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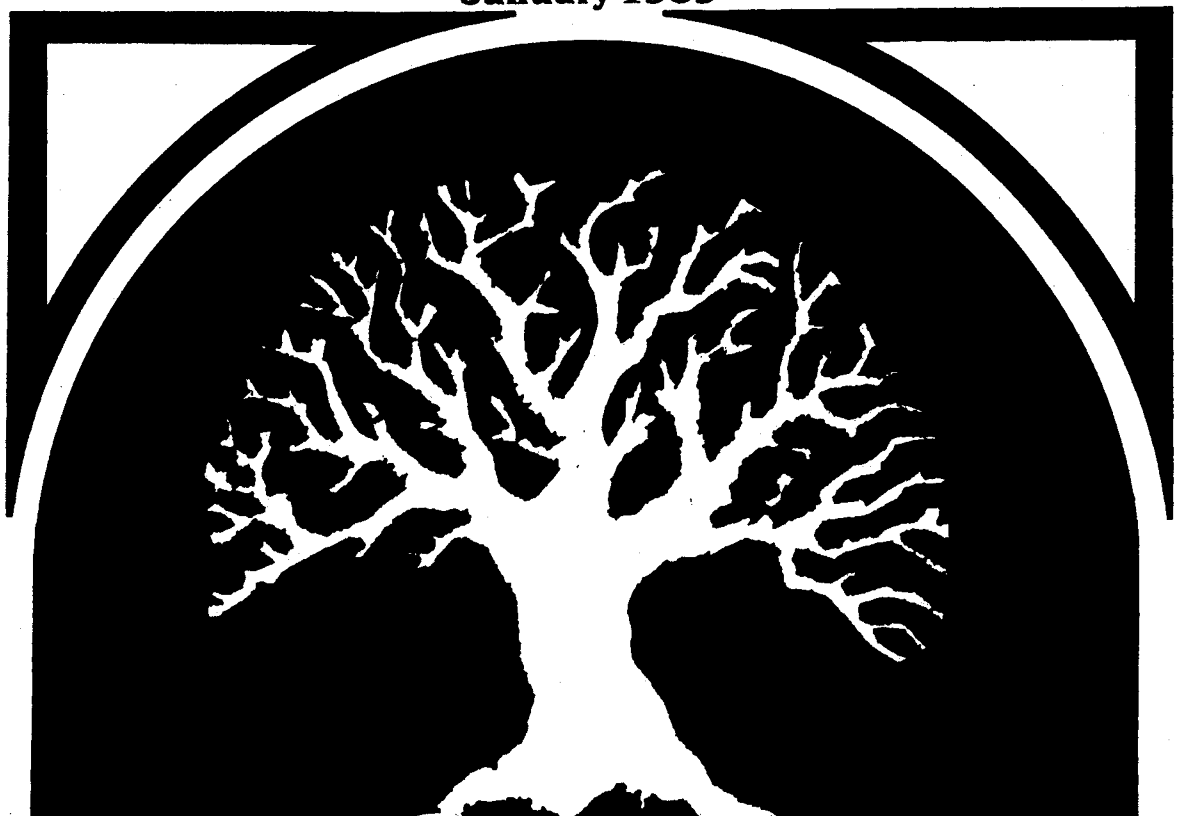

Oak Decline

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Oak Decline

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Foreword

Occurrence of decline and mortality in this nation's hardwood forests has been documented in reports for the past 130 years. From 1856 through 1981, more than 26 decline events were reported from eight eastern states affecting almost all species of oaks. Fourteen factors have been implicated as either primary or secondary agents responsible for decline and mortality.

In recent years, incidence of decline and mortality in the South's natural stands of oak has increased. Since 1974, foresters have reported instances of oak decline and mortality ranging from a few trees to several hundred acres in Mississippi, Alabama, Oklahoma, Arkansas, Tennessee, and Kentucky. Suggested causes of decline and mortality in these instances were changes in land use, drainage, climatic history, disease and insects, and other environmental alterations. The lack of understanding of the factors responsible, especially the interactive effects of host, stand, site, climate, and pathogenic organisms is of considerable concern among professionals directly and indirectly associated with this valuable natural resource. The ability to predict stand susceptibility and potential losses is unattainable with the existing data base.

The complexity of oak decline will require information from a diverse group of scientists. Our research group includes pathologists, entomologists, soil scientists, and technical staff assistants. The approach has been to first stratify the Midsouth hardwood forest along two main drainage systems, the Mississippi and the Tennessee-Tombigbee. Within each drainage system, field plots representing various levels of decline have been established. Data collected include edaphic characteristics (soil type, slope, aspect) and biological entities (host type, age, dbh, growth rate, height, live crown ratio, stand composition, and insects and diseases associated with roots and stems). From these data, a predictive model will be developed for oak stands in the Midsouth. This model will allow forest land managers to apply silvicultural treatments to oak stands on a priority basis. Managers will be able to identify areas requiring silvicultural treatments and to predict the probability of decline/mortality associated with selected stand manipulations.

First among the major objectives identified in this 5-year cooperative study is to conduct a comprehensive literature review on oak decline and mortality and to make this information available to all forestry-related user groups. This Technical Bulletin contains the results of this endeavor.

Oak Decline

Introduction

Oaks are among the most important timber resources in the United States. They provide about a third of the nation's hardwood sawtimber volume. Approximately 90 percent of the oak volume is located in the eastern states. Most of these oaks occur in oak-hickory or oak-pine forests that occupy about 38 percent of the forest land in the eastern states. A large block of these mixed forest types extends along the Appalachian Mountain range from New England to Mississippi and Alabama. Another block extends from Minnesota to Texas. Oak-pine forest types are most common in southern areas, particularly Tennessee, Georgia, Alabama, and Mississippi. About 20 oak species are considered commercially important timber species in the eastern U.S., although five species account for most of the volume harvested.

It is inevitable that such a valuable resource has generated a great deal of research interest, especially when oak trees die by the millions over large areas during a short time span. Oak decline is the term used to describe a highly variable complex of adverse environmental factors and organisms of secondary action, which have been implicated in the death of many oaks. Decline has been scrutinized increasingly in recent years because of widespread damage to oak timber and the difficulty of understanding the complex relationships of the many factors involved in decline.

Decline is considered by some to be a stress triggered disease because severe environmental trauma, such as a drought or a late freeze, often appears to initiate the decline syndrome. Insect defoliations may also play a part in decline. Some authors consider insect defoliations to be a major initiating factor, but in many cases tree growth has decreased slowly for several years prior to heavy defoliation. Anthropogenic causes, such as pollution and mechanical damage, have also been implicated in the decline process. Once decline begins, secondary agents, such as root rots and wood borers, may accelerate oak mortality.

Species of Oaks

The genus *Quercus* consists of approximately 500 species of oaks widely distributed throughout the world. Seventy-nine species are native to North America exclusive of Mexico. Oaks hybridize freely, causing taxonomists to differ on the exact number of species.

The oaks are subdivided into two subgenera; *Leucobalanus* (white oaks) and *Erythrobalanus* (red oaks). White oaks are characterized by leaves without spinose teeth or bristle-tipped lobes; summerwood pores that are angled, small, and thin-walled; and fruit that matures in one season. Red oak leaves have bristle-tipped lobes, or, if unlobed, margins, apices, or both with spines or bristles. Red oak has summerwood pores that are rounded, large and thick-walled, and fruit that usually matures in two seasons.

Most species of North American oaks, which are believed to have originated in Mexico, are evergreen in the warmer regions of their range. However, deciduous species become more prominent northward through the range. Oak species tend to have small, shallow lobed or unlobed, thickly waxed leaves in dry regions. Northern species often have deeply lobed, larger leaves. Although oaks grow more commonly on well-drained soils of hillsides and mountain slopes where moderate precipitation prevails, they also may be found growing in low, wet areas, dry rocky mesas, and sea coasts.

Oaks support a wide variety of wildlife. Acorns form part of the diet of wild turkeys, wood ducks, squirrels, raccoons, hogs, bears, deer, and many other animals.

White oak is the most important oak species used for commercial timber in the United States. It is a slow-growing tree that occurs from southern New England to northern Florida to east Texas. Although maximum growth occurs in coves and on northern lower slopes, white oak can be found on wet bottomland and on most upland aspects except dry, shallow-soil ridges. Young white oak trees are shade tolerant, but become less tolerant as they mature. It is rarely found in pure stands, but occurs with many other trees, including other oak species and hickories. The light brown wood is hard, tough, strong, and close-grained.

Chestnut oak has a more limited range than other upland oaks. It occurs from southern Maine to Georgia and Alabama, excluding the southeastern coastal plain. Chestnut oak occasionally occurs in almost pure stands on rocky ridges. It usually is found in association with white and black oak as well as red maple, black cherry, hickory, and white and pitch pine. This species' performance is superior to the other upland species on dry, coarse soils, although maximum size is attained in well-drained coves. Its growth is faster than that of white oak but slower that that of northern red oaks. Chestnut oak is intermediate in shade tolerance between white oak and scarlet oak.

Northern red oak occurs further north than other upland oaks. It is commonly found on middle and low slopes and coves with northern or eastern aspects. Although northern red oak grows on sites with soils that range from clay to loam and deep stone-free to shallow rocky soil, the most favorable sites have deep, fine-textured soils with a high water table. Northern red oak is similar in shade tolerance to chestnut oak and grows more rapidly than other upland oaks.

Black oak occurs throughout most of the eastern United States on upper slopes and dry sandy or rocky ridges. It occurs on all aspects and slope positions and tends to grow on drier sites than white or northern red oak. Young trees develop long tap roots and grow more rapidly than other upland oaks (except northern red oak). The species is relatively short lived. Black oak is intolerant of shade and is found in mixed stands only when its crown is in the upper canopy.

Scarlet oak is found in most states east of the Mississippi River except Wisconsin and Florida. It often is found growing in poor, dry soils on middle to upper slopes and ridges. Scarlet oak grows rapidly and matures early. It is the most shade tolerant of the eastern oaks and is usually found as a dominant tree in a stand.

Southern red oak occurs from southern New York to northern Florida and east Texas. It often is divided into two varieties, *Q. falcata* Michx. *falcata* (southern red oak) and *Q. falcata pagodifolia* Ell. (cherrybark oak). Southern red oak frequently is found growing on dry, sandy, or clay upland soils and many loams. Although cherryback oak occurs on dry ridges and south or west facing hilltops, it attains greatest size in moist, fertile bottomland. Southern red oak is moderately fast growing and may live 100 to 150 years. Cherryback oak is limited to southern portions of the southern red oak range. It occurs in well-drained loamy bottomlands and on fertile uplands. Cherryback oak tends to have a straighter, more branch-free trunk than does southern red oak.

Live oak is an evergreen oak that grows along the lower coastal plain from southeastern Virginia to southern Florida and southern Texas. It occurs in moist rich woods and along streams, but is most common in low sandy soils near the coast growing in association with water oak and laurel oak. Live oak has very dense wood, a wide spreading, rounded crown, and fast growth. It is tolerant of short-term flooding, persisting even where roots may be inundated at high tide.

Water oak occurs along the coastal plain from New Jersey to central Florida and westward to eastern Oklahoma and Texas. It grows along streams, and rivers and in floodplains, attaining its largest size in well-drained silty clay or loams.

Laurel oak occurs along the coastal plain from southeastern Virginia to Florida and southern Texas. Maximum growth occurs in well-drained soils in moist woodlands along streams and in swamps. It grows rapidly, maturing in approximately 50 years.

Willow oak occurs along the coast from New York to Georgia and from southern Kentucky west to eastern Texas. It grows best near swamps and streams or in rich upland soils, although it can be found on terraces and hammocks. It grows rapidly and has a long lifespan.

History of Oak Decline

The history of decline and death of oaks in the United States has been documented in reports covering more than 130 years. Beal (1926) cited a report of a late freeze that occurred in June 1856, in Bland County, Virginia, in which "the killing of many white oaks" was noted (Hopkins 1902). The association of *Armillaria mellea* with dying oaks in New York was reported by Long in 1914. He observed that a high percentage of declining oaks in the eastern United States were colonized by this fungus. He also reported instances where only two-lined chestnut borers (*Agrilus bilineatus* Weber) were associated with dead trees. Long stated that the relationship between *A. mellea* and borers may not be as important as originally perceived because borers infested healthy trees in addition to trees colonized by *A. mellea*.

Chapman (1915) stated that "at the present time the two-lined chestnut borer, *A. bilineatus* Weber, is commonly associated with the death of many oaks (*Quercus* spp.) in the southeastern part of Minnesota." Chapman further acknowledged that reports as early as 1885 called attention to damage inflicted on oaks by this insect in Massachusetts and Minnesota. Chapman noted the preference of this insect for black oaks over white oaks, and the interaction of the two-lined chestnut borer and Armillaria root rot. In some cases, adult borers appeared to prefer trees in a certain locality and/or selected trees. In general, this preference was associated with trees growing under stress caused by drought, crowding, cultivation, injury, and disease. It was noted however, that trees showing no signs of stress were attacked and killed by this insect.

A year later, F. C. Craighead (1916) suggested that oak mortality was due to the additive effects of the two-lined chestnut borer, Armillaria root rot, drought, late spring frosts, and insect defoliation. Six years later, Burgess (1922) claimed that defoliation by gypsy moth caused 26 percent mortality of red oaks in his New England plots over a 10-year period. Baker (1941) reported similar effects of gypsy moth defoliation in New England from 1912 to 1921. He observed that the greatest economic losses attributable to gypsy moth defoliation in New England occurred among oaks, which were highly susceptible as a group, and pines. He reported that thrifty hardwoods rarely were injured by single complete defoliations, but that repeated strippings at short intervals caused mortality. Baker qualified his diagnosis by stating that tree mortality may not have been entirely a result of defoliation but may have been aided by development of secondary agents.

From 1912 to 1915, an outbreak of two-lined chestnut borer populations in eastern New England may have increased decline incidence and death of trees stressed by heavy gypsy moth defoliation and drought. Baker documented heavy defoliations of black and white oaks at intervals separated by 2 to 3 years between 1912 to 1921, and continuous defoliation of scarlet oaks resulting in their progressive decline. Growth among oaks with 81 to 100 percent defoliation was half that of trees with defoliation ranging from 0 to 20 percent. In addition, growth reduction fluctuated inversely with percent defoliation and occurred the same year as defoliation. Continuous, heavy defoliation of scarlet oaks over a period of 6 years reduced their vitality such that they failed to recover. Baker noted greatest mortality occurred during a 3-year-period following a severe drought among those trees stressed by defoliation and borer activity.

Effects of gypsy moth defoliation on tree performance in New England also was recorded by Minott and Guild (1925). Their experiment consisted of 14,610 trees (representing 37 species of hardwoods) growing on 4,000 square miles in the northeastern United States. Gypsy moth defoliation on red, scarlet, black, and white oak averaged 36.5 percent per year over a 10-year-period from 1912 to 1922. Forty-seven percent of the trees subsequently died, and growth in terms of wood produced was only 62 percent as great as that of the previous decade. These two authors were among the first to note the tremendous variation among oak's ability to tolerate defoliation. Nearly half of the observed dominant white oaks died one year after complete defoliation. However, they concluded that even moderate defoliation is debilitating and, if frequently repeated, will lead to decline and death.

J. A. Beal (1926) concluded that the extensive mortality of white oak during this same period in Bland County, Virginia, was caused by freezing temperatures recorded on May 26 and 27, 1925. He further described occurrence of mortality only in valleys and hollows, where white oaks were in a succulent condition. He noted that there was no insect or disease damage associated with dead trees and that larger mature trees sustained the most damage. This, he concluded, was due to droughty conditions prevalent throughout the region during the summer of 1925.

R. E. Balch (1927) attributed red, black, and scarlet oak decline and death in the southern Appalachians during the late 1920's to drought, root rot, and borer attack. Although he did not identify a primary cause, he speculated that severe late frosts in April 1927, killed new foliage throughout much of the Bent Creek Experimental Forest in North Carolina. Balch concluded that vigor of trees already weakened by age and competition was further reduced by frost and drought, and that subsequent attack by *Armillaria* sp., *Agrilus* sp., and *Prionus* sp. caused tree mortality.

Another oak decline event in the Bent Creek Experimental Forest was believed by C. R. Hursh and F. W. Haasis (1931) to be caused by a severe drought. These authors noted browning and premature defoliation of trees growing on ridges and upper slopes in August and September 1925. Leaf browning and early leaf fall were more pronounced among younger trees. More foliar symptoms of drought were present in trees with logging or fire scars than in those with sound boles. Chestnut oaks were injured only slightly and in the following spring showed no evidence of permanent injury attributable to drought. Leaves of black oaks were injured severely. With few exceptions, the response of red and scarlet oaks was similar to that of black oaks. Increment cores taken from recovered trees showed that only a minor reduction in growth had occurred during the drought period and during the years immediately following. Growth of trees that died within 4 years after the drought, however, showed a definite reduction during the 4-year decline period.

Soils in the Bent Creek area seldom exceed 18 to 20 inches in depth. Bedrock is close to the surface, with frequent rock outcrops, and the topography is steep with slopes ranging from 50 to 100 percent. Hursh and Haasis (1931) suggested that species which had established themselves on upper slopes and rocky soils during cycles of favorable precipitation for the 25 years preceding the drought were severly injured or killed because of this catastrophic event. This suggests that the minimum of a fluctuating precipitation range should be considered in determining sites for species selected for planting in the southern Appalachians.

Red, black, scrub, scarlet, white, and rock oaks growing in Pennsylvania were severely defoliated and believed to be killed by the fruit-tree leaf roller and the elm spanworm (Knull 1931). Knull noted that heavy defoliation for a period of years reduced vitality such that trees were attacked by chestnut borers, which contributed to mortality. Scarlet oaks appeared to be most susceptible to injury and were the first to die. An explanation offered for the severe injury was believed to be the altered forest condition. The section in Pike County where infestation was highest was originally a white pine area. Commercial removal of white pine was followed by fire, then a slow conversion into an American chestnut, chestnut oak, pitch pine ecotype. Chestnut blight converted some of these forests into pure stands of oaks.

McIntyre and Schnur's (1936) assessment of oak decline in 1929 and 1930 was that growth reduction was due primarily to drought and discounted the importance of insects or disease.

True and Tryon (1956) wrote a similar report after observing widespread injury to oaks in West Virginia in the early 1950's. The symptoms they observed most frequently were top dieback and stem cankers on trees growing primarily on ridgetops characterized by shallow, coarse soils. Scarlet, red, and black oaks incurred the most damage whereas chestnut and white oaks were rarely injured. Cankers were more common and damage most severe on the south side of stems. In addition, no one species of fungus was found to be regularly associated with cankered trees.

Gillespie (1956) also observed the general condition of oaks growing in West Virginia following the 1953 drought, and reported that a similar decline of oaks had occurred in Pennsylvania, New Jersey, and New York during the summers of 1953, 1954, and 1956. Scarlet oaks were affected most, followed by red and black oaks, and to a lesser extent, white, and chestnut oaks. Other associated tree species were not affected. Gillespie reported that affected trees occurred most frequently on southern and western slopes of foothill ridges and rarely in coves or near creeks. He also observed that while the overall decline pattern appeared to follow tilted Devonian shales from which very poor, shallow soils develop, these same shales were present in drought areas of northern West Virginia where decline was rare.

Gillespie also noted that declining oaks were in the dominant or codominant classes and that foliar symptoms occured suddenly in late July or August when leaves quickly turned brown, died, and remained attached. New leaves were often small and chlorotic, stump sprouts were rare, diameter growth was reduced for 6-8 years, root systems showed no evidence of disease, and fungi likely to be a casual agent were not isolated from branch and twig samples collected in 1953, 1954, and 1955.

Fergus and Ibberson's 1956 report of oak mortality in Pennsylvania in the 1950's again identified red, scarlet, and black oaks as the species most severely affected, whereas most white oaks and non-oak species remained unaffected. All age and crown classes of the former group were affected. In addition, declining trees showed a significant growth reduction. Symptoms included a failure of leaf buds to open either over large areas of the crown or on single branches, resulting in apparent dieback. Leaves from buds that did open failed to develop to normal size and many leaf blades aborted. Foliage growing at outer branch tips was slightly chlorotic. Some fully-formed leaves died and turned brown, but no wilting or defoliation occurred. This gradual decline eventually resulted in tree death. Decline occurred from the top down and from the outside in.

Fergus and Ibberson failed to isolate pathogenic organisms from twigs, branches, trunks, or roots of affected trees. Armillaria was found, but only on trees which had been dead for more than 2 months. Decreased radial growth in healthy and dying scarlet oaks was associated with successive periods of drought. Change in radial growth from year to year in response to drought was greatest on better sites. Trees on poorer sites were injured more severely and were not as able to recover during years with adequate rainfall as vigorous trees growing on better sites. Hemlock (a moist-site species with shallow roots) growing on the same bites as dying oaks, grew more slowly during drought, but there was no relationship between ring width and July-September rainfall of the preceeding year, as occurred with scarlet oak. The authors concluded that "hemlock, after becoming established on a poor site, is not so sensitive to late summer droughts, as is mature scarlet oak."

Fergus and Ibberson pointed out that tree age may be a factor, since "the dying scarlet oaks examined were between 53 and 92 years old, growing on sites well below average productivity." They quote Hepting and Kimmey (1949) as stating that decay cull visually causes serious breakup of scarlet oak stands over 80 years old, but most other oak species will pass 150 years without major loss from decay. While noting the difficulty of proof, the authors conclude that "drought played an important part in causing death of these trees."

Staley (1965) conducted an extensive study of red and scarlet oak mortality in Pennsylvania in a 60-year-old affected stand near Livonia, and a 43-year-old healthy stand 30 miles away at Snowshoe Summit. He also compared climatic and edaphic data from those areas with the area in West Virginia studied by Tyron and True (1958). Scarlet oak was the most severely affected species. Black oaks were rarely killed and healthy black oaks were observed growing adjacent to dying scarlet oaks. White oaks were seldom observed declining. Many associated chestnut oaks were killed, but only where scale insects were present. Other tree species, such as hemlock, hickory, white pine, and red maple growing in declining areas usually exhibited a temporary reduction in growth and increased dieback of twigs, but were otherwise unaffected.

Initial symptoms of red and scarlet oak decline were reduced radial and terminal growth over a 2 to 7-year period, and chlorotic and aborted foliage, most apparent in spring, but becoming less apparent by late summer with production of new leaves and greening of chlorotic leaves. Additional symptoms included reduced crown density (most apparent in June but still detectable in mid-August), production of sprout foliage by stems and larger branches, dieback of small upper crown twigs and their replacement by additional shoots, production of "Juhannistrieb" or "Lammas shoots," diminished starch reserves, reduced acorn production, and rootlet mortality less than 30 percent.

Mortality was first observed as a failure of buds to break following winter dormancy. Death usually occurred in August and September. Symptoms accompanying late summer mortality included subnormal crown density, prominent yellowing of foliage, followed by wilting and retention of withered brown leaves, successful attack by two-lined chestnut borer larvae, absence of detectable starch reserves, and necrosis of 50-90 percent of rootlets growing in the upper foot of soil.

Insect defoliators appeared to be closely associated with decline. Staley observed high populations of oak leaf roller larvae and a closely related form *A. Albicomana* Clem.) selectively defoliate red, scarlet, and scrub oaks. Except for an occasional lightly infested black oak, associated species were not injured. Greenhouse and field experiments indicated that insect defoliation alone could be the primary cause of oak decline. However, since two-lined chestnut borers attack only weakened trees, they play a secondary role in oak decline. The impact of chestnut borers and Armillaria root rot appeared to be interrelated and difficult to distinguish. Staley consistently isolated *A. mellea* and an unidentified imperfect fungus from necrotic roots of declining and dying trees, but concluded that both were secondary, weak pathogens. He was unable to consistently isolate fungi from dead branch tissue.

Even though unfavorable soil conditions are usually found associated with oak decline, they were not consistent. Oak decline was not limited to unfavorable aspects of slope positions and it appeared to be more widely distributed and less closely associated with unfavorable soils than was mortality.

Drought was considered more closely associated with mortality than initiation of decline and favored increased populations of oak leaf rollers and borers. Frost was not believed to initiate decline even though it may contribute to decline and mortality.

Three groups of factors were associated with oak decline; those that reduce photosynthate production, those that destroy weakened organs, and those that cause moisture stress. Staley suggested that factors contributing to tree decline and mortality may best be resolved by considering the effect of each factor on carbohydrate metabolism of affected plants.

Approximately three-fourths of the oaks that died in Pennsylvania from 1951 to 1967 were in the red-black oak group (northern red, scarlet, and black oaks) (Nichols, 1968). "Killed trees exhibit 2 to 3 years of serious radial growth reduction, frequently preceded by 2 to 10 years of gradual loss in radial growth. Symptoms of crown decline normally start in the top portion with several dead branches, reduced terminal growth, chlorosis, and stunting of foliage with reduced density. Symptoms progress downward and inward in subsequent years, or in one year, until all that may remain is a stagheaded tree with sprouting on the stem and larger branches." Nichols also observed several areas where dominant trees of several oak species abruptly declined in 1 or 2 years and concluded that insect defoliation or severe frost damage preceded mortality in all red oak areas and areas dominated by oak. Most dying and recently killed trees were infested with two-lined chestnut borers.

Nichols claimed to have traced 75 percent of chestnut and white oak decline and mortality to periodic outbreaks of pit-making oak scale. Death of other chestnut oaks occurred after 2 to 3 years of heavy defoliation by fall cankerworms. Most scale-caused mortality was restricted to nearly pure stands of chestnut oak growing on poor sites. White oak was insect-damaged only when associated with chestnut oak. Oak leaf tiers were the major defoliators of trees in the red oak group. Twenty-two additional insects were identified as contributing to defoliation. Defoliation was most severe on lower slopes and valley bottoms in almost pure stands of trees in the red oak group.

Nichols concluded that "droughts are not a primary casual agent in the present oak decline and mortality situation in Pennsylvania, but their effects are roughly equal to those caused by moderated defoliation." He also stated that "data from each mortality area on aspect, slope, soil condition, tree age, crown class, relative vigor prior to heavy defoliation, site index, and stand density showed no obvious or consistent relation to decline and mortality."

Kegg (1971, 1973) reported 35 to 40 percent mortality among scarlet, white and red oaks and 11 and 16 percent mortality in chestnut and black oaks, respectively, in the Morristown National Historical Park, New Jersey, following gypsy moth defoliation. He observed many defoliated oaks had recovered by July, that new leaves wilted and trees began to die in late August, and that most trees entering fall with sparse foliage did not survive the winter. *A. mellea* and the two-lined chestnut borer were found associated with wilted trees. Soils in the park were moderately deep, well-drained, with a coarse, rock subsoil. Precipitation was about normal.

Kegg's 1973 report on gypsy moth defoliation of oak in the Newark Watershed described stands consisting of 63 percent oak growing on fair to poor sites with shallow soil and frequent rock outcroppings where 90 percent of the white and chestnut oaks were declining or dead. Decline and death of red, black, and scarlet oaks was 65-75 percent. Most dead and dying oaks were infested with Armillaria and two-lined chestnut borers. Kegg, also noted that mortality was greater on southwestern, southern, and southeastern aspects.

Schmidt and Seymour (1972) observed decline in southern live and laurel oak in Florida. Typical decline symptoms included sparse foliage, branch dieback, and sprouts from adventitious buds. The authors concluded that roots damaged by site preparation and weed control activities served as infection courts for *Ganoderma curtisii* (Berk.) Murr. Trees succumbed slowly over a period of years, and decline symptoms intensified during times of drought. Saprophytic fungi, especially a species of Hypoxylon, colonized affected trees. Herbicides, fumigants, irrigation, and fertilization were also mentioned as possibly contributing to decline.

Skelly (1974) reported a 50 percent growth reduction in scarlet oaks following decline initiation until tree death. Smaller diameter, suppressed trees died twice as fast as larger diameter, dominant trees of similar age classes.

Dunbar and Stephens (1975) attempted to establish the role of two-lined chestnut borers and Armillaria to oak mortality in Connecticut. They reported that decline and death of black, red, scarlet, and white oaks was half that of chestnut oak and that mortality was highest where defoliation occurred early and frequently. Fifty to 100 percent of oaks dead one year or more had visible borer emergence holes. Borers had been present in almost all dead chestnut oaks and in many dead white and red oaks. This insect infested significantly more dead trees in the white oak group than in the red oak group. Mycelial fans of *A. mellea* were not found on healthy or dying trees, but were found on trees dead one year and on occasional trees which had recently died. The authors concluded that Armillaria was mainly saprophytic.

Wargo (1977) also studied this fungus-insect relationship relative to oak decline. Investigations were conducted in Pennsylvania on chestnut, white, scarlet, red, and black oak. Wargo's examination of excavated root systems indicated that Armillaria was present long before mycelial fans were evident at root collars. He also found that all dead and dying trees were attacked by borers, but not by Armillaria. Some trees heavily colonized by Armillaria were only lightly infested with borers. Wargo concluded that chestnut borers are dominant on some trees and Armillaria on others. He suggested that oak decline and mortality could not be separated into primary and secondary causes and reiterated the notion that mortality results from a sequence of events that starts with stress; predisposing trees to invasion by organisms that subsequently kill them.

Feder et al. (1980 reported a progressive dieback, beginning in upper crowns, leading to decline and death of English oaks on the north shore of Cape Cod. They noted many symptoms of fungus attack in vascular systems and isolated an unknown fungus.

Lewis (1980) reported drought related oak mortality during 1978 and 1980 in black and willow oaks in Arkansas and Mississippi, southern red oak in Texas, and laurel oak in Florida. Ninety-five percent of declining and dead trees were infected with *Hypoxylon* spp. *Ganoderma lucidum* was found on dead and dying trees with root decay in Arkansas, Mississippi, and Florida. Many affected oaks in Arkansas were attacked by the two-lined chestnut borer. Lewis concluded that oak mortality in the South was triggered by drought and that borers, hypovirulent canker, and root decay fungi were contributing factors.

Tainter and Benson (1982) studied an unusaully high incidence of red oak declne and death in the Nantahala National Forest, North Carolina. Believing that insects and diseases were not involved, the authors statistically analyzed relationships between several climatic variables and growth. They found that "average temperature for December of the year prior to growth and for current February and April had positive effects, whereas current May precipitation had an inverse relationship (to earlywood growth). For latewood growth, average temperature and total precipitation for July or the year prior to growth had positive effects, whereas average current August temperature had an inverse effect. Average current temperature for May and total July precipitation had positive effects. Decline was probably due to a series of drier than normal years from 1975-78."

Tainter et al. (1983) reported extensive oak decline and death along the South Carolina coast in 1981. Willow, laurel, water, and southern red oaks were particularly affected. Decline and mortality were attributed to a prolonged drought, plus a period in 1979 to 1980 where precipitation was the lowest recorded for 30 years. Fruiting bodies of Hypoxylon canker were associated with most dead trees and many declining trees. Once stromata appeared, trees rarely survived more than a few weeks. Soils in oak decline areas were wet, sandy soils on broad ridges.

Factors Involved in Oak Decline

Climate Change (Preparatory Factors)

Hepting (1963), in his review of relationship between climate and forest diseases, makes several points of interest in the study of oak decline. First, he suggests that the most stable characteristic of climate is change. Far from being a "steady state" under which an equilibrium climax forest might be attained, climate is a history of major fluctuations in temperature and precipitation. Not only do temperature and precipitation means change; so do their extremes. These changes in extremes are probably more important to forest health than the changes in means. Consequently, Hepting asks "is the climax forest concept valid?" Can a true climax be attained since climate changes so rapidly?

Drawing on Holloway's (1954) arguments, Hepting says "the crux of his hypothesis is that climatic changes could have been so recent that existing forests bear the imprint of old forest; that existing forests are in a plastic and unstable condition, and that existing forest types and species distribution may be largely out of phase relative to present climates." The argument that climatic changes would affect species only at the limits of their range is refuted by Hepting based on the thesis that geographical races (provenance)means that climatic change would affect a species throughout its range. Indeed, he states "the 'provenance' or local adaptation characteristic of a strain of trees and the fact that long-lived trees will keep their genetic makeup throughout their life while local climate may change could be reasons why some general declines of tree species have been taking place over wide areas."

Even if climate were stable over many years, however, particular species might be found growing in areas and under conditions for which they are not well suited. Knull (1932) suggested that the single most important contributing factor to forest declines is encroachment of civilization. He noted that in Pennsylvania, virgin white pine forests were cut; fire followed, and an American chestnut, chestnut oak, pitch pine forest developed. Chestnut was removed by chestnut blight, leaving an almost pure stand of oaks. These oak stands were then very vulnerable to widespread insect attack. Human activities and commercial interests have considerable influence on forest composition in the United States and are therefore not in a "climax" state relative to climate. Consequently, most forested areas in the United States are in a state of flux accompanied by some degree of stress that influences their vulnerability to decline and pests.

Almost all authors identify drought as a factor in oak decline. Some argue that drought is the major factor, others consider it a contributing factor, and some regard moisture deficiency as a minor, inconsequential stress. Drought can weaken trees, predisposing them to other injury or be the primary cause of death (Hursh and Hanes 1931, Lewis, R. , Jr. 1981, Tainter and Benson 1982). Drought is believed to be favorable for development of defoliating and boring insects (Staley 1965, Houston 1973). Drought may also alter tree physiology, making trees more attractive and nutritious to defoliating and boring insects and root rot fungi (Feeny 1970, Parker 1975, Thomas and Boza 1983). In almost all studies where radial growth has been measured, from 2 to 10 years of reduced growth occurs before decline symptoms become obvious (Fergus and Ibberson 1956, Nichols 1968). Drought could well account for the initial growth loss.

Drought is usually measured in terms of precipitation received for a given period of time. Because recording stations are several miles apart, measurements of drought are difficult to assign to soil moisture availability to individual trees. In addition, length of time a tree is undergoing moisture stress is difficult to determine from precipitation records. Direct measurement of soil moisture is, of course, impossible for past decline times, and laborious and expensive for present decline events.

One should expect drought injury where edaphic factors are unfavorable for moisture storage. The literature indicates that oak decline is most frequently associated with shallow, coarse, rocky, and excessively drained soils although declining trees have been observed growing in apparently favorable soils.

Site Factors

The influence of site factors on tree performance appears to be primarily related to moisture availability, although soil fertility may be involved. Some authors have found that trees most likely to decline are those growing on southern aspects (southeastern to southwestern) Gillespie 1956, Kegg 1973). Excessive drainage due to extreme slopes has also been noted (Gillespie 1956, Tyron and True 1958). Slope may also affect decline via its moderating influence on temperature. Often, only trees at slope bottoms are injured by late freezes (Beal 1926). In addition, steep slopes are often characterized by shallow, well-drained soils (Gillespie 1956, True and Tyron 1956).

Coarse, shallow, poor soils are believed by many investigators to be involved in tree decline because of their more fragile moisture/fertility characteristics (Hursh and Haasis 1931, Tyron and True 1958, Staley 1965, Hursh and Haasis 1981, Tainter et al. 1983). Staley (1965) observed declining stands where heavy clay soils restricted internal drainage, causing overly wet soil conditions during early parts of growing seasons. Low fertility was mentioned by Kegg (1973), Tyron and True (1958), Staley (1965), and Gillespie (1956) as a factor to be considered in decline. Nichols (1968), however, found that "aspect, slope (and) soil condition...showed no obvious or consistent correlation to decline and mortality."

Host Factors

In general, the red/black oak group appears to be more susceptible to widespread decline and mortality than the white oak group (Knull 1932, Fergus and Ibberson 1956, Gillespie 1956, True and Tyron 1956, True and Tyron 1958, Staley 1965, Nichols 1968, Kegg 1971, Skelly 1974. Lewis 1981, Tainter et al. 1983). Exceptions appear to occur where frost (Beal 1926), insect defoliators (Knull 1932, Kegg 1973, Dunbar and Stephens 1975), or pit-making oak scale (Staley 1865, Nichols 1968) are involved. Among the red/black oaks, scarlet oak appears to be most susceptible, followed by northern red and black oak. White and chestnut oak decline more often than other members of the white oak group.

Struve and Moser (1984) reported that scarlet oak had a relatively coarse, unbranched root system which made transplanting difficult. This anatomical characteristic may be of significance in explaining this species, sensitivity to decline. They also discovered that girdling had no effect on numbers of roots initiated or average new root length of seedlings. These data suggest that scarlet oak root growth is more dependent on mobilization of stored food reserves in roots than on newly photosynthesized materials. The observation that starch reserves are usually low in roots of declining trees provides additional evidence to explain sensitivity of scarlet oaks to decline in that the energy required by scarlet oak is insufficient to allow root systems to expand adequately into new sources of moisture and nutrients.

Hinckley et al. (1979) reported that stomata on northern red, white, and black oak were closed 32.9 percent, 22.7 percent, and 19.7 percent of the days measured, respectively. If one were to use control over stomatal closure as a drought resistance mechanism, these data do not fit earlier observations where northern red oak was ranked most susceptible followed by black then white oak. If, however, one considers that at stomatal closure time increases, photosynthesis decreases, then relative rankings of these three species, reaction to drought becomes clearer. A partial explanation follows that depletion of food reserves rather than insufficient water accounts for decline and species susceptibility previously described. Seidel (1972) also ranked black and white oak relatively high in drought tolerance.

Dougherty and Hinckley (1981) list characteristics they believe account for tolerance of white oaks to drought, including: (1) moderate to high photosynthesic capacity; (2) relatively low light saturation levels; (3) relatively high, broad temperature optimum for net photosynthesis; (4) low threshold water potential for stomatal closure; (5) long duration of functional leaves; (6) long persistence of leaf area; (7) deep and extensive root systems. They also observed that white oak roots grow most of the year even under moderate to low soil water conditions. They compared these data to growth requirements reported for northern red oak and concluded that white oaks are better suited to survive drought than red oaks.

Seidel (1972) and Hinckley et al. (1979) ranked black oak similar to white oak in drought tolerance. However, Hinckley et al. (1978) noted that black oak is a pioneer species with high light saturation requirements. An interpretation is that mature black oaks are less successful than white oaks in synthesizing and maintaining adequate starch reserves under adverse conditions, explaining why black oaks sometimes decline along with scarlet and red oaks while white oaks remain unaffected. Estes (1970) stated that "since black oak normally grows on drier sites than white oak, it may be assumed to be the more xeric of the two species and probably better adapted physiologically to the drier climate of northwestern Arkansas than is white oak. Black oak usually develops a long taproot, especially on the poorer sites. This enables it to reach deeper underground water supplies and to be very drought resistant. Black oak is more sensitive to climatic fluctuations than is white oak or shortleaf pine."

Frost

Frost has been implicated as a contributing factor in several accounts of oak decline (Beal 1927, Hursh and Haasis 1931, Staley 1965, Nichols 1968, Skelly 1974). Only Beal and Nichols give details. Beal attributes mortality of many white oaks in Bland County, West Virginia, to a severe late freeze. Dead trees appeared only in valleys and hollows, primarily among large, over-mature oaks. Other than an occasional hickory or red oak, only white oaks were killed, due primarily to the more succulent condition of white oak leaves. Trees failed to produce new leaves the following spring. Beal reported that a drought occurred the following summer, which may have contributed to mortality.

Nichols also believed that late frosts were a major factor in decline situations he studied, followed by insect defoliation. He noted that in nine areas where only dominant oaks were affected, frost damage was the primary factor leading to mortality. In agreement with Beal, Nichols believed that frost had its greatest effects on mature, dominant trees growing in hollows with poor air drainage, but indicated that damage was not limited to these areas. Injury was greatest when frost occurred just prior to or immediately after bud break.

Insects

Insects implicated with oak decline are either defoliators or borers. Borers are generally considered to infest only those trees weakened by other agents. Defoliators, however, are considered to be primary initiators of oak decline.

Nichols (1968) listed 23 insects associated with oak defoliation in Pennsylvania. He considered only five of major importance. Defoliators most commonly identified as major factors in oak decline are gypsy moths, oak-leaf tiers, fruit-tree leaf rollers, and elm spanworms. Burgess (1922) reported a widespread loss of red oak in New England to gypsy moth defoliation. Knull (1932) attributed mortality of oaks in Pennsylvania to fruit-tree leaf rollers and elm spanworms. Staley (1965) stated "the only primary casual factor suggested by this study is defoliation by the oak leaf roller *Argyrotaxa semipurpurana* (Kearf.)." Kegg (1971, 1973) assigned heavy oak mortality in New Jersey to gypsy moth defoliation; Dunbar and Stevens (1975) believed gypsy moths and elm spanworms responsible for oak mortality in Connecticut.

A mechanism of decline associated with insect defoliation appears to be depletion of carbohydrate reserves. Production of new leaves each spring places a heavy demand on energy stores. Regeneration of leaves following defoliation could possibly deplete carbohydrate reserves and account for smaller, chlorotic, and fewer leaves (Staley 1965, Magnoler 1970, Stephens et al. 1972). Baker (1941) reported that ". . .outright killing of thrifty trees by single complete defoliations is confined largely to the conifers and . . .thrifty hardwoods are never injured so severely, although repeated stripping at short intervals may kill them."

Nichols (1968) noted that either 2 consecutive years where spring defoliation between 60 percent to 100 percent occurred, or 3 years of severe defoliation were necessary to initiate mortality. He observed that 2 to 3 years of moderate defoliation occurred before heavy attacks began and that several years of moderate defoliation followed by one heavy defoliation were rarely enough to cause mortality.

However, Minott and Guild (1925) recorded 50 percent losses among dominant white oaks after one complete gypsy moth defoliation. They found a single tree that survived five complete strippings and concluded that even though there was considerable genetic variation among trees, a moderate degree of defoliation was injurious and could lead to tree mortality if it occurred repeatedly.

Staley (1965) induced decline symptoms by artificially defoliating red oaks. He concluded that foliar symptoms of oak decline and leaf roller defoliation were identical and that insect defoliation could be a primary cause. Presence of large numbers of defoliating insects is often related to climatic factors. Effects of drought and defoliation are often compounded in the northeast because defoliator outbreaks frequently accompany hot, sunny periods when soil moisture is low. Leaf cell contents become more concentrated allowing insects feeding on them to develop more rapidly (Houston 1974). Houston observed that trees growing on sites frequently subjected to severe environmental alterations are most likely to be defoliated, but that they may not succumb as readily to a given level of defoliation as those growing on sites rarely disturbed. In 1984, Valentine and Houston reported that stands susceptible to gypsy moth defoliation generally consist of many small, slow-growing trees whereas resistant stands tend to contain relatively large, fast-growing trees. Differences among these stands are probably due to climatic and site factors.

Many reports of oak decline fail to mention insect defoliation (Chapman 1915, Beal 1926, Balch 1927, Hursch and Haasis 1931, McIntyre and Schnur 1936, Gillespie 1956, Fergus and Ibberson 1956, Tyron and True 1958, Tainter and Benson 1982 and Tainter et al. 1983). Even Nichols (1968), who is an advocate of the primary role of insect defoliators, states that "killed trees exhibit 2 to 3 years of serious radial growth reduction, frequently preceded by 2 to 10 years of gradual loss in radial growth." The question remains, what caused the long-term loss of radial growth?

Many reports identify the two-lined chestnut borer as a primary causal agent of oak decline. However, the general concensus is that it is a secondary factor, attacking trees previously weakened (Dunbar and Stephens 1976, Cots and Allen 1980, Haack and Benjamin 1982). Stressed trees are believed to be located by attraction to host plant volatiles (Dunn et al. 1986, Wargo 1983). Dead trees are not attractive to adult borers and larvae do not survive in dry, dead tissue (Wargo 1977, Haack and Benjamin 1982). Felling infested trees is believed to kill many larvae by causing desiccation of cambial tissues (Haack and Benjamin 1982).

Borer eggs are laid in deep cracks in oak bark from which larvae burrow into the cambium making galleries as they grow. Larval development requires four instars. The fourth, overwintering instar larvae exhibit a strong tendency to burrow perpendicularly to the grain, which increases the probability that infested trees will be girdled by one or more galleries (Chapman 1915, Haack and Benjamin 1982). Actively conducting portions of xylem and phloem tissues are thin, especially in the red oak group, making oaks vulnerable to girdling (Haack and Benjamin 1982). Two-lined chestnut borers attack all portions of selected trees (Chapman 1915). Infestation usually begins in crown tops and proceeds down over a 2 or 3-year period without reinfesting areas previously killed (Haack and Benjamin 1982). Complete infestation and death may occur in one year. Girdling of branches and stems may induce wilting and subsequent death of leaves and branches above girdled areas or these parts may die in late fall or the following spring.

Although chestnut borers are generally believed to attack only stressed trees, healthy trees have been infested (Chapman 1915, Nichols 1968, Dunbar and Stephens 1975). Dunbar and Stephens (1975) reported that upper boles of 9 of 23 apparently healthy trees were infested with borers. Evidence of borer attack consisted mainly of adult emergence holes in bark and larval galleries under the bark. Adult emergence holes were not present where larvae failed to reach maturity. However, larval galleries injured trees. It appears that infestation of lower boles, a characteristic associated with mortality, is the last stage of an attack that may have begun 1 to 3 years previously. Early infestations are characterized by chlorotic and aborted foliage, production of sprout foliage, reduced crown density, and dieback of branches. If small, early instar larvae partially or completely girdle upper crown phloem tissues without seriously affecting xylem tissues, they may reduce starch reserves in roots while not markedly affecting crowns (Haack and Benjamin 1982).

There is general agreement among scientists that late summer infestations of boles by chestnut borers are responsible for considerable oak mortality following a period of decline. Attacks are characterized by chlorosis, wilting, browning, and retention of dead foliage caused by the complete girdling of stems. Attacks often coincide with late summer moisture stress.

Armillaria Root Rot

It is generally agreed that this fungus is a pathogen that attacks only weakened trees or injured tissues (Staley 1965, Wargo and Houston 1974, Wargo 1977). *A. mellea* appears to be stimulated by chemical alterations in roots including increases in glucose, fructose, and certain amino acids and production of ethanol (Weinhold and Garroway 1966, Wargo 1972, Wargo 1982). Defoliation, drought, flooding and other injuries can reduce these chemical changes in oak roots (Wargo 1972, Parker and Patton 1975, Crawford and Baines 1977, Wargo and Montgomery 1983). This root rot fungus is frequently found in roots of trees infested with chestnut borers even though there is no requirement of one for the other (Wargo 1977). Some investigators have suggested that the presence of *A. mellea* at root collars may be used as evidence of root infection to classify trees as attacked or not. Wargo (1977), however, has demonstrated that a tree's root system may be extensively colonized by *A. mellea* without any signs produced at root collars.

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Scientific Names

Insects

Two-lined Chestnut Borer	*Agrilus bilineatus* Weber
Gypsy Moth	*Porthetria dispar* L.
Fruit-tree Leaf Roller	*Archips argyropsilus* Walker
Oak Leaftier	*Croesia albicomana* (Clem)
	Croesia purpurana (Kearfott)
Elm Spanworm	*Ennomos subsignarius* (Hbn).
Oak Leaf Roller	*Argyrotaxa semipurpurana* (Kearf.)
Pit-making Oak Scale	*Asterolecanium minus* Lindinger

Fungi

Armillaria Root Rot Fungus	*Armillaria mellea* (Vahl.) Quel.
Hypoxylon Canker Fungus	*Hypoxylon atropunctatum* (Schw. ex Fr.)
Heartrot Fungus	*Ganoderma lucidum* (Leyss. ex Fr.)
	Ganoderma curtisii (Berk.) Murr.

Other Oak Hosts

English Oak	*Quercus robur* L.
Bur Oak	*Quercus macrocarpa* Michx.
Scrub Oak	*Quercus ilicifolia* Wangenh.
Rock Oak	*Quercus montana* Willd.

Decline Events

Date	Location	Oak Species	Factors	Citation
June 1856	Bland County, VA	White	Late Freeze	Beal (1926)
Late 1800's & early 1900's	Massachusetts and Minnesota	White Bur Red Scarlet	Two-lined Chestnut borer (TLCB)	Chapman (1915)
Early 1900's	New York	Oaks	Armillari root rot (ARR)	Long (1914)
1912-1920	–	Oaks	TLCB ARR Drought Late spring Frosts Insect defoliations	Staley (1965)
1912-1922	New England	Red	Gypsy moth	Burgess (1922)
1912-1922	New England	Scarlet Red Black White	Gypsy moth TLCB ARR	Baker (1941)
1912-1921	New England	Scarlet Red Black White	Gypsy moth	Minott & Guild (1925)
1925	Bland County, VA	White	Late Freeze Drought	Beal (1926)
1927	Southern Appalachians	Red Black Scarlet	Late Freeze Drought Overmaturity & Competition ARR TLCB	Balch (1927)
1925-1929	Southern Appalachians	Black Red Scarlet	Drought ARR TLCB	Hursh and Haasis (1931)
1925-1931	Pike County, PA	Red Black Scrub Scarlet White Rock	Fruit-tree leafroller Elm spanworm TLCB	Knull (1932)
1930-1931	Pennsylvania	Scarlet	Drought	McIntyre and Schnur (1936)
1953	West Virginia	Scarlet Red Black White Chestnut	Drought	Gillespie (1956)
1953-1955	West Virginia	Scarlet Red Black	Drought	True and Tyron (1956)

Date	Location	Oak Species	Factors	Citation
1955	Pennsylvania	Red Scarlett Black	Drought ARR	Fergus and Ibberson (1936)
1956-1961	Pennsylvania	Red Scarlet Black Chestnut	Insect defoliation Oak leaftiers	Staley (1965)
1957-1967	Pennsylvania	Red Scarlet Black White Chestnut	Insect defoliation (23 species) Late frost Drought TLCB ARR	Nichols (1968)
1960-1970	Virginia	Scarlet	Gypsy moth Drought Root rot Frost Woodboring insects	Skelly (1974)
1967-1970	New Jersey	White Scarlet Red Black Chestnut	Gypsy moth	Kegg (1971)
1969-1973	Connecticut	Black Red White Chestnut	Gypsy moth Elm spanworm TLCB ARR	Dunbar and Stephens (1975)
1971-1975	Pennsylvania	White Red Black Scarlet Chestnut	Gypsy moth TLCB ARR	Wargo (1977)
Late 1970 's	Massachusetts	English	Unknown fungus	Feder et al. (1980)
1976-1980	Wisconsin	Red Black White	Drought Ice storms Fall cankerworm TLCB Man-made disturbances	Haack and Benjamin
1978-1980	Arkansas Mississippi Texas Florida	Water Willow Southern red Laurel	Drought Hypoxylon canker Ganoderma root rot TLCB	Lewis (1981)
1979	North Carolina	Red	Drought	Tainter and Bensen (1982)
1981	South Carolina	Willow Laurel Water Southern red	Drought Hypoxylon canker	Tainter et al. (1983)

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