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Hypovirulence in chestnut blight in Connecticut improves the condition of chestnut trees

By Sandra L. Anagnostakis

Chestnut blight, caused by the fungus *Cryphonectria parasitica*, was identified in New York City in 1904, and all attempts to halt its spread were futile. The first official report of chestnut blight in Connecticut is in the 1909 list of plant diseases diagnosed by the Plant Pathology Department of The Connecticut Agricultural Experiment Station. By 1913 the blight was found in several nurseries in the state, and by 1920 most of the mature American chestnut trees were dead or dying.

Asian species of chestnut resist the blight, but most are not immune. Since Asian trees were freely imported into this country before plant quarantine restrictions, they may have been a source of the blight fungus that so easily kills our native American species.

Chestnut blight spread throughout the native range of American chestnut, from Maine to Georgia, in 50 years. Trees were killed above the ground, but the fungus was unable to enter the roots. Although large trees failed to recover, smaller trees sprouted from the ring of live stump tissue just above the ground, called the "root collar." Today, 84 years after the discovery of chestnut blight in this country, trees still sprout, are killed back, and sprout again.

European chestnut trees are similar to their American cousins and also susceptible to blight. The disease was first reported in Italy in 1938 and spread was rapid. However, within 15 years it was clear that something unusual was happening. Hope for control of this canker disease came in 1965 with the discovery in Italy of strains of the fungus that were less virulent when introduced alone into the bark, and that stopped blight expansion when introduced into cankers caused by virulent strains. These "hypovirulent" strains were described by Jean Grente and Suzanne Sauret in Clermont-Ferrand, France. Scientists at The Experiment Station imported some of these hypovirulent strains in 1972 and found that they contained double stranded RNA molecules (dsRNA) that resemble those found in fungal viruses.

The Experiment Station then began testing hypovirulent strains of *C. parasitica* for blight control in the laboratory and greenhouse. Station scientists have found that the genes on the dsRNA in hypovirulent strains from France and Italy keep *C. parasitica* from making its normal orange pigment and interfere with growth. The white appearance of the European strains makes them easy to recognize when they are isolated from cankers on chestnut trees. Hypovirulent strains that are quite different have been found in this country in Michigan, Virginia, and Tennessee. All of the American hypovirulent strains have normal pigment, and in the laboratory some grow almost as well as virulent strains. Several scientists are comparing native American with European hypovirulent strains of *C. parasitica* for the "relatedness" of their dsRNA molecules, and for their efficiency in controlling blight.

In 1978, former staff member Richard Jaynes set up an experiment in northeastern Connecticut to test survial and spread of hypovirulence.

The test areas were in two partially-cleared forests; one in the Goodwin State Forest in Hampton (called T1), and one on private land in Pomfret (T2). The cankers were treated with a mixture of hypovirulent (dsRNA containing) strains of *C. parasitica* at least once a year for four years (1978-1981). Nine years later, in the summer of 1987, I found abnormal cankers on sprouts up to 245 feet from the edge of the areas treated. Such abnormal cankers usually contain hypovirulent blight strains, usually do not kill trees, and are the type now found commonly on chestnut trees in Italy and France.

Chestnut trees in and near the treatment areas looked better than trees in areas where no treatments had been done, but objective proof was needed. I chose two areas as controls: one in Ellington (C1) where the chestnut trees were growing in the understory, as is typical in Connecticut, and one (C2) on land in Pomfret that had been cleared at the same time as the Pomfret treatment area and kept open by occasional selective harvesting. I started in the centers of T1 and T2 and cut transects through the dense blueberry bushes and small saplings of birch, cherry, and maple. These transects went through the cleared areas where chestnut cankers were treated, through adjacent areas where clearing had been done, but no cankers were treated, and ended 330 feet from the original centers of the plots in forest where the chestnuts were in the understory. We counted and measured chestnut sprouts in 30-foot-wide swaths along these transects to determine how many of the stumps that were still sprouting had live stems that were at least an inch in diameter. The results are presented in Table 1.

More sprout clumps in the treated areas had large, live stems than clumps in the control areas where no treatments had been done, indicating continued protec-

Table 1. Number of live sprout clumps of American chestnut in 30-foot-wide swaths along transects through Connecticut test areas.

	# sprout clumps	% stems >1 in. diameter
C1 (understory)	114	35%
C2 (cleared)	51	16%
T1		
cleared, treated	22	77%
cleared, not treated	7	86%
understory, not treated	39	38%
T2		
cleared, treated	34	71%
cleared, not treated	21	67%
understory, not treated	16	50%

tion by hypovirulent strains. Even more interesting, there were more clumps with large stems in cleared areas adjacent to treated areas than in control area C2 where clearing had been done but no hypovirulent strains were used. Chestnut trees farther from the places where hypovirulent strains were introduced were struggling to grow in the understory. Although data for T1 understory sprout clumps is the same as that for the nontreated understory area, C1, there were more sprout clumps with large, live stems in the understory around the T2 clearing.

Our other method of comparing treated and nontreated chestnut areas used counts of the numbers of cankers on each stem. If a small (one inch diameter) chestnut tree is infected by a virulent strain of *C. parasitica*, it will be killed in one season. If, however, hypovirulence is present in that canker the tree should live longer, and may become repeatedly infected. Chestnut trees growing in the understory in typical nontreated, forest areas rarely have more than one canker. We counted cankers in our understory and cleared control areas, and in the two treatment areas and the cleared areas adjacent to them, where no treatments were done. We were able to compare our findings with the original 1978 data on the trees. As we had expected, 46% of the live stems (one inch diameter or larger) in the understory control area C1 had no cankers at all, and none of them had three or more cankers. The cleared control area C2 was decimated by blight, and only one small sprout was free of blight.

The comparison of data for T1 and T2 for 1978 at the start of the experiment and 1987 is in Table 2.

Even though T1 and T2 started out with different amounts of blight, they now have similar average numbers of cankers; many more per stem than are found in places where cankers were not treated with hypovirulent strains. The fact that the stems have survived to sustain more cankers is very encouraging, and this is our evidence for improved chestnut tree condition. I believe that this improvement is due to hypovirulence being sustained in the plot and spreading beyond the places where hypovirulent strains were introduced.

We took bark samples from 151 cankers in and around the treated plots T1 and T2, isolated the fungus, and tested for dsRNA. About half of the strains contained dsRNA molecules about the same size as those in the hypovirulent strains used in the treatments from 1978 to 1981. We still don't know, however, whether the dsRNA that we now detect in these plots is genetically the same as that used in 1978, or whether it has mutated to become better "adapted" to our Connecticut *C. parasitica* strains and the environment and trees of northeastern Connecticut. Our tests for dsRNA were combined with tests for strain identification (vegetative compatibility types; see Frontiers, 1981). We found that dsRNA is now present in strains different from those used for treatment in 1978, indicating that dsRNA molecules with hypovirulence genes have spread to other strains and have been maintained in the pathogen population.

We will continue to search for better ways to increase the chances for the return of the American chestnut to a place of prominence in our Connecticut woodlands.

Table 2. Percent of live American chestnut sprouts at least one inch in diameter free of chestnut blight cankers and with three or more cankers. Data are from plots T1 and T2: in cleared central parts cankers were treated with hypovirulent strains of *C. parasitica* (1978-1981), and in cleared adjacent areas cankers were not treated.

	No cankers		3 or more cankers	
	1978	1987	1978	1987
T1				
treated	61%	27%	4%	50%
nontreated	58%	25%	9%	58%
T2				
treated	88%	13%	1%	48%
nontreated	88%	23%	0	62%

Further Reading

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What happens to organic pollutants during municipal composting?

By Kenneth D. Racke

Concerns about air and water quality, problems with disposal of ash from incinerators, a growing shortage of landfill space, and a new emphasis on recycling have all increased interest in composting as an alternative means of disposal of organic waste.

Composting involves the decomposition of organic wastes in the presence of sufficient oxygen by heat-tolerant microorganisms. When a large pile of sufficiently moist and well aerated organic material is formed, naturally occurring microorganisms in the waste dramatically increase in numbers and activity as they begin to decompose available nutrients. Great

quantities of carbon dioxide are produced as easily degradable organic materials are mineralized by the microorganisms. Metabolic heat generated in the process increases the temperature of the pile to as high as 175° F, when specialized heat-tolerant microorganisms become active. The most common municipal composting method was developed by United States Department of Agriculture scientists. It involves the construction of large windrows (9 feet high, 15 feet wide, 50 feet long) of mixtures of sewage sludge and woodchips or leaves through which air is drawn with blowers to maintain aerobic conditions during a 3 week to 3 month composting cycle.

One continuing problem is disposal of sewage sludge in an environmentally sound manner. Approximately 60,000 tons of sewage sludge are generated yearly in Connecticut during treatment of municipal wastewater. About two-thirds of this sludge is incinerated, with the remainder dumped in landfills. Two municipalities, Greenwich and Bristol, compost their sewage sludge with leaves or woodchips, and a number of others are constructing composting facilities or are exploring composting options.

Composted sewage sludge has been shown by Station research to stimulate plant growth, and is, therefore, useful as a horticultural soil amendment. Another benefit is that pathogenic microorganisms in sludge are destroyed by the elevated temperatures produced during composting. However, because little is known about the fate of organic pollutants in sewage sludge or other organic wastes during composting, I addressed this question experimentally.

My studies were conducted with a laboratory composter developed by USDA researchers. The benchtop apparatus can compost as little as 2 lbs of waste under controlled conditions and accurately simulates composting in the field. The system consists of a water bath in which an airtight vessel containing the material to be composted is immersed. Compressed air is passed through the compost vessel to maintain aerobic conditions and exhaust gas is bubbled through an alkaline liquid to trap carbon dioxide for analysis. A device monitors the temperature of the composting material and maintains the temperature of the water bath slightly below that of the compost.

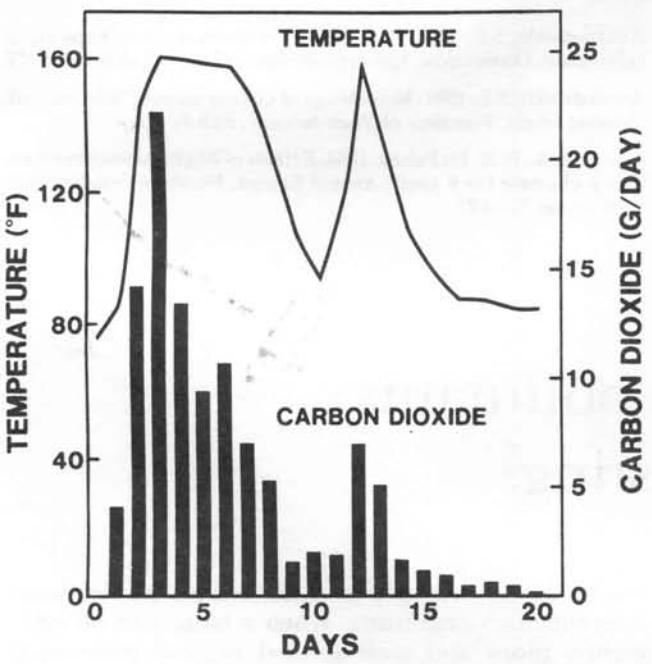

Figure 1. Temperature and carbon dioxide emission profiles for sewage sludge-woodchip mixture during laboratory composting.

As shown in Figure 1, I found that mixtures of sewage sludge and woodchips in the laboratory composter rose rapidly to around 160° F shortly after mixing. This rise in temperature was accompanied by generation of much carbon dioxide, which is indicative of the tremendous microbial activity associated with composting. During each composting experiment the temperature dropped after having been around 160° F for several days and briefly rose again before gradually cooling upon completion of composting. This may have been because microorganisms can easily generate too much heat, and excessively high compost temperatures can cause a temporary decline in microbial composting activity. Recovery of microbial activity was indicated by the secondary peak of carbon dioxide production that coincided with the secondary rise in temperature.

I chose several organic chemicals to study during composting. The first was glucose, which is not a pollutant, but was used as an indicator of how fast a ready nutrient would be degraded during composting. I discovered that glucose decomposed very rapidly with over 75% of the applied glucose converted to carbon dioxide during 20 days of laboratory composting. I next chose two pollutants to study, phenanthrene, a common sludge contaminant that is a member of the important polyaromatic hydrocarbon class, and carbaryl, a commonly used pesticide. To determine the fate of these pollutants during composting, I added 5 ppm of each to the sludge-woodchip mixture which was then composted in the laboratory for up to 3 weeks. Degradation to carbon dioxide was monitored during the composting cycle, and upon completion, the compost was analyzed for pollutant and breakdown products. I used radiolabelled pollutants to allow a complete accounting.

Phenanthrene was resistant to degradation (Table 1). I recovered almost 92% of the phenanthrene unchanged after 20 days of composting at temperatures up to 160° F. A small portion of the phenanthrene had been partially degraded and incorporated into the organic matter of the compost, but only a trace was completely degraded to carbon dioxide. To see how phenanthrene would be affected by not allowing compost to reach microbially inhibitive temperatures, I also conducted an experiment in which I limited the maximum temperature of the compost to 130° F. However, phenanthrene was just as persistent at this lower temperature.

The fate of carbaryl during composting was different. As shown in Table 1, only a trace of the carbaryl

persisted through the composting process. The great majority of carbaryl had been converted to unextractable product that had probably been incorporated into the compost organic matter. This conclusion was supported by the fact that a portion of the applied carbaryl was converted to products that were associated with high molecular weight humic compounds extracted from the compost. A small amount of carbaryl had been completely degraded to carbon dioxide during composting, but not nearly as much as is commonly observed when carbaryl is degraded in soil. To test whether reduced levels of oxygen in the compost might be limiting mineralization of carbaryl to carbon dioxide, I conducted one experiment in which I alternately supplied air and pure oxygen during the first 10 days of composting. The results in Table 1 show that although increasing the supply of oxygen greatly increased the total amount of carbon dioxide produced by the compost, the amount of carbaryl degraded to carbon dioxide was not similarly affected. Apparently, the supply of oxygen is not the most critical factor in the complete degradation of carbaryl.

My investigations indicate that although some organic pollutants undergo little decomposition during composting, others will be almost completely degraded. Study of other pollutants should reveal the types of degradative reactions that commonly occur during composting. This knowledge will help determine which organic pollutants may need to be monitored in finished composts and will also be useful in evaluating the environmental impact of compost application to soil.

Table 1. Composting conditions and the fate of phenanthrene and carbaryl after 20 days of laboratory sewage sludge composting.

PHENANTHRENE		
composting conditions:		
Maximum temperature (°F)	158.4	131.0
Aeration gas	Air	Air
Carbon dioxide evolved (g)	30.3	36.2
% of applied phenanthrene recovered as:		
Phenanthrene	91.9	89.8
Compost-bound residue	14.9	16.9
Carbon dioxide	0.7	0.8
CARBARYL		
composting conditions:		
Maximum temperature (°F)	159.1	156.2
Aeration gas	Air	Air/Oxygen
Carbon dioxide evolved (g)	27.5	46.2
% of applied carbaryl recovered as:		
Carbaryl	<0.1	<0.1
Extractable humic-bound	3.5	2.6
Compost bound residue	94.9	96.0
Carbon dioxide	3.3	4.6

Mass spectrometric technique measures Dioxins in Connecticut

By Lee Huang and Harry M. Pylypiw, Jr.

Analytical techniques for Dioxins have been the subject of considerable interest due to their high toxicity. The public is interested in where Dioxins are found, how they are formed and how they are introduced into the environment, particularly around waste disposal sites. Incineration of municipal wastes has become necessary due to the shortage of land disposal areas. The fly ash formed during the incineration of plastics and paper is believed to be the major contributor of Dioxins to the environment.

Dioxin is a general name for a group of chlorinated organic compounds that have a common structure. There are 75 possible Dioxin compounds, each having from one to eight chlorine atoms at various positions in its structure. Each individual compound is known as a Dioxin isomer. One important Dioxin isomer is 2,3,7,8-Tetrachlorodibenzo-p-dioxin (2,3,7,8-TCDD).

Several isomers of Dioxin are considered to be among the most toxic compounds discovered. A measure of the toxicity of a chemical is its LD_{50}, the dose necessary to kill half a test population of laboratory animals such as rats. The LD_{50} for 2,3,7,8-TCDD is 0.00000035 moles /Kg body weight, as compared to an LD_{50} for cyanide, which is 0.0002 moles/Kg body weight. These figures indicate that this Dioxin might be 1000 times more toxic than cyanide.

The complex nature of samples containing Dioxins challenges a chemist in many ways. Environmental samples might contain many or just a few of the individual Dioxins along with other compounds which complicate the analytical procedure. Dioxins in environmental samples are not easily detected and quantitated. They are usually found at levels of a few parts-per-billion (ppb) or less; concentrations which are analogous to one drop in a swimming pool.

Connecticut regulations allow only 1 picogram of Dioxin (one trillionth of a gram) in air. Since the allowable level for Dioxin is extremely low, an ordinary chemistry laboratory, operating with routine instruments, cannot perform accurate sample analysis. To perform accurate Dioxin analysis, a laboratory must possess up-to-date technology, and use sophisticated instruments.

The Department of Analytical Chemistry has received soil and water samples collected by the Department of Environmental Protection, and has been testing them for the most toxic Dioxin compound, 2,3,7,8-TCDD.

The following is an overview of the analytical process. Samples are extracted and the extract purified by a cleanup procedure which utilizes several different column chromatographic techniques. The Dioxins in the final extract are separated by high resolution gas chromatography and the exact amounts measured and confirmed by low resolution mass spectrometry. Specific analytical procedures for water and soil samples are given below.

Before and after the extraction process, a small amount of isotope-labeled Dioxin is added to each sample as a reference standard. Dioxins present in the samples and isotope-labeled Dioxin have similar chemical and physical properties except for molecular weight. The mass spectrometer, which will be described later, can differentially detect and measure the amounts of Dioxin in each sample based on the amount and response of the reference standard added to each sample.

Water samples are prepared by solid-phase extraction (SPE). This method enables the detection limit to be at the low part-per-trillion (ppt) level. Water sample size is 2 liters and isotope-labeled 2,3,7,8-TCDD (2 ppt) is added as the first reference standard. An SPE cartridge containing 100 mg of C-18 bonded silica is used to extract the Dioxins from the water. The 2 liter water sample is passed through the SPE cartridge, and the Dioxins are adsorbed onto the cartridge. After the entire sample has passed, the Dioxins are removed from the SPE cartridge with 2 ml of hexane.

Isotope-labeled 1,2,3,4-TCDD (2 ppt), a second reference standard, is added to the extract prior to the final concentration step. The concentrated water sample extract is now ready for analysis by gas chromatography. Addition of a second reference standard is necessary to calculate extraction efficiency and Dioxin recovery throughout the entire procedure. If recovery does not fall within the acceptable range of 40-120%, a second analysis is performed. Our recovery of 2,3,7,8-TCDD usually averages 95% and has always been greater than 70% (Table 1).

Soil samples present a greater problem to the analyst since they contain a wide variety of other chemical compounds. Because these compounds interfere with the determination of the Dioxins, additional cleanup steps are necessary. Soil samples are first extracted with solvent and then interfering compounds in the extract are separated by column chromatography using silica gel and alumina. Each soil sample must be analyzed in duplicate along with Dioxin-fortified soil for verification that the procedure is accurately measuring the Dioxins. Analysis of one soil sample takes three days as opposed to three hours for six to ten water samples.

The water and soil extracts are analyzed by a high resolution gas chromatograph coupled to a low resolution mass spectrometer. The analytical chromatography column is a 0.25 mm x 50 M DB-5 capillary column. This column is able to separate most of the Dioxin isomers found in the samples over an analysis time of nearly 45 minutes.

Three samples of soil from a waste incinerator firm in Bristol were tested. One sample contained 1.03 ppb of 2,3,7,8-TCDD and a trace of 1,2,3,7-TCDD. The other two samples did not contain Dioxins above our detection limit. Three water samples were tested from landfills in Bristol, Hartford, and Shelton. None of these samples contained Dioxins above the 1 ppt detection limit for water. Proper separation is important for correct identification of the Dioxins, since 2,3,7,8-TCDD is the most toxic compound of all of the 75 Dioxin isomers, while other isomers such as 1,2,3,4-TCDD are essentially non-toxic.

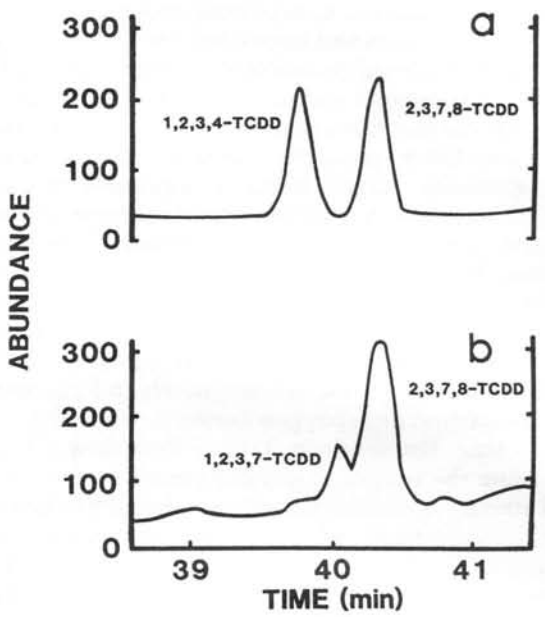

Figure 1. Chromatogram of a) baseline separation of 1,2,3,4-TCDD and 2,3,7,8-TCDD and b) detection of trace amount of 1,2,3,7-TCDD in a soil sample.

Operation of the low resolution mass spectrometer is in the selected ion monitoring mode. This technique enhances the sensitivity of the analytical technique with some sacrifice of compound specificity. The ions monitored for each Dioxin isomer are selected as recommended by the United States Environmental Protection Agency. The limit of detection for 2,3,7,8-TCDD is 100 ppt in soil and 1 ppt in water. Figure 1 illustrates the detection of 1.03 ppb 2,3,7,8-TCDD and trace amounts of 1,2,3,7-TCDD in a soil sample collected from Bristol.

The Station is now improving its capability for Dioxin analysis by installing a high resolution mass spectrometer. The instrument resolves compounds by measuring their exact masses and thus provides a high degree of confidence for Dioxin analysis. Furthermore,

Table 1. Recovery of 2,3,7,8-TCDD in 2 L water samples by Solid Phase Extraction

	Spiked Concentration (ppt)		
Substance	5.0	2.5	1.0
2,3,7,8-TCDD	81%	96%	84%
$^{13}C_{12}$-2,3,7,8-TCDD	118%	105%	70%

[1]Recovery of 40-120% is within EPA recommended range.

this instrument can eliminate chemical interferences that an analyst may encounter in samples containing Dioxin and compounds similar to Dioxin. For example, the mass of 319.8965 is a characteristic ion for 2,3,7,8-TCDD, while an interfering compound might have a mass of 320.1065. Our present low resolution mass spectrometer would identify both masses as 320. To resolve these two compounds with our current instrument, extensive sample cleanup is required, but the result is sometimes unsatisfactory due to the limited chemical resolving power of our present instrument. With greater resolving power, a high resolution mass spectrometer can differentiate between Dioxin and interfering compounds. We will be able to detect Dioxins in soil samples at the low part-per-trillion level and in water samples at the low part-per-quadrillion level without the need for rigorous cleanup.

Inventories at 10-year intervals reveal changes in Connecticut's forests

By Jeffrey S. Ward

In 1926 scientists at this Station began one of the oldest and most comprehensive studies of forest dynamics in the world. Although their original objective of relating soil types to forest composition was not achieved, they provided a benchmark of natural changes against which forest management practices can be compared and which can be used to estimate future forest composition.

The study was begun in the Turkey Hill Tract of Cockaponset State Forest. Cabin, Cox, and Reeves Tracts in Meshomasic State Forest were added the following year. North-south strip transects 16.5 feet wide were established in each tract. The combined transects covered 13.75 acres. The 1927 inventory recorded the location of all trees greater than 0.6 inches dbh (diameter at 4.5 feet above ground) together with the tree's diameter, species and crown class (the relative position of a tree's crown in the canopy) on strip maps. The second inventory was in 1937. Beginning with the 1957 inventory, the minimum diameter was lowered to 0.5 inches dbh. Inventories were repeated in 1967, 1977, and 1987.

The present database includes nearly 41,000 stems distributed over 55 species. To simplify analysis of changes over the past 60 years, species were assigned to one of seven species groups: Maples (*Acer* spp.), Birches (*Betula* spp.), Oaks (*Quercus* spp.), Hickories (*Carya* spp.), Beech (*Fagus grandifolia*). Other species of economic value (white ash, tulip poplar, hemlock, etc.) were assigned to the Commercial species group. The final group was the Non-commercial species group and included species such as grey birch, American hornbeam, and flowering dogwood. These species are small at maturity and do not grow large enough to form part of the main canopy.

The 1927 inventory revealed marked differences in species composition among moisture classes (Figure 1). Dry sites had three times more Oak, five times more Hickory, and 14 times more Beech than moist sites. Density of Non-commercial and Commercial was twice as high on moist compared to dry sites. Density of Maple and Birch was similar on all sites.

From 1927 to 1957 density declined from 1440 to 640 trees/acre. The decreasing number of trees was not indicative of a declining forest; rather it resulted from trees growing larger. Large trees need more resources (light, moisture, nutrients) than small trees. As individual trees grow and utilize more and more resources, one or more of these resources become limiting. Trees which are not as competitive as others decline and die.

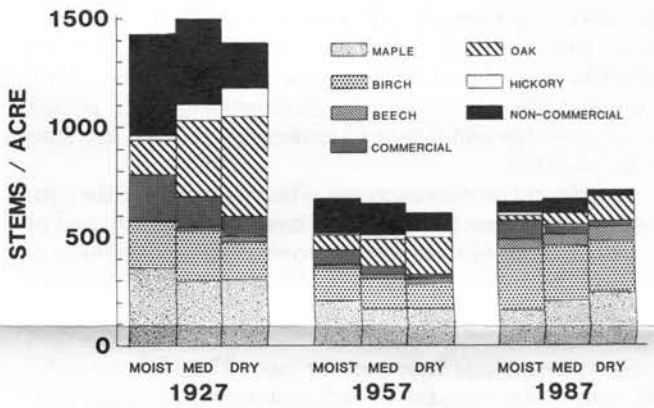

Figure 1. Distribution of all trees greater than 0.5 inches diameter by species group, soil moisture and year.

Our forests have been constantly changing since the first inventory. There was a steady decline in the number of Hickory (91% decrease), Non-commercial (86% decrease), Oak (83% decrease), and Commercial (68% decrease) species. During the first 30 years, Maple and Birch declined by approximately 40%. Since then, Maple density has increased 16% and Birch density has increased by 83%. Beech is becoming increasingly important (260% increase since 1927) and is the only species which has exhibited an increase during each of the inventories. By 1987 the differences between moisture classes had become relatively minor. Maple, Oak, and Beech had higher densities on the drier sites, while Birch and Commercial had higher densities on moister sites.

Grouping species to simplify the analysis has masked some compositional changes within species groups along the moisture gradients. The 1987 data show that sugar

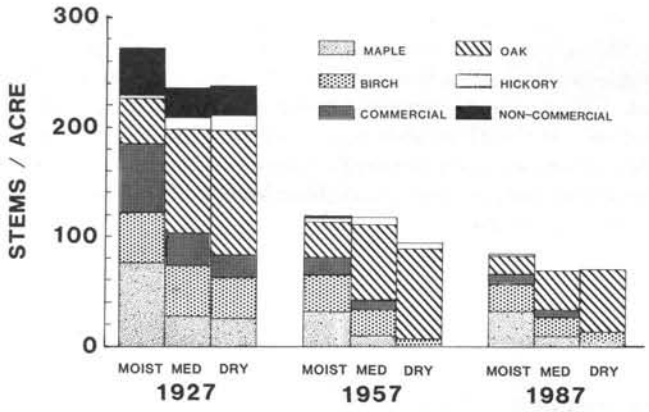

Figure 2. Distribution of canopy trees by species group, soil moisture and year.

maple and yellow birch are more common on moist sites, while red maple and black birch are more common on dry sites. Northern red oak accounts for 67% of all oaks on moist sites, but only 29% of all oaks on dry sites. On dry sites black, scarlet and chestnut oaks are more abundant. On moist sites 73% of Commercial trees were tulip poplar or pepperidge and 80% of Commercial trees on dry sites were sassafras.

A different picture emerges when we examine the canopy trees (Figure 2). These are trees with the top and at least two sides of their upper crowns exposed to the sun. In 1927 Oak was predominant (48% of all trees) on the dry sites while a mixture of Maple, Birch, and Commercial (68% of all trees) dominated the moist sites. Medium sites were intermediate between the two. Time has accentuated the differences between the sites. Oak accounted for 79% of canopy trees on the dry sites in 1987, while 78% of canopy trees on moist sites were either Maple, Birch, or Commercial. In 1987 canopy trees on medium sites were evenly divided among Oak and a mixture of the remaining species groups. These changes were not caused by an increase in the density of any species group; instead they are the result of some species groups decreasing more slowly than others. For instance, by 1987 there were less than three trees/acre of Maple in the canopy on dry sites, a 91% decrease from the 25 trees/ acre in the canopy in 1927. Over the same period, density of canopy Oaks decreased from 114 to 56 trees/acre, only a 51% decrease. By comparison on moist sites density of canopy Maples decreased 58% and density of canopy Oaks decreased 59%.

Another way we can study forest dynamics is to examine changes in the number of trees of different sizes. Trees were assigned one of three diameter classes: sapling (0.5-4.5 inches dbh), pole (4.6-10.5 inches dbh), or sawtimber (>10.5 inches dbh). From 1927 to 1987 there has been a convergence in the number of trees on the different moisture classes within each of the diameter classes (Figure 3). This is interesting because of the distinct species mixtures which occur on the different moisture classes. There was a steady decrease in the density of saplings through 1957. The more recent increases in sapling density may be attributed to defoliation and drought of the early 1960s (see below). Pole density rose from 1927 to 1937 before beginning a 50-year decline which lasted until 1987. We expect to see an increase in pole density in the 1997 inventory as saplings that were established in the 1960s grow larger. Sawtimber density on all moisture classes appears to be reaching a plateau of around 60 trees/acre.

During 1957-67 annual mortality rates for canopy trees were only 0.25%/year higher than for the 1937-57 and 1967-87 periods. This is not to say that mortality rates of some species groups were not affected. The 1957-67 mortality of Oak was nearly twice that of 1937-1957 at 7.2%/year and 3.7%/year, respectively. Although the study areas have been defoliated since the 1960s, Oak mortality has continued to decrease and during 1977-87 was only 1.2%/year. This suggests much of the 1957-67 Oak mortality was concentrated in trees susceptible to defoliation or those which were already weakened. The net effect of the defoliation was not a change in mortality rates, but a concentration of mortality within the Oak group.

If mortality for 1957-67 did not increase, why was there an increase in sapling ingrowth following defoliation? The probable answer is that the mortality occurred quickly instead of being constant over the 10 year period. The effect was similar to what happens when the canopy is opened following thinning. With many trees removed at once, the resulting holes in the canopy allow increased light to reach the forest floor. Soil moisture also increases because the dead trees do not transpire water. Increased light and soil moisture allowed more seedlings to grow into the sapling size class. The number of trees large enough to be measured for the first time averaged 10.3 trees/acre/year for 1937-57. The number increased from 11.4 trees/acre/year for 1957-67 to 29.7 trees/acre/year for 1967-77, a 160% increase. The distribution of ingrowth among the species groups was not greatly changed by the defoliation and drought of the 1960s.

Sixty years of this research has provided solid documentation of the dynamics of Connecticut's hardwood forests. Current research in the long-term plots includes work on volume growth, seedling recruitment, and shrub communities. In the next 60 years these forests will shift from even-aged to uneven-aged as many of the trees comprising the upper canopy die and are replaced by new recruits. Continual monitoring of these forests will enable us to more completely understand the processes which shape our forests.

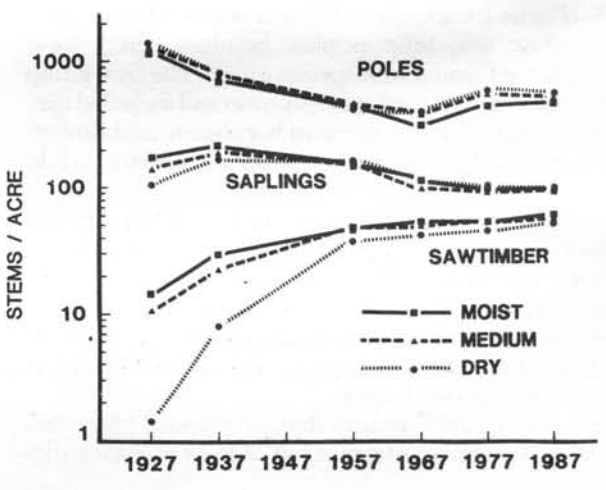

Figure 3. Distribution of all trees by diameter class, soil moisture and year.