find Dr. Fred Hebard's piece on creating the first map of genes controlling chestnut morphology as a way to identify those hybrids which have a greater percentage of American traits, which is crucial if we are to move ahead quickly. You'll also find Jill Willson's story of her father and how his simple action became one of the highlights of his life. Donald Swecker offers up a delightful, lyrical remembrance of youth and the American chestnut.

Thanks to Dr. Doris Armstrong-Goldman's initiative we have a picture of how American chestnut was used by the Pennsylvania Dutch last century. (She rewrote parts of her piece on deadline while administering cold tablets and soup to several sick children!) Dr. Fred Paillet takes chestnut ecology and focuses both inward and outward - his explanation of how the American chestnut grows and disperses seedlings gives us a new understanding of this tree's ecology, which in turn, carries implications for explaining ancient ecological patterns. A former Associated Press journalist, Jack Stillman, paints a portrait both of chestnut and a unique woodworker who scouts for downed trees in his area.

Finally, studies in Illinois of a stand of apparently blight-free American chestnut can proceed thanks again to Paillet and to Dr. Eric Ribbens. But thanks also to the landowner who realized he had something special and permits ACF entry, and thanks to Illinois Chapter members, who, as you read this, probably have someone stationed outside amid fall's chill wind watching squirrels bury nuts for us.

We can all contribute to the restoration of the American chestnut!

Rachel Kelly

Meadowview Notes 1993

F.V. Hebard, Superintendent
Wagner Research Farm

Overall, we had a very good year in Meadowview in 1993. We had adequate rain although it was very dry in June and July; all the rain falling on the Midwest bypassed us. The dry, hot weather reduced nut set below the banner years of 1990 and 1991. But we did harvest about one nut per pollinating bag, which is not bad. (Table 1)

1993 NUT HARVEST

Thanks to Peter Devin, who made crosses in Connecticut and sent us pollen from the 'Graves' and 'Clapper' first backcrosses, we were able to bag many more trees in the Virginia mountains in 1993 than in previous years, more than doubling the yield of backcross nuts in comparison to previous years. (Table 1).

Additionally, the trees at the farm produced enough female flowers to make controlled pollinations at the farm worthwhile for the first time. These factors combined to allow us to place more than 2,000 pollination bags, almost a 50% increase from our previous best effort of about 1,400 in 1990. However, due to the relatively poor nut set, we harvested "only" 2,003 nuts from controlled pollinations, about 75 more than our previous best harvest in 1990. The 1993 count does not include harvests by cooperators at other locations.

Among these nuts were our first crop of third backcrosses. This year, we will begin routine screening of second backcross trees for blight resistance. Next year, we will begin producing third backcrosses in earnest. This year, in 1994, we should almost complete our work to advance the 'Graves' and 'Clapper' first backcrosses to the second backcross generation.

For their assistance last year, I would like to thank Peter Devin, Chandis Klinger, Mike Webb, Lou Silveri, Henry Heckler, Ginny Webb, Laurie and Scott Spangler, Bernie Monahan, Bill Sladen, Paul Gross, Darren Corrigan, Joann Alexander, Wayne Wise and Elize Biederman for helping with pollination at Meadowview and pollinating at other locations.

PLANTINGS

We now have a total of 5,220 trees and planted nuts in the ground at Meadowview (Table 2). These include 2,094 second backcross trees, 242 first backcrosses and 385 F1s, as well as 936 American chestnuts. We have more Americans than we will need because 600 were installed to test methods of accelerating flower formation, although we have accelerated flower production about as much as possible. Most trees, including pure American chestnuts are setting male catkins 2 to 3 years after planting and setting female flowers 3 to 4 year after planting.

Tree growth was adequate in 1993 because we got good rains in August and September. But the dry weather in July forced us to stop fertilizing, so the new seedlings did not grow as much as in previous years. Also, some did not harden off at the top because of the late growing season.

The Tennessee Valley Authority (TVA) responded to our earlier grant request by giving us 18,000 feet of irrigation pipe, worth about \$7,000. With their knowledge, I plan to sell it so we can install the type of irrigation system we need, namely micro-sprinklers or drip tape fed through plastic main lines. A plastic system would allow fertilizer to be injected, which would save time and labor. The TVA pipe is aluminum, which is easily corroded by fertilizer.

Also, the plastic could be placed underground, out of the way of other equipment. Finally, we do not have an adequate water source to irrigate with regular sprinklers. This year, we are using some of the TVA pipe to irrigate a few critical orchards.

BLIGHT RESISTANCE TESTING

In 1993, we inoculated about 200 F2s and 400 BC1-F2s, and 50 BC2s, as well as controls, to test Dr. Charles Burnham's hypothesis that the blight resistance of Chinese chestnut can be backcrossed into American chestnut. We failed to reject the hypothesis, which indicates that the backcrossing method should indeed yield highly blight-resistant, American-type chestnut trees. Even more encouraging, we found highly blight-resistant trees in both the F2 and BC1-F2 populations, and we found some BC2s as blight-resistant as F1s, which indicates that blight

resistance is controlled by just a few genes. The results indicate that blight resistance is probably controlled by two incompletely dominant genes. Control by one gene, three genes, or four genes is less likely.

One caution, here, these results are from only one growing season; agricultural scientists generally believe that data must be collected in the course of two or three seasons before results can be accepted as valid. This year, 1994, we are continuing to monitor the trees inoculated last year, and we have inoculated an additional 166 BC2s and 20 BC1s. We also have backcrossed as many of the highly blight-resistant F2s as possible to American chestnut and backcrossed blight-resistant BC2s to American chestnut to confirm our assessments of their blight resistance.

TABLE 1
American Chestnut Foundation
1993 Nut Harvest from Controlled Pollinations.

| Nut | Type | Female Parent | Pollen Parent | pollinated | | | Pollinated | | | Un |
|---------------------|------|-----------------|-------------------------|------------|------|------|------------|------|-------|----------|
| | | | | nuts | bags | burs | nuts | bags | burs | American |
| | | | | | | | | | Lines | |
| BC ₂ | | American | Clapper BC ₁ | 528 | 471 | 1170 | 27 | 43 | 103 | 8 |
| BC ₂ | | American | Clapper BC ₁ | 528 | 471 | 1170 | 27 | 43 | 103 | 8 |
| BC ₂ | | American | Clapper BC ₁ | 528 | 471 | 1170 | 27 | 43 | 103 | 8 |
| BC ₂ | | American | Graves BC ₁ | 746 | 616 | 1415 | 28 | 61 | 129 | 8 |
| BC ₃ | | American | Clapper BC ₂ | 301 | 154 | 463 | 4 | 12 | 33 | 6 |
| Chin B ₁ | | Meiling Chinese | Nanking F ₁ | 94 | 171 | 378 | 5 | 17 | 45 | |
| F ₁ | | Meiling Chinese | American | 327 | 394 | 1021 | 8 | 37 | 109 | 4 |
| LS F ₁ | | American | Big Mac American | 5 | 29 | 74 | 2 | 3 | 8 | 1 |
| LS F ₁ | | American | Floyd American | 2 | 48 | 87 | 0 | 3 | 2 | 1 |
| Total | | | | 2003 | 1883 | 4608 | 74 | 176 | 429 | |

LS - large surviving

TABLE 2

Type and Number of Chestnut Trees at the ACF Wagner Research Farm in April, 1994, with the Number of Sources of Resistance and the Number of American chestnut lines in the Breeding Stock.

| Type of Tree | Number of | | |
|--|-----------|------------|----------------|
| | Trees | Resistance | American Lines |
| American | 936 | 0 | 14 |
| Chinese | 307 | 29 | |
| Chinese x American: F ₁ | 385 | 6 | 23 |
| American x (Chinese x American): BC ₁ | 242 | 9 | 15 |
| American x [American x (Chinese x American)]: BC ₂ | 2094 | 2 | 29 |
| American x (American x [American x (Chinese x American)]): BC ₃ | 69 | 1 | 1 |
| (Chinese x American) x (Chinese x American): F ₂ | 236 | | |
| [Amer x (Chin x Amer)] x [Amer x (Chin x Amer)]: BC ₁ -F ₂ | 422 | | |
| Chinese x (Chinese x American): Chinese BC ₁ | 88 | | |
| Castanea sequinii | 48 | | |
| Japanese | 3 | 2 | |
| American x Japanese: F ₁ | 4 | 1 | 1 |
| Chinese x Castanea pumila : F ₁ | 2 | | |
| Large, Surviving American (code large surviving) | 125 | 10 | 10 |
| Irradiated American | 199 | | 4 |
| Luther Burbank Cultivars | 7 | | |
| Other | 53 | | |
| Total | 5220 | | |

* We will have to make additional crosses in in some lines to achieve the desired number of 75 progeny per generation within a line.

A Chestnut Treasure

by Jack Stillman

Recent generations have never seen the like of the American chestnut tree. It towered over the forests of the Appalachians, lined the eastern United States and swept into the Midwest - that is until it was virtually wiped out by a mysterious fungus nearly a century, ago.

There were whole groves of these majestic trees in Pickens County, Georgia, until the late 1930's; by the 1940's they were all dead. Now, for those willing to tramp deep into the woods, new American chestnuts can be seen rising from the old root systems which never died.

Researchers and a few hardy woodsmen like Tom Brock, who operates a unique wood-working shop in Pickens County, hold out a faint hope that the disease which doomed these unusual trees can be conquered. Almost everyone who lived in the mountains felt the loss, it was so tragic. The chestnut forests affected the lives of so many people because the nuts, bark, leaves, sap and wood were important to their daily lives. Now, few people would even recognize the leaves of a chestnut tree if they stumbled across one. They are that rare.

Shortly after the turn of the century, the previously unknown fungus wiped out millions of trees, simply by forming a canker around the tree's base and choking off the flow of water and sap. The blight cannot thrive beneath the soil, so the roots are not affected.

Each year Brock discovers a few new trees, sprouts from the old root systems which refuse to die. It is on these millions of shoots that spring up every year that researchers are pinning their hopes that a solution to the mysterious blight can be found.

"Wouldn't that be wonderful if we could do that," Brock commented. "We have destroyed so many things on this earth, it would be simply wonderful if we could bring back something that is all but extinct."

Tom Brock has staked out a few stands of new trees. He has watched them through the past few years. One tree grew to a height of about 25 feet and produced nuts.

"I discovered it because I saw the nuts first," he said. "It may have been the only chestnut tree bearing fruit in the mountains."

It was near the side of a road. One day he found it toppled over. A truck had backed against it. It was the biggest of the new trees that he has found although its trunk was only about four inches in diameter.

The typical mature American chestnut a century ago was 90 feet tall, 5 or 6 feet in diameter and 500 years old.

Since the destruction of the 25-foot tree, Brock has found another one that is about 18 feet tall. Its trunk is about two and one-half to three inches in diameter and is perhaps five years. It will likely not live much longer, however, because the blight is already forming its deadly canker a few inches above the ground.

Sometimes Brock is discouraged by what seems to be a relentless fate for the chestnut: he finds clusters of new chestnut shoots three to four feet high, flourishing and giving no outward appearance that they are in trouble, but he knows they will never be allowed to grow to maturity.

They will not tower high in the canopy, nor will they become fine woodwork, moldings or other furnishings under Brock's hand.

Brock's shop is no ordinary millwork shop. He harvests hardwoods which he dries in his own kilns. Much of his work involves making moldings and trim for historical restorations. He reproduces patterns that are not available anywhere else.

Tramping through the woods with Brock is an adventure in itself for he is in his element. Trees that were merely trees turn into something special. There are vague marks on one which would have gone unnoticed until Tom explains they are the marks of a bear.

The dried earth here and there is full of animal signatures: the footprints of the fox, the cloven dash of deer, and in the early evening, the call of the coyote can be heard, all of which would mean nothing unless you are a part of Tom Brock's world.

For most of his work he uses poplar, red oak or maple. But occasionally he will discover a chestnut log, half buried, where it was felled by the blight 50 to 60 years ago. He hauls the logs to his mill, where he cleans off the outer decay. The inside is hard and solid as the day the tree fell. One such log yielded boards two feet wide - a chestnut treasure.

Most of the original moldings in the older buildings in Atlanta were made of hard pine. Although practically

unavailable now, this wood came from the center of the huge virgin pines which used to be so numerous in northern Georgia. The old-timers called it "lightard" because it was used as kindling to start fires. There are a few of these huge pines remaining, including one loblolly on Brock's property. That tree is more than a hundred feet tall with a diameter of about 12 feet and about 120 years old.

But to Brock nothing is as exciting as coming upon a new stand of American chestnuts, their huge leaves waving valiantly in the evening breeze as if to signal they are on their way back!

ONE MAN'S DREAM- THE RETURN OF THE AMERICAN CHESTNUT

By Jill Wilison
*In memory of her father,
Charles Tracey Matthews*

My father, Charles Tracey Matthews, was born in Amonate, West Virginia. At the age of 7, when his father died, his family moved back to his mother's home in Nelson County, Virginia. That was in 1938, and American chestnut trees were still being logged in

the area. There were still some very large trees, but they were disappearing fast.

My father's ancestors were all from Virginia and most can be traced to colonial times. His people were farmers, some more successful than others, and some of them were loggers. Those that were not certainly logged wood as the need arose, for the wood itself or to clear fields. He and his brothers hauled wood when he was young and one of his brothers is still in the logging business. One of his great uncles made a fortune in logging, especially chestnut wood, and the corresponding land deals. Chestnut trees were still being heavily logged in the face of the blight when his family returned to central Virginia in 1938. There were still some very large trees, but they were disappearing fast.

My father had an interest in trees and growing things.

However, he was especially concerned with the American chestnut.

It was sort of a passion for him. American chestnut had been a staple cash crop, at least in this part of the country. The wood could be used for almost anything. It did not rot and it was resistant to bug infestation. Houses and fences and furniture were made from chestnut and they lasted. The boards were wide and strong. Loggers could make their living on chestnut trees. The forests were full of them. Even in the 1950's and 1960's the remains of log cabins made from chestnut were found all through the mountains in this area. Another of my father's brothers built a log cabin antique store from chestnut logs gathered from abandoned cabins.

I think my father felt a sense of loss for this great tree and wanted to see it return to the forests of Virginia and elsewhere. He felt that there had been no tree to replace the strength, size, versatility and value of the American chestnut tree. Or its sweet nuts which he enjoyed roasting.

Dad grew up on a farm and, as a boy, walked all over the mountains in the area. Among other things, he would look for wood to make whistles. Though he used willow and other woods, American chestnut was his favorite. At that time, the size of the live chestnut trees he could find were barely large enough to make a whistle. In more recent times he was able to find larger trees.

"Nowadays you can find them from 8 to 16 inches in diameter," he'd say. "Though they are diseased, the tree is slowly winning the battle." He knew the chestnut would not recover in his lifetime, or even mine, but he felt he saw positive signs that recovery had already begun.

I don't think my father ever stopped being a boy. That is, as long as I knew him, he always loved fishing, frog hunting, turtle hooking, swimming and bathing in streams and rivers (versus a bath!), morel mushroom hunting, apple picking... He knew so much about his natural surroundings. He knew when anything was ripe, what plant was which and where to find things. He was a country boy. These things were part of his training. He enjoyed the woods, and at one time depended on them for much of his food. He never outgrew this desire to be outside and natural.

As an adult, my dad stayed very close to nature and visited his home in Nelson County often. He had attempted to work for a large corporation and we moved several times over 10 years to larger and larger cities farther and farther from his home. In 1968, he quit and returned to live in Charlottesville, only 30 miles from "home". I suspect he always knew of the Mawyer and maybe the Amherst tree. He would hunt things like that down. In addition to moving back into the area, he was divorced from my mother in 1969 and, without a family in his daily life, was more free to go "home" and do the things he liked to do again. He found out that there were other people interested in the American chestnut, such as Dr. Richard Jaynes of the Connecticut Agricultural Experiment Station and that there was a chestnut foundation.

On March 27, 1969, Dr. Jaynes returned his letter and asked how the trees were doing and whether he should examine them. Dad wrote back, inviting Dr. Jaynes to visit these trees with him and forwarded some scions from the tree on Tom Mawyer's place. He also warned Dr. Jaynes that the people of Nelson County were still suspicious of outsiders and it would be best if he visited the trees in his company.

On April 21, 1969, Dr. Jaynes flew to Charlottesville, Va., on his way to a chestnut planting near The Priest in Amherst County. He set aside that afternoon to visit the trees my father had written about. They visited the tree at Tom Mawyer's house (Uncle Tom he called him) and a tree in Amherst County on the Cash/Ross farm. Dr. Jaynes was impressed with "the size of the trees, especially the one at the Cash/Ross farm."

"Wish I could explain why the main trunk is alive even though infected, while some of the sprouts are dying from infections," Jaynes later wrote in a letter to my father about the Amherst tree. The Mawyer tree has died since then, but the Amherst tree is still alive and has been used in testing and breeding programs.

After Dr. Jaynes' visit, I don't think much happened. He knew the Amherst tree was special and how important it was that he had identified it. Yet science and the foundation did not include him any further in the work. Periodically, my father did visit the tree and he took me there a few times.

Dad thought, if I remember right, that the Amherst tree was a mutant. He felt that the same oddity that made it a sterile tree (unable to produce fully developed nuts) was also responsible for its survival. The inability to reproduce was either linked in some way to its resistance, or made it somehow stronger against the blight. He never talked much about the Mawyer tree, that I remember. He did think that there were old trees that had somehow survived and occasionally other trees that make it despite the blight.

My father planted several chestnut trees, including American, Chinese and crossed trees, but none ever grew to his satisfaction. He followed planting programs and obtained sapling trees to plant. He looked in the woods for old trunks and for trees that struggled to survive despite the blight. He also made several attempts over many years to grow the right black walnut tree, but never quite made it. He did grow a tree with large nuts, easier to crack, that he felt might rival the Thomas Walnut. However, the last crop I gathered from the tree rotted in the shells in the drying process, though the previous crop had been good.

When Dad was dying of cancer, I asked him what his most significant accomplishment in life was, what he wanted to be remembered for. He replied his work with the chestnut trees and the walnut trees. He felt he had failed or run out of time with the walnut tree, but he felt a great deal of satisfaction in having identified the Amherst tree for research and breeding. I had to piece together, after his death, who he had contacted and find out exactly what he had done, to feel that intense pride of accomplishment. I found the letters to the foundation in his files.

I learned from my father the joy of being in the woods, identifying trees, growing my own apple and peach trees, planting a garden, foraging for wild fruit and nuts ... in the same part of the country where he grew up. I own land that has forests and would like to see the

chestnut return as a viable tree. I watch several large chestnut trees to see how they are doing. From one of my trees, very infested with blight, I obtained leaves and burs to place on his coffin.

Shortly before his death in July 1992, my father said, "The American chestnut will be back before the experts think it will, one to two generations more. The trees have come so far just in my one lifetime."

PENNSYLVANIA- GERMAN TRADITION AND THE AMERICAN CHESTNUT

by Doris Armstrong Goldman

The Pennsylvania Germans originally lived in rural areas where the American chestnut constituted up to half of the trees (4), and thus played an important role in the culture and daily lives of these people.

The Pennsylvania Germans came to America between 1710-1820 from places where European chestnuts were grown and are still appreciated in cooking, such as Alsace-Lorraine, Switzerland, and especially the Pfalz, or Palatine region of western Germany (3,8).

In a book on British medicinal uses of plants published in 1772 (1), Dr. R. Brookes says that chestnuts are "windy and hard to digest, so they seldom agree with any except laborous working people", but he added that chestnuts were much eaten in continental Europe, and were prepared by boiling or roasting. Since the Pennsylvania Germans were already familiar with chestnuts, they probably made use of the American nuts soon after they arrived. Notably, they called one of their garden plants, *Cyperus esculentus* (now known as yellow nutsedge) by the name of Grund Keschde, or ground chestnut (8). English speakers called the plant - which is raised for its edible tubers - ground almond, nutsedge or chufa.

Many of the Pennsylvania Dutch words for tree parts use the very "flat" sort of Pfalzer German spoken in regions where chestnut was important to daily life rather than formal high German. Chestnut tree = Keschdebaum. The chestnut burr or fruit husk Iglra or Keschdigla, the nuts were Kesche or Keschde (8).

The Pennsylvania Germans learned so many of their folk remedies from the native American Indians that to brauche mit, which meant to use a folk medicine or charm, a Brauchmittel, was to "pow-wow in English. Like the Indians, they treated whooping cough with a medicine prepared with the liquid left after boiling chestnut leaves in water (8). The Indians also used a tea of chestnut leaves as a sedative and tonic, used the bark as a dye and as a treatment for worms (7). They also cooked with chestnut meal and chestnut oil (9, 2).

The Pennsylvania Dutch used durable, rot-resistant chestnut wood for furniture, musical instruments, caskets, shingles, houses, barns, and for long-lasting fences, barrels, and pump parts.

Chestnut was considered to be poor firewood (8).

Chestnut tanbark, which was used for tanning leather, was prepared first by removing the bark in the spring when the sap was ascending with a tan spud, or Rinnascheeler (8). Then the material was ground up fine and soaked for several days to extract the tannin which would be used to work the leather.

Chestnut timber was cut in August and December, probably during relatively slow periods on the farm, and preferably during the old moon which they believed was the time when the wood would be free of worms (8). Among carpenters and woodworkers, American chestnut was often the favorite wood both for personal preferences and utility's sake; the wood was used for a wide variety of purposes.

One barn built in central Pennsylvania in the 1800's still stands and is completely made of chestnut. Although another barn of about the same era contains no chestnut, even though it was built by a farmer who also ran a tannery (Terry Pelton, restoration craftsman, personal communication) just a few miles from forests where chestnuts still sprout. Fencemaking also involved chestnut (6). Field fences were constructed largely of chestnut wood and according to specific designs, the favorite being the split-rail style.

The rail-splitting tool or froe was the Schpaltmesser, and the plane was the Howell. Posts were chestnut or locust, hewn with a broad ax to be about "6.5 to 7 ft. long, 7 to 8 ins. wide and 3 ins. thick." They were sunk deep enough to leave 4 ft. 4 ins. above ground. So that posts would "grow into the ground" and not be frost-heaved, they were set when the old moon was in declension (8) or were set upside down (3). Posts were spaced 11 ft. apart, and were connected by 12-foot long chestnut rails, put flat side out through holes 6 ins. from the top and bottom of the posts. The family kitchen garden, often called a four-square garden because of its layout, was surrounded by a picket fence or Glabbordfens, partly for display and partly to keep animals out. Each 11-foot section was called a Gfach, or Daerli. Only two rails were needed to support the pickets, which were made of chestnut, oak or pine, and spaced about 1 in. apart.

One family made pickets by splitting 4-foot chestnut logs into billets 4 to 5 ins. wide and 6 to 7 ins. thick and then into 6 or 7 pickets. A 45-degree saw cut at the top put a point on the picket (6). The "white picket fence"¹ celebrated

in American culture was certainly a part of Pennsylvania Dutch homelife. Typically they whitewashed many wooden structures on the farm, which gave a neat appearance and helped preserve the wood. The author works at a park site in which the farm, built in the 1700's also has a lime kiln on the property. Studies indicate that at least by the 1800's the typical Glabbordfens was white-washed annually (6).

Elsewhere in the garden, chestnut bordered the raised beds and made boardwalks and coldframes. Grape arbors and poles for hops and beans were made from chestnut or red cedar (6).

In the spring, children used to slip the bark off chestnut shoots to make whistles called Keschedpeifa (chestnut pipes), but in the fall, they had to go out to the woods to help gather chestnuts for harvest. Some children disliked the task because the spiny burs pricked their hands and feet (8). A proverb used when someone pouted or made a sour face (for example, after stepping on a chestnut bur!) was En Maul macha wie en Fuchs wanner Keschedigla fresset or "the fox makes a terrible face when he eats a chestnut bur" (8).

Several Pennsylvania German proverbs about chestnuts predict the size of the nut crop judging by the weather in early summer. These may have a factual basis, because if it's too rainy or cold during pollination and fertilization or fruit set, the crop is poor.

Wann uf di Pingschte regert, gebts ken keschte, which means "Rain on Pinkster means no chestnuts." Pinkster, known as Whitsuntide or Pentecost, usually falls in mid-May.

Wann di Maciche nass iber der baerik get, gebts ken keschte, which means "When the Virgin gets wet as she goes over the mountain there will be no chestnuts." this means that when it rains on the visitation of the Virgin (July 2 the day commemorating the visit of Mary to her cousin Elizabeth), the chestnut crop will fail.

Wann regert uf der Tschann Huss, gebts ken nuss, which means "When it rains on Jan Huss' Day (July 6) there will be no nuts." Jan Huss was a Czech religious reformer burned at the stake in the 1400's.

Wabbs regert uf der Siberschleffer gebts ken keschte, which means "When it rains on the day of the Seven Sleepers (July 27) it gives no chestnuts."

Some of these proverbs are nearly identical to proverbs from western Germany (3), but this one is truly American: Wanns ufer firt Tschulei regert waern di keschte waermich, which means "When it rains on the 4th of July the chestnuts will be wormy."

Finally, in the fall, Fil hikerniss, haselniss, walniss un keschte bedeite en haerter winter" or "Full hickory nuts, hazel nuts, walnuts and chestnuts foretell a hard winter."

These tidbits came entirely from my library research. Older people with a Pennsylvania Dutch background likely have many interesting first-hand stories. Chestnuts also undoubtedly figure in the folklore of other parts of the country. It would be interesting to learn more about the similarities and differences of the tales and traditions from region to region.

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RESEARCH UPDATE: PATTERNS OF REPRODUCTION OF AMERICAN CHESTNUT IN A BLIGHT-FREE HABITAT - SAVANNA, ILLINOIS

Research conducted by Fred Paillet,
Eric Ribbens and the Illinois ACF Chapter

The basic premise of our study seems to be panning out - the initial data show that this is a location where we can see the pattern of reproduction from a single pair of introduced American chestnut trees, and at the point in time when the "offspring" from the initial pair of trees have just begun to bear fruit on their own, writes Dr. Fred Paillet in his notes on the study.

Scientists and ACF members completed the first phase of their research in June of this year and submitted a promising progress report.

The project, funded at \$2,080 by The American Chestnut Foundation, focuses on the ecology of American chestnut reproduction in a blight-free habitat. Two sites are under study: one in which chestnut trees are reproducing well, and one, at the Mississippi Palisades State Park, in which seedlings do not seem to be establishing themselves successfully. Both are located near Savanna, Illinois, in the northwest corner of the state.

The grant covers the cost of fence materials, seed traps, supplies, and basic transportation expenses. Labor is either volunteered or paid by other sources, graphic work including photography and manuscript preparation is covered by the U. S. Geological Survey. Lodging is accommodated by camping.

The study focuses on surveying and interpreting patterns of nut dispersal, the influence of rodents caching seeds, the survival of sprouting seedlings, and the effects of various ecological disturbances, such as logging, brush mowing, and extensive oak blight, on the reproduction of the chestnut trees.

The information gathered from this study will hopefully prove very useful in re-establishing chestnut once blight resistant varieties are created through ACF's breeding program. The study will also likely shed light on the role of chestnut in prehistoric forests under neoglacial climate conditions, research of interest to and being conducted by the USGS.

The work is being carried out over a three-year period and will rely strongly on the time and insight provided by ACF Illinois Chapter volunteers. In June, during Phase One, Paillet, Ribbens and a cadre of volunteers spent an intensive week preparing site number one, which will hereafter be referred to as the Lang property. The property is private land, a parcel of about 10 acres containing approximately 120 trees that seem to have all developed from two individual trees of between 70 and 100 years of age. The team's notes follow.

1. All chestnut stems greater than 10 inches in diameter at approximately 1 meter above ground level were mapped. All trees were classified as to location, diameter, crown shape and reproductive status (based on fertile burs on the ground). The pattern shows the "foot-print" of reproduction centered on the pair of original trees. The pattern shows a definite concentration around the larger of the two trees, which was cut about 10 years ago. This pattern probably results for two reasons. First, because that tree was larger, it was probably a better seed source. Secondly, the remaining tree is now at the edge of the woodland and may have been growing under more open conditions in the past where the ground below would have been unsuitable for seedling establishment.

2. All chestnut stems from seedlings to trees were mapped on 300 meters of 10-meter-wide transect. The single outstanding feature of this mapping was the lack of recent chestnut reproduction. We found only one seedling from last fall's nut crop, and only two (probable) 2-year-old seedlings. This compares to literally hundreds of oak and hickory seedlings on the same plots.

3. Two 10-meter-square plots for enclosures and one control plot were mapped. All stems and other features such as logs and stumps were mapped in the plots. Non-nut stems less than 0.25 cm., such as elm and

mulberry were not mapped; these species generate many young seedlings, relatively few of which survive to maturity. All chestnut, oak, walnut, and hickory seedlings, however, were mapped. Stems and nut seedlings were listed and mapped for each 2 x 2 meter sub-plot. Plots were located near access roads to permit easy access of equipment while installing fences. Locations were also selected to minimize tramping through the woods, while still lying within the woodlot and in areas designed to capture chestnut seedfall.

4. Outlying reconnaissance. A preliminary search was made along the periphery of the distribution on the Lang property (including an adjacent preserve) and the area surrounding the two chestnut trees at Mississippi Palisades State Park. Two outlying trees were found on the Lang property, but none in the preserve. No outliers were found in the state park, but such a search could not be thorough in the available time and during a part of the season where the understory is the most dense. We note the fact that the outliers on the Lang property seem to be among the biggest of the offspring from the original pair of trees.

5. The two exclusion fences were installed by Gerry Kopf and a crew of local volunteers from the Illinois Chapter of the ACF. Stakes were used to identify the corners of the control plot. The land owner, Dan Lang, has been urged to make no changes in land use (mowing of open areas, grazing of livestock, etc.) that would impact the experiment.

COMMENTS

The main focus of the work completed so far has been to set up transects and test plots with fences, map the basic distribution of chestnut stems at the site, and observe the nature of ongoing reproduction. The number of new chestnut seedlings was expected to be smaller than the number of oak and hickory seedlings. Even so, we found the lack of recent reproduction striking. We know the chestnut trees are reproducing here, we just can't seem to catch them doing it!

The spatial pattern of reproduction around the source trees probably says something about the nature of seed dispersal superimposed on the effect of microsite. We need to observe how nuts are being dispersed this fall, and to spend more time mapping the most distant outliers. There may be other trees we haven't yet mapped out there. The best time to do this would be in the fall when there is less interference from the underbrush, and when the distinctive yellow-brown of chestnut leaves can be used to find any more distant trees.

In general, the work is progressing as planned except that we have made transects shorter and wider than as planned (300 meters long and 10 meters wide versus 500 meters long and 2 meters wide) because seedlings were so few, and smaller chestnut stems seemed more tightly concentrated in the vicinity of the original trees.

The paucity of reproduction also forced us to set up exclusion fences and only one control so that the plots were directly underneath the largest expected seedfall. Another issue is also worth mentioning. The landowner completed a selective logging operation on one corner of his property to salvage diseased red oaks. No new chestnut seedlings were observed in the logged area, but the openings and soil disturbance associated with logging lies just adjacent to the largest "offspring" chestnut. This area offers the chance to check the effects of such disturbance on chestnut reproduction. We expect to identify small test plots for monitoring in this area on our next visit.

Finally, we note that a tree approximately 20 centimeters in diameter of the typical "clean" form of a chestnut sapling was found completely dead, even though the shape of this tree indicated it had been making rapid growth into the subcanopy. There is a slight chance that this is in fact a dead chestnut tree. But the lack of any basal sprouting in response to what appears to have been a fungal infection suggests that this was a red elm. Young elms have the same growth form and

ray-free ring porous wood that we identify with chestnut. Another more recently killed red elm (presumably by Dutch elm disease) was found with this same growth form, and this tree could be identified positively as an elm. Therefore, we do not think this is a case of chestnut blight.

Continued research is scheduled for this fall. Seed traps will be established to record nutfall in time for the 1994 nut season and observers will be stationed to view dispersal, particularly by squirrels and rodents. Artificial seed caches will be established using nuts obtained from the seed crop, and wildlife foraging observed at various times over the following year. Throughout the three-year period, measurements of seedlings and saplings will be taken, and patterns of establishment charted.

GENETIC MAPPING OF CHESTNUT

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Readers of The Journal know that The American Chestnut Foundation is attempting to backcross the blight resistance of the Chinese chestnut tree into its American cousin. To do this, we cross a Chinese chestnut with an American chestnut tree to obtain offspring which are one-half Chinese and one-half American. These one-half trees are referred to as first hybrids, or F1s in genetic symbolism. An F1 is backcrossed to a pure American chestnut tree to obtain offspring which, on average, are three-fourths American, one-fourth Chinese. We select blight-resistant trees from among these first back-cross, or BC 1 progeny, and backcross them again to another American chestnut tree to obtain offspring which are seven-eighths American and one-eighth Chinese, on average. An additional cycle of selecting and backcrossing yields offspring which are fifteen-sixteenths American and one-sixteenth Chinese, on average. These hybrids should closely resemble their American parents, but carry the blight resistance of their Chinese great-great grandparent.

The purpose of the successive backcrosses to American chestnut is to dilute out all traits of the Chinese tree, except for blight resistance, for which we are selecting. However, please note in the description above that I always used the key words, "on average," when describing the proportion of American and Chinese parentage in each backcross generation. Theoretically, first backcross trees can range from one-half Chinese to one-hundred percent American. They are only three-fourths American when we take an average across a large population of trees. Individual trees will display a fair amount of variation around the average value. We can take advantage of this variation by studying the proportions of Chinese and American parentage in each backcross generation and selecting trees which have more American parentage than the average. This can speed up the breeding process.

For instance, it would be possible to recover a first backcross tree with blight resistance that was seven-eighths American. Doing so would have diluted out as much Chinese chestnut parentage in one cycle of backcrossing as is normally accomplished in two cycles. We might then backcross that seven-eighths tree a second time and recover a blight-resistant second backcross tree that was thirty-one, thirty-seconds American instead of fifteen-sixteenths. Thus, we would have accomplished in two cycles of backcrossing what is normally accomplished in four.

So how does one pick out backcross trees that are more American than average? One way is to examine the appearance of the trees, or, in botanical jargon, their morphology (which means the science of form). For example, Chinese chestnut leaves and stems are hairy whereas American chestnut leaves are hairless, so one would select backcross trees with hairless rather than hairy leaves and stems. Another approach to picking the most American-like tree in a set of backcross progeny is to examine proteins which vary between Chinese and American chestnut. Then one could select trees with American forms of the proteins. The proteins that are examined most commonly are enzymes, which catalyze chemical reactions. An example of an enzyme is amylase, found in our saliva. Amylase catalyses the conversion of starch to sugar. Many enzymes exist in several forms, and these forms are called iso-enzymes, or isozymes. Isozymes are the most commonly examined proteins for detecting differences between species, because their catalytic ability makes them easy to detect.

A third approach to picking the most American-like trees is to examine the genetic material itself, the DNA, or deoxyribonucleic acid. There exists a bewildering array of these molecular genetic techniques, with acronyms such as RFLP, AFLP, RAPD, and VNTR, which are used to examine DNA. The bottom line for us is that each of these molecular techniques might be used to select backcross trees with a high proportion of American DNA.

So which approach is best? The morphological approach is the fastest and most inexpensive, by far. However, there are not enough morphological differences between American and Chinese chestnut even to identify all the chromosomes in chestnut. So, after two or three rounds of selection for American morphology, we probably would not be able to distinguish our backcross trees from American chestnut, but the backcross trees could still possess a large complement of Chinese genes.

Thus, it would be best to complement the morphological approach with the isozyme and/or molecular approaches. To do this, it would be necessary to use isozyme and molecular markers which do not identify the same region of the chestnut genome as morphological markers. And in order to identify such markers, we need to map all of them onto the chestnut genome. In other words, we need to prepare a genetic map of chestnut.

GENETIC MAPS

An obvious question at this point is, what is a genetic map? First, we have to introduce the concept of linkage. I mentioned above that Chinese chestnut leaves are hairy while American chestnut leaves are hairless. Chinese chestnut stems are also green or tan-colored while American chestnut stems are red. In a first backcross to American chestnut, one-half of the progeny will have hairy leaves and one-half will be hairless if leaf hairiness is controlled by one dominant gene. Likewise, one-half will have red stems and one-half will have green stems if stem color is controlled in a similar fashion. (In actuality, both traits are inherited in a more complicated fashion). For both traits, the two forms of each trait are found in 1:1 ratios, if each is controlled by one gene. If we find that backcross trees with hairy leaves show red and green stems in a 1:1 ratio, while trees with hairless leaves also show red and green stems in a 1:1 ratio, then the two traits, leaf hairiness and stem color, are said to be unlinked. On the other hand, if plants with hairy leaves have more green than red stems, while plants with hairless leaves have more red than green stems, then the two traits are linked.

The strength of the linkage between traits is usually expressed as percent recombination, and these percentages are used to construct a genetic map. Recombinant plants are those that do not show the combined traits of the parents. Remember that Chinese chestnut has hairy leaves and green stems while American chestnut has hairless leaves and red stems. Recombinant backcross chestnut trees would be those with hairy leaves and red stems or hairless leaves and green stems. If we found 20 recombinant plants out of 100 in a backcross population, that is, 20 with either hairy leaves and red stems or hairless leaves and green stems, then the recombination percentage would be 20 percent. Recombination percentages can vary from 0 to 50 percent, where 0 indicates complete linkage and 50 indicates no linkage.

If we were to examine a third trait, such as stipule size, (stipules are small leaflike structures that appear on either side of the leaf base) we might find that leaf hairiness, stem color and stipule size are all linked. The recombination percentage between stipule size and stem color might be 10 percent while that between stipule size and leaf hairiness might be 30 percent. Geneticists have found that recombination percentages are related to each other in a linear fashion, so that, in this case, the distance between stipule size and stem color, 10 percent, plus the distance between stem color and leaf hairiness mentioned above, 20 percent, adds up to the distance between stipule size and leaf hairiness, 30 percent.

Genetic maps are constructed by examining numerous traits and determining the recombination percentages between all of them. Using the linear property of recombination percentages, one then deduces the order of the linked genes. This order, with the distances between genes, is the map. In the hypothetical example discussed above, the order is stipule size, stem color and leaf hairiness.

Geneticists have found that there will be several groups of traits linked to each other, with no linkage of traits between groups. The number of groups should correspond to the number of chromosomes. A great deal of study is needed to assign each group of traits to a particular chromosome.

A MAP OF MORPHOLOGICAL TRAITS IN CHESTNUT

I began this mapping process in chestnut - for which no genetic map has been constructed - by examining morphological traits in the Chinese and American parents, their F1 hybrid, first and second backcrosses to American chestnut, and F2 and BC1-F2 progeny. F2 progeny are the offspring of two F1 hybrids crossed with each other, while BC1-F2 progeny are the offspring of two BC1s crossed with each other.

Concurrently with my work, there is also work in progress using the isozyme and molecular approaches. The isozyme approach is being pursued at Auburn University by Hong-wen Huang and Joe Norton. The molecular approach is being studied by Jain-su Zhang and Robert Bernatzky both of the University of Massachusetts and Robert Doudrick and Warren Nance of the U.S. Forest Service in Gulfport, Miss. David Mulcahy of the University of Massachusetts also has been using the molecular approach to search for linkages with blight resistance genes.

Mulcahy and Bernatzky discussed some of their work on pages 33-36 of Vol. VII, No. 1 of this journal.

For the more curious, a complete paper describing the mapping for morphological traits should be published in the September, 1994, issue of the Journal of Heredity. Here, I present a summary of the results and the important conclusions. A preliminary report on the inheritance of leaf and twig hairiness appeared on pages 119-121 of Vol.

VI, No. 2 of this journal.

Seedlings were examined for hairiness on the leaves, leaf veins and twigs. They also were examined for stipule size, bud shape and stem color. Figure 1 depicts most of these traits in Chinese and American chestnut. I might note that many of the traits were determined in midsummer on seedlings in their first year of growth. On older trees and at other times of the year, traits can vary, especially stem color.

Table 1 presents all of the easily observed morphological differences between Chinese and American chestnut of which I am aware. Obviously, I could not examine traits related to burrs and nuts in the young seedlings. Several other traits were not easy to score or gave inconclusive results.

Table 2 presents a summary of most of the traits I did score in more than 1,300 seedlings, together with the number of genes which controlled each trait, the method by which those genes controlled the trait, the dominant parent for each trait and the symbol assigned to the gene(s) which controlled the trait. I also scored the 1,300 seedlings for bud shape, but no simple genetic hypothesis was found to explain the data.

TABLE 1
Morphological differences between Chinese & American chestnut

| Organ | Chinese | American |
|----------|---|---|
| LEAVES | 1)shiny (waxy) 2)leaves growing in full sun are hairy; underneath have a whitish cast 3)leaves are ovate 4)teeth not pronounced 5)angle between leaf base & petiole can be acute petiole never acute 6)leaves leathery | dull leaves not hairy; green underneath leaves lanceolate teeth pronounced angle between leaf base & leaves not leathery |
| STIPULES | 1)0.5-1 cm broad at base triangular narrow from tip to base 2)persistent on stem | 0.1-0.2 cm broad at base drop soon after leaf expands |
| TWIGS | 1)tan or pea green 2)hairy 3)lenticels (white spots) large, 0.5mm | reddish brown to brownish green not hairy lenticels small, 0.1 mm |
| BUDS | 1)tan to dull brown 2)rounded: almost as wide as they are long 3)closely appressed to stem 4)main axis parallel to stem 1)tips tend to be rounded 2)hairs generally only around tip 3)in white part (base), vascular bundles frequently not visible | reddish brown to yellowish brown pointed, only half as wide as long stick out from stem main axis not parallel to stem tips pointed hairy down 1/3 to 2/3 of length vascular bundles clearly visible, arranged in a sunburst pattern |
| BURS | 1)spines about 1 mm in diameter, 1-2 cm | spines about 0.5mm in diameter, 2-3 cm long |

Most of the genes were not linked with each other, but there was some linkage, and Figure 2 shows how those genes were mapped, and the distance between them in percent recombination, with standard errors.

Taking all traits together, 3.4% of 119 BC1s and 8.8% of 297 BC2s had all-American morphological traits, namely,

no interveinal hairs, a low density of vein and twig hairs, small stipules, red stems and cylindrical, pointed buds. Currently, we attempt to grow only 75 trees in each backcross line partly because controlled pollinations are so laborious. We expect one-quarter or one-eighth of the 75 trees to possess all major genes for blight resistance. Thus, when we select for both blight resistance and all-American morphological traits, given no linkage between blight-resistance and these other traits, we can expect the following results. Only one or two individuals, on average, from a BC2 line will possess all major genes for blight resistance. (Seventy-five trees multiplied by one-fourth, to account for blight resistance, multiplied by 8.8% to account for those with all-American traits equals 1.65 trees with all required characteristics). Thereafter, selection for American traits using only morphological markers will suffice prior to the third backcross

TABLE 2
Number of genes, interaction type, dominant parent, and symbol for traits observed in crosses of Chinese and American chestnut

| Trait | Number of Genes | Gene Interaction | Dominant Parent | Symbol |
|---|-----------------|------------------|-----------------|-----------------|
| Leaf Interveinal Hair Occurrence with modifiers | 1 | Single Factor | Chinese | Inh |
| Leaf Vein Hair Density incompletely dominant | 3 | Multiple Factor | Chinese | Vnh 1,Vnh2,Vnh3 |
| Twig Hair Density incompletely dominant | 2 | Multiple Factor | Chinese | Twh ;,Twh2 |
| Stipule Size incompletely dominant | 2 | Multiple Factor | American | Stp1 ,Stp2 |
| Stem Color | 2 | Complementary | American | Red1, Red2 |

Once we have accumulated enough scientific knowledge and financial resources to score progeny for molecular or isozyme genetic markers, the genetic mapping of morphological markers described here will enable us to use fewer of the more expensive markers to accomplish our goal of producing blight-resistant, American-type chestnut trees in the shortest time possible.

ECOLOGY AND PALEOECOLOGY OF AMERICAN CHESTNUT IN EASTERN NORTH AMERICAN FORESTS

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INTRODUCTION

The American chestnut (*Castanea dentata* (Marsh.) Borkh.) was an important tree in the eastern deciduous forests of North America (3), but it was removed from the forest canopy after 1900 by an introduced pathogen (2), the chestnut blight fungus (*Cryphonectria parasitica* (Murr.) Barr). As a result, relatively little is known about the ecological characteristics of the American chestnut in preblight forests (20).

Nonetheless, there is a renewed interest in its ecology due to several factors. These include: an interest in reconstructing the role of chestnut in preblight forests (5, 6), the apparent association of chestnut with climate changes over the past 2,000 years inferred from pollen data (12, 22), the unexplained abundance of chestnut sprouts in modern forests (1, 13, 14, 21), and an interest in understanding how chestnut ecology may relate to the control of blight and the establishment of blight-resistant chestnuts in future forests (8).

This paper reviews more than a decade of research on chestnut ecology and discusses how these results may be used to interpret the role of chestnut in prehistoric forests inferred from studies of fossil pollen in New England.

CONCEPTS

Recent surveys of surviving American chestnut populations demonstrate that chestnut sprout clones - groups of genetically identical shoots that sprout from preformed buds on the root collar at the base of existing stems - are an important part of the understory in many eastern woodlands, and may be increasing as a percentage of total stand biomass. Studies in southern New England indicate that most chestnut sprouts originated as seedlings rather than developing from the root collars of former canopy-dominated trees.

Woodlands with many logs from former large chestnut trees and few surviving sprouts may indicate that chestnut was not reproducing in some former chestnut stands.

Comparative studies of chestnut and chinquapin, which have similar growth forms, also provide insight into the ecology of the American chestnut, as do studies of the frequency of chestnut pollen found in bogs, forest hollows and soils.

MATERIALS AND METHODS

Mapping and distribution. The locations of chestnut sprout clones, large logs and stumps of former chestnut trees were mapped at several locations in New England. Most of these study sites are in south-central Connecticut, northeastern Massachusetts and southern New Hampshire (12, 13, 14).

Chestnut population densities were characterized as absent, low (less than 20 clones per ha), moderate (between 20 and 100 clones per ha) and abundant (more than 100 clones per ha). The precise locations of individual sprouts, logs and stumps were mapped over selected areas of from 0.2 to 1.0 ha, and along 2 m-wide transects extending over distances from 0.3 to 2.0 km. The number of clones and stumps counted ranged from a few to hundreds.

Sites where chestnut clones found were classified as old fields, former woodlands that had been regularly harvested, former pastures, etc., according to available land use records and physical inspection of the sites.

Growth form. Chestnut sprouts in mapped areas at the study sites were separated into classes based on number of stems, height, stem shape and estimated age class. Overall clone vigor was given by the average yearly elongation of terminal shoots on primary lateral branches, one of the most active and vigorous growing parts of the tree. Dead chestnut wood was identified using the criteria given by Panshin et al. (18). The color, ring structure and lack of ray cells made chestnut easy to recognize in the field. In oak, so-called rays reinforce those cells which run vertical or parallel to the trunk by connecting them radially. As a result, oak resists splitting, but it also bears the streaked appearance we prize.

Dead chestnut was classified according to size, number of stems and type (sawed stump, snag, fallen log, etc. (14)). The size and shape

of root collars, and number of preformed buds were noted for sprout clones in some of the mapped areas. Similar

studies of growth form were conducted in a small, naturalized but unblighted chestnut stand in Wisconsin (16), and in chinquapin (*Castanea pumila* (L.) Miller) stands in Arkansas and Virginia (15) for comparison with blighted chestnut in New England.

Dendrochronology. Increment cores were taken from numerous living chestnut sprouts and canopy trees (oak, pine and birch) adjacent to sprouts and the remains of large, blight-killed chestnut trees. Cross-sections also were taken from chestnut stems of various sizes in order to determine the ages and reconstruct the growth histories of these stems. Ring increments were measured using a wood microscope by the U.S. Geological Survey Tree Ring Laboratory in Reston, Va. Increment series were processed and analyzed using the techniques described by Fritts (7) and Paillet (13).

Pollen analysis. Pollen samples were recovered taken from soils and moss polsters (typically round, clumps of moss) within a naturalized chestnut stand in Wisconsin, a modern chestnut forest which served as a control for studying the ecology of past forests. Samples were treated as described by Paillet et al. (17), Heide (9) and Winkler (23). All pollen data are given as percentages based on a minimum of 300 counts per sample.

RESULTS AND DISCUSSION

Mapping and distribution. Mapping the distribution of chestnut sprouts at various sites in New England indicates that sprouts are abundant, but very irregularly distributed in old forests. Some local areas of dense populations include sites where chestnut sprouts completely dominate the understory. The concentrations of sprouts sometimes coincide with the location of former large chestnut trees, and are separated by areas of very low population densities. In other locations, there are many large chestnut stumps, yet few or no living sprouts. At still other sites, the modern distribution of sprouts indicates a "halo" around the location of former woodlots that had been dominated by chestnut, but now are dominated by hemlock.

In Connecticut, chestnut sprout densities seem to be related to local terrain features, with concentrations of sprouts around old stone walls, roadsides and on the edges of swamps and streams (14).

Only those sprouts clearly arising from the base of former canopy chestnut trees showed a relationship to preblight chestnut trees. Chestnut sprouts develop only from the root collar, so that sprouts arising from former canopy trees are always closely associated with the stump of the former tree. Seedlings and sprouts look alike, except that one originates from a chestnut and the other from a bud located on the root collar of a seedling, sapling, or tree. The sprouts only arise from buds already formed and long dormant on the root collar, as opposed to other trees and shrubs where the sprouts can come from any location (roots, stems and root collar). The point is, you can tell if a sprout came from a big tree because the remains of the stump will be there. There are questions about whether sprouts without such a stump are from seed, or from a small stem that was already there - an "old" seedling.

Most sprouts (more than 95% in New England) appear completely independent of former trees. Instead, they must have been "old seedlings"- seedlings that have been resprouting since they started from the seeds produced by fruiting trees before blight appeared 80 years or more ago. This result agrees with similar results given by Keever (10), and documented for preblight forests by Zon (24).

These results also suggest that the modern distribution of chestnut sprouts effectively represents the distribution of chestnut seedlings in New England at a time when agricultural lands were being abandoned to the forest.

So few new seeds are being generated now, that one can infer we are seeing the pattern of seedlings that were established at that time. The pattern of sprout distribution shows a concentration of sprouts on the edges of what were woodlots between 1900-1920 populated by stands of young birch, pine and oak - trees characteristic of abandoned agricultural fields. If these woodlots had been established forests one would expect to find maple, beech and hemlock.

Growth form. Most chestnut sprouts in New England are 1-3 m tall, 2-8 cm in diameter 1 m above ground level, 10-40 years old and consist of a single main stem. About 60% of the clones mapped in Figure 1 consisted of a single stem or one large stem with one or more much smaller secondary stems in 1983. Shoot elongation on the largest lateral branches varies from 2-10 cm per year. Less than 5% of the clones in undisturbed woodlots indicate the presence of an active blight infection during the previous two years, but nearly 100% of clones in areas where chestnut is released - typically by a natural disturbance such as a windstorm, disease to the overstory, or fire, but also evidenced by human disturbances such as logging or road construction - are infected by blight within 5 years after removal of the overstory.

Comparison of the growth form of chestnut and chinquapin indicates that they have similar growth forms, but that chestnut sprouts are slightly larger and tend to have fewer stems per clone (15). They apparently have similar life cycles involving long periods of suppression, during which they compete against overstory trees for light, nutrients

and moisture; once released from these limited conditions, both chestnut and chinquapin direct their energy to producing seed and generating a larger stem, with chinquapin generating seed more rapidly than chestnut.

The only significant difference between chestnut and chinquapin, in addition to overall size, is that chestnut sprouts are consistently found with root collars that originated with the current stem, whereas chinquapin stems originate from the same root collar over many generations of sprouts.

Chestnut actively walls off new sprout tissue from the old root collar, and generates a new root collar and root system in each cycle of sprouting. Chinquapin retains the entire root collar and old root system as a locus for continued sprouting throughout the lifetime of individual stems. These differences probably reflect adaptations for maintaining a relatively defect-free stem for a long-lived canopy tree (chestnut) and for efficient reversion to shrub form for a sub-canopy tree or shrub (chinquapin).

The chestnut also exhibits sprouting characteristics suited for multiple cycles of release and reversion to shrub form. It is a tree suited for long-term survival in the understory of relatively open, oak-dominated forests.

The high density of chestnut sprouts originating as seedlings and the long period since a chestnut seed source was present in New England demonstrate the ability of chestnut to "store" reproduction in the understory. It is proposed that the life cycle of chestnut is a two-step process: seedlings first are established in the understory, later, after disturbance, they attain a position in the canopy. Many other temperate and tropical tree species have a similar ecological life cycle (11, 19), but chestnut appears to use this strategy more effectively than any other deciduous tree in eastern North America.

Dendrochronology. Increment borings indicate that most chestnut sprouts have stems that increase in diameter by about 0.20 cm per year. However, chestnut sprouts were found growing less than 0.05 cm per year where they were heavily suppressed, and at rates of more than 1.5 cm per year when they were released.

Increment borings on oaks and chestnut trees released by the blight destruction of chestnut indicate that blight reached southern Connecticut by 1910, and extreme northeastern Massachusetts before 1925 (13). The oldest chestnut sprout stems found in New England are now about 40 years old, and thus originated long after blight killed the canopy chestnut trees in New England.

One can conclude that these clones originated from "old" seedlings and have had at least two generations of stems. Analyses of variations in ring widths otherwise indicate that chestnut was unusually insensitive to short-term variations in climate (R.L. Phipps, personal communication).

Pollen analysis. Analysis of pollen obtained from soil and moss polsters in a naturalized American chestnut stand in Wisconsin indicates that chestnut is slightly over-represented in pollen deposits located directly under the source trees. Paillet et al. (17) conclude that measured percentages of chestnut pollen need to be multiplied by a factor of 0.8 to estimate the local percentage of chestnut in the pollen-producing canopy.

By contrast, chestnut pollen is poorly dispersed above the canopy, so that chestnut is severely under-represented in the sediments of lakes and bogs. Paillet et al. (17) conclude that the percentage of chestnut pollen counted in such sediments needs to be multiplied by a factor of 3.0 to approximate the percentage of chestnut in the forest canopy contributing pollen to the bog catchment (Figure 4). However, it is important to note that a large area (many square km) contributes to the pollen influx into lakes and bogs, while a small area (probably a few ha at most) contributes to the soil pollen.

The correlation between chestnut pollen and chestnut abundance in prehistoric forests (17) can be applied to pollen studies published by researchers at the Harvard Forest (S, 6).

Paleoecology of chestnut in New England. The correlation between chestnut pollen sampled from lake sediments and chestnut tree populations in prehistoric forests (17) can be used to interpret pollen data from sites in New England. Analyses of pollen in bog sediments, forest hollows and soils at a site in north, central Massachusetts indicate an abrupt increase in the percentage of chestnut pollen about 2,000 years ago as a result of early land use, which is similar to increases at about the same time found at most other locations in southern New England (4, 22). Pollen in lakes is seen to increase from 7-8% to about 15% which translates into an "average" chestnut proportion of 20% in prehistoric times increasing to 50-60% in early historic times.

However, studies of forest hollow sediments, where chestnut is better represented in the total pollen influx, reveal some chestnut pollen in sediments as old as 4500 years (5). The regional chestnut pollen influx of about 5% in bog sediments indicates a relatively steady population of chestnut in the regional forest in the last 2,000 years. By contrast, the pollen records from soil and small catchments directly under the forest canopy indicate that local chestnut populations were variable, and that large increases in chestnut pollen followed such disturbances as fire and windfall (5, 6).

These results suggest that although the regional average chestnut population was stable, this average was composed

of a continuously shifting mosaic of local chestnut-dominated stands. The abrupt increase in chestnut about 2,000 years ago was apparently related to a subtle change in disturbance regime (prehistoric human activity, fire and windstorm frequency, etc.) and other environmental effects, rather than the direct result of a simple change in climate, or delayed migration from glacial refuge as hypothesized by Davis (4).

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