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Stand Dynamics in Connecticut Forests: The New Series Plots (1959-2000)

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Most of Connecticut appears as a sea of hills swathed with trees when viewed from a high overlook. This seemingly never-changing cloak of trees is, in fact, a constantly changing assemblage of individual trees. Most of our forest, including the tracts discussed in this bulletin, have arisen after harvesting or farm abandonment in the 1800's (Ward and Barsky 2000). The young saplings which grew on those cutover and abandoned lands are now the large, upper canopy trees in our forests today.

Because forest growth and development are long-term processes, patterns of forest development have been largely derived using indirect methods such as stand reconstruction and comparing stands of different ages. Indirect methods have outlined the general framework of forest stand dynamics. However, they are of limited utility in providing a specific prediction on the future development of an individual stand of trees with its unique initial composition and disturbance history.

Ultimately, forest stand development is the aggregate of the growth, or demise, of many individual trees. Understanding the causal factors that affect the future growth and survival of individual trees will lead to better comprehension of how these factors influence forest succession. This requires a large long-term database with detailed information on individual trees. Fortunately, four large, permanent tracts, the Old-Series plots, were established in young forests (~25-years-old) in central Connecticut in 1926-27. These tracts were reexamined in 1937, 1957, 1967, 1977, 1987, and 1997. These tracts are invaluable because of the length (since 1926-27), depth (43,357 trees, 41 species), and breadth of information (species, dbh, crown class, spatial location, etc.). In addition, their continuity and replication on four sites make these tracts unique.

Earlier reports (Stephens and Waggoner 1980, Ward et al. 1999) have described changes occurring during seventy years on the Old-Series plots. Changes in growth, mortality and ingrowth were related to soil moisture and defoliation. These data have also been used to examine the long-term effects of wildfire (Ward and Stephens 1989), gypsy moth defoliation (Stephens 1971), and individual tree development (Ward and Stephens 1994, 1996, 1997). However, all four tracts lie relatively close to one another, contain few conifers, and have an uneven distribution among soil moisture classes.

Therefore, four additional tracts, the New-Series plots, were established in 1959-1960. These tracts were established on sites with either dry or moist soil moisture classes. Data from these plots were used to determine the relationship between defoliation levels and subsequent mortality (Stephens 1971, 1981). These four tracts represent a wider geographical distribution, a more even distribution among soil moisture classes, and a greater differences in age of trees. Two of the tracts contained abundant conifers: eastern hemlock and eastern white pine (scientific names of woody plants are in Appendix 1). A survey of the permanent tracts in 2000 documented forty years of dynamic change in forest composition. These changes in forest composition will affect the quality and variety of forest resources that are available to future generations and wildlife. Therefore, it is prudent from both ecological and economic perspectives to understand these changes and their possible consequences.

TRACT LOCATIONS AND HISTORY

Because the initial report of these tracts (Stephens and Hill 1971) is out of print, descriptions of the forests are repeated here. The four tracts all lie in the upland region of metamorphic rocks and glaciated soils. The Eastern tracts, Gay City and Natchaug, are relatively younger hardwood forests. The Western tracts, Catlin Woods and Norfolk, are older and have a significant conifer component. The tracts vary in soil, climate, and history.

The Gay City tract, mostly in the Meshomasic State Forest near Gay City State Park, is a mixed hardwood woodland with few conifers. One portion occupies the crest of a north-south ridge at an elevation of about 850 feet. The abundance of rocks, the presence of old charcoal hearths and stone walls and the absence of a plow layer suggest that the land was cleared, but never tilled. In 1980, dominant trees on the somewhat excessively drained ridgetop were found to have originated between 1905-1910 and the smaller trees, between 1910-1920. Scattered dominants originated before 1900 on the moister sites and around 1880 on the poorly drained site. The remaining smaller canopy trees on these sites originated around 1910. This tract lies closest, about 10 miles northeast, to three of the

Old-Series plots reported in an earlier bulletin (Ward et al. 1999).

The Natchaug tract is a stand of mixed hardwood in the Natchaug State Forest in Eastford, about 25 miles northeast of Gay City. Its gently rolling topography ranges in elevation from 700 to 750 feet and its north-facing slope varies from one to seven percent. Stone walls indicate that the land was once cleared, but abundant rocks and absence of a plow layer suggest it was never tilled. In 1980, the larger scattered dominants were found to have originated between 1890-1900, while smaller canopy trees originated between 1910-1920.

Catlin Wood is a stand of hemlock, white pine, and transition hardwoods on a nearly flat plain at about 900 feet elevation in the White Memorial Foundation in Litchfield. Slope ranges from one to four percent. Catlin Wood is the oldest of the four tracts in the New Series. This stand was established around 1795. Its origin is obscure, but since early 19th century the main disturbance has been cutting or windthrow (Smith 1956). Removal or death of chestnut permitted a second age group of mixed hardwoods and hemlock, originating around 1910-1920, to develop.

The Norfolk tract in the privately owned Great Mountain Forest, lies about 18 miles north of Catlin Wood in a region of rugged terrain in the lower Berkshire Hills. Its east-facing slope varies from one to fifteen percent and lies between 1400 and 1500 feet elevation. In 1980 the larger white ash and red oak were found to have originated between 1880-1890. The presence of sprout clumps and charcoal hearths suggest the area was heavily cut around 1880. Smaller and younger beech, yellow birch and black cherry about 90 years old suggest a second disturbance in 1910. Hemlock was not used for charcoal, but it may have been removed at a later date. Persistent stumps reveal that chestnut was also present earlier. The absence of fire scars suggests that this tract was not burned.

Site Characteristics

On the Gay City tract, soils have formed on friable glacial till derived chiefly from Bolton schist. The somewhat excessively drained, shallow Hollis soil predominates. The remainder of the tract lies about 0.6 miles east at 500 to 550 feet elevation on an east-facing slope of 4 to 11 percent. The well drained Charlton soil occupies the upper slopes, the moderately well drained Sutton occupies the lower slopes, and the poorly drained Leicester occupies the drainage swales.

On the Natchaug tract, soils have formed on compact glacial till derived from Eastford granitic gneiss. Hardpan is present throughout the area sampled. The well drained

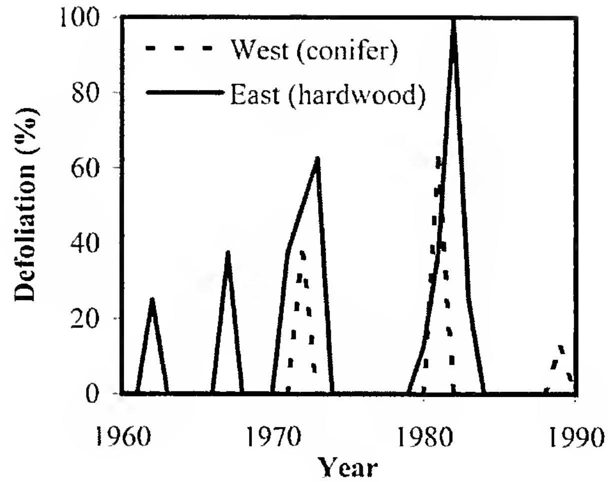

Figure 1. Estimated canopy defoliation (%) on New-Series plots between 1960-1990. There were no observed defoliation episodes after 1989.

Woodbridge soil on the upper slope gives way to the poorly drained Ridgebury soil on the lower slope.

At Catlin Woods, the underlying bedrock is mostly Brookfield diorite gneiss. The soils developed on glacio-lacustrine sands which thinly mantle the underlying glacial till. On the lower slopes, the glacial till forms a weakly developed hardpan at depths of 20 to 30 inches. On the upper slopes, the well drained Agawam and the moderately well drained Sudbury soil formed in sand and gravel. The poorly drained Walpole soil occupies a broad drainage swale at the base of the terrace.

On the Norfolk tract, soils are formed on compact glacial till derived principally from Canaan Mountain schist. Hardpan is present at depths of 20 to 30 inches, restricting downward drainage and creating seepage areas near the base of the slope. Well drained Paxton soil occurs on the upper slopes, moderately well drained Woodbridge on the lower slopes, and the poorly drained Ridgebury soil occurs at the base of the slope.

Insects and Disease

Annual defoliation maps prepared from aerial reconnaissance by the State Entomologist were used to estimate defoliation on the tracts. The eastern hardwoods tracts were defoliated more frequently, and more severely, than the western conifer tracts (Fig. 1). The eastern tracts had partial defoliation by gypsy moth *(Lymantria dispar)* and canker worm (*Paleacrita vernata*) during 1962 and 1967. Severe multi-year defoliation episodes were noted during 1971-73 (gypsy moth and elm spanworm (*Ennomos*

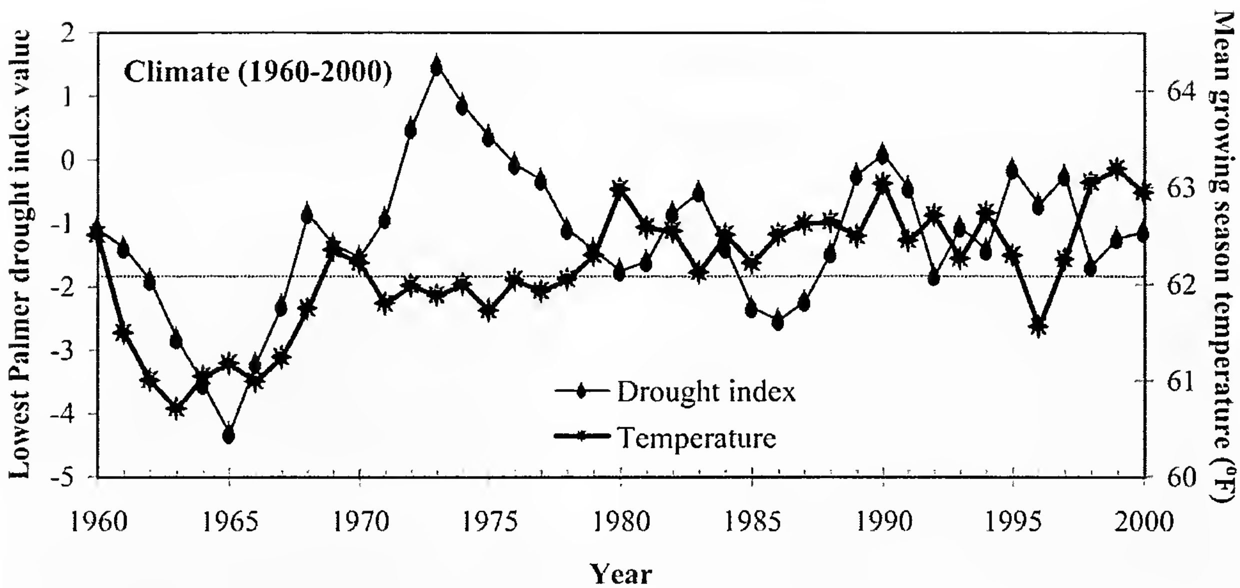

Figure 2. Mean growing season temperature and lowest Palmer drought severity index values during the growing season (April-September) between 1960-2000. Running three year averages are shown.

subsignarius), and 1980-1983 (gypsy moth). In contrast, defoliation was noted in the western tracts only in 1972, 1981, and 1989. The 1989 defoliation was controlled by the gypsy moth fungus (*Entomophaga maimaiga*). Gypsy moth populations in Connecticut have continued to be controlled by the fungus.

Introduced diseases have also influenced the composition of these forests. American chestnut have been recorded on all the tracts. However, chestnut blight fungus (*Cryphonectria parasitica*) has largely relegated this formerly regal species the status of an understory shrub. Dutch elm disease (*Ceratocystis ulmi*) reached the Gay City tract (the only one with elm) before the first survey in 1959. Because elms were never abundant in these forests, the disease had less impact than chestnut blight.

Beech bark disease, a complex of beech scale (*Cryptococcus fagisuga*) and a fungus (*Nectria coccinea* var. *faginata*), was found on 14% of American beech. Beech bark disease weakens, and may kill trees, by both feeding on sugars flowing through the branches and trunk, and by killing tissues that feed and produce the bark. A native canker, Nectria canker (*Nectria galligena*), was also present. It was found on nearly 4% of black birch in these tracts, about half the rate of 8% observed in the Old-Series tracts (Ward et al. 1999). Although it rarely kills trees, Nectria canker can weaken trees and cause considerable loss of commercial wood production.

Weather

Climate varies somewhat among tracts because of their distribution over the state. In general, the western conifer tracts in the Litchfield Hills are cooler and moister than the eastern hardwood tracts. Climatic data used here are from Bradley Airport in Windsor Locks, Connecticut. Gay City is approximately 20 miles southeast of the airport. Catlin Woods, Norfolk, and Natchaug are slightly more than 30 miles from the airport and lay southwest, west, and east, respectively. The area is in the northern temperate climate zone. Mean monthly temperature ranges from 25°F in January to 73°F in July. There are an average of 176 frost free days per year. Average annual precipitation is 44.4 in per year, evenly distributed over all months.

Soil moisture is replenished during winter months because trees do not remove water via transpiration. Adequate rainfall during the growing season is crucial if trees are to maximize growth. A wet August or September can mask the presence of a drought during the early summer. Therefore, we determined the lowest (most severe) Palmer drought index value during the entire growing season (April-September) for a given year. The lowest Palmer drought severity index values, along with the mean temperature during growing season, are presented for the period between 1960-2000 (Fig. 2). Three year averages are shown to emphasize trends by smoothing the often dramatic year-to-year fluctuations. Climate values were obtained from the National Oceanic and Atmospheric Administration (NOAA 2004).

The climate in northern Connecticut has oscillated between wet and dry during the past forty years. The first decade (1959-1970) was the coldest and driest period. The following decade (1970-1980) was the wettest period and had average temperatures. Temperatures between 1980-2000 were slightly elevated from the previous twenty years and had average to slightly moister than average conditions. It should be noted that there were years within each 10-year period when drought severity differed significantly from the average for the decade.

FIELD METHODS

In each tract a base line was established generally perpendicular to the contour and across a series of drainage classes. Along the base line, soils were identified according to profile morphology and slope position. Drainage classes were identified according to the Soil Survey Manual (Anon. 1951). Within each drainage class, transects were established parallel to the contour on one or both sides of the base line. The transects were 16.5 feet wide (5 m) and 66 feet (20 m) to 394 feet (120 m) long. The end of each transect segment was permanently marked with an iron t-bar and rock cairn at 66-feet intervals. Where possible, approximately equal areas were sampled in each drainage class (Table 1). The drainage classes were grouped into three sites: moist, containing the very poorly drained, poorly drained and somewhat poorly drained soils; medium moist, containing the moderately well drained and well drained soils; and dry, containing the somewhat excessively drained and excessively drained soils.

Along the transects, each stem with a diameter of at least 0.5 inches at 4.5 feet above ground, was plotted on a map, identified, and described. The 1959-60 tree descriptions included species, dbh, crown class, and whether the stem was part of a sprout clump. Diameters were measured to the nearest 0.1 inch. The Norfolk, Gay City, and Catlin Woods tracts were established in 1959. The Natchaug study area was established in 1960.

Crown class is a qualitative measure of a tree's position in the canopy relative to its neighbors (Smith 1962). The upper canopy of a forest is comprised of dominant and codominant trees (Fig. 3). Upper canopy trees have well-developed crowns that receive direct sunlight from above and partly on the side. Intermediate and suppressed trees form the lower canopy. Intermediate trees only receive direct sunlight from above. Suppressed trees are found under the other crown classes and receive no direct sunlight, except for occasional sunflecks.

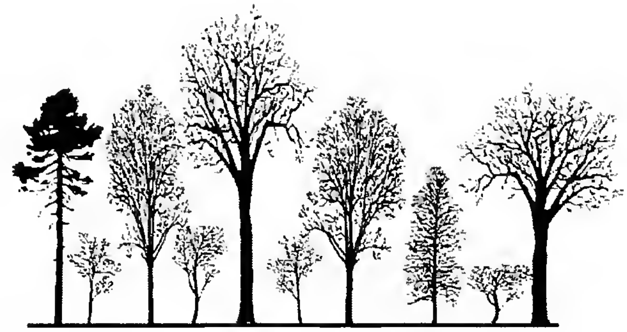

Figure 3. Schematic drawing of crown classes. D-dominant, C-codominant, I-intermediate, S-suppressed.

Individual trees were relocated using maps from the previous survey for the surveys in 1970, 1980, 1990, and 2000. A total of 2831 stems were included in these surveys. Mortality of previously counted stems and ingrowth (stems that had grown to at least the minimum dbh since previous survey) were also recorded. Total height of all dominant trees and every tenth other tree was measured to the nearest foot in 1980. Trees measured for height were also examined for stem and crown defects. The defects were of form and symmetry and external injury to crown and stem. Internal defects such as heartrot were not included. Beginning with the 1980 survey, the perpendicular distance of each stem from the centerline of the transect was measured and recorded. Stems were measured using the metric system during the 1990 and 2000 inventories. Diameters were measured to the nearest 0.1 cm and the minimum diameter was slightly decreased to 1.2 cm (0.47 inches).

Regeneration (stems < 0.5 inches dbh) was first inventoried in 1980 using 1/300 acre circular plots. The center of each regeneration plot was located halfway, or 33 feet, between the cairns with stakes. A slightly smaller 1/1000 hectare (1/405 acre) circular plot was used for the 1990 and 2000 inventories. Stems were tallied by species in one-foot height classes (<1, 1-1.9, 2-2.9,..., ≥ 9 ft tall). For this Bulletin, regeneration was categorized as either seedlings (< 4 feet tall) or saplings (≥ 4 ft tall and < 0.5 inches dbh).

Species groups

There were 26 major tree species represented, 7 minor species, and 13 shrub species which included small understory trees, chestnut sprouts and large shrubs. Species are categorized into similar groups to simplify the discussion. As before, extensive tables with summaries by

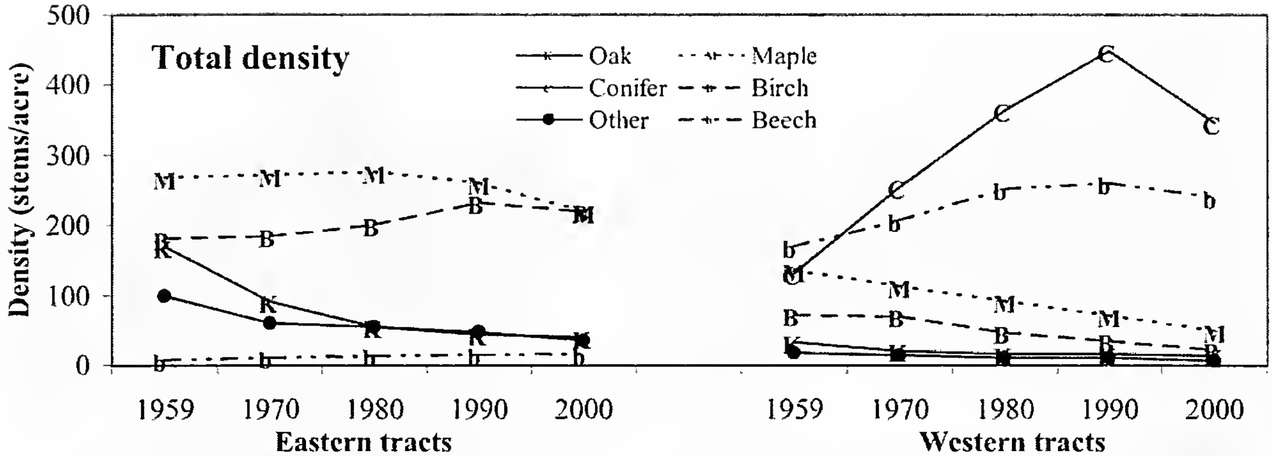

Figure 4. Total stand density (stems/acre) by species group and survey year for New-Series plots.

individual species are provided. These are found at the end of the Bulletin. Preceding these tables is a species list with their common and scientific names.

The OAK group included northern red, black, scarlet, white, and chestnut oak. The BIRCH group includes black, yellow, and paper birch. The MAPLE group includes red and sugar maple. American beech is the sole species in the BEECH group. The CONIFER group includes eastern white pine and eastern hemlock. The OTHER group includes those species that can form part of the upper canopy in a mature forest, but were found at low densities on these tracts. To fit the individual species tables on a page the following species were combined: green and white ash, slippery and American elm, the various species of shadbush.

MINOR species are those species that do not grow large at maturity and generally do not appear in the canopy except in very young stands. This group includes intolerant pioneer species (e.g. gray birch) and species that can grow and develop in the understory (e.g., flowering dogwood, blue-beech, shadbush, and hophornbeam). American chestnut is also included in the MINOR species category because chestnut blight kills stems before they grow large enough to enter the upper canopy. Species that do not grow tall enough to form part of the upper canopy (e.g. witchhazel and highbush blueberry, and spicebush) were included in the SHRUB category.

COMBINED CROWN CLASSES

Density

For the reader's convenience, all tables are at the end of this Bulletin. To simplify the analysis presented in this Bulletin, the similar eastern hardwood tracts (Natchaug and Gay City) were combined, as were the similar western tracts (Catlin Woods and Norfolk) that had a significant conifer component. Total tree density is the mean density (stems/acre) of the combined species over all moisture classes.

In 1959 the number of stems per acre varied among tracts and sites. The relatively younger eastern tracts had higher densities than the older western tracts. This difference has largely disappeared over the past forty years. These tracts are increasingly dominated by late-seral or "climax" species. Between 1959-2000, Maple/Birch/Beech have increased from 44% to 59% of stems in the eastern tracts. In the western tracts over the same time period, the proportion of Maple/Beech/Conifer increased from 70% to 90%.

Species that require more sunlight to reach the forest understory for their seedlings to grow, and depend on more severe disturbances to increase the sunlight, have been declining in numbers over the past forty years. This group includes the oaks, ashes, aspens, and black cherry. It is likely these species will continue to decline in numbers until there in a major disturbance event such as a hurricane or intense wildfire.

The decline in oak and other more shade intolerant (sun loving) species is not unique to this study, other unmanaged forests (Christensen 1977, Nigh et al. 1985, Barton and Schmelz 1987, Ward and Parker 1989, Ward and Stephens 1993) or forests that are partially harvested (Heiligmann et al. 1985, Jokela and Sawtelle 1985, Smith and Miller 1987, Abrams and Scott 1989, Abrams and Nowacki 1992). This will lead to large scale changes in the landscape from even-aged to uneven-aged forests, and may accelerate the shift in dominance from midtolerant to tolerant species. Stand growth rates may slow when stands become dominated by

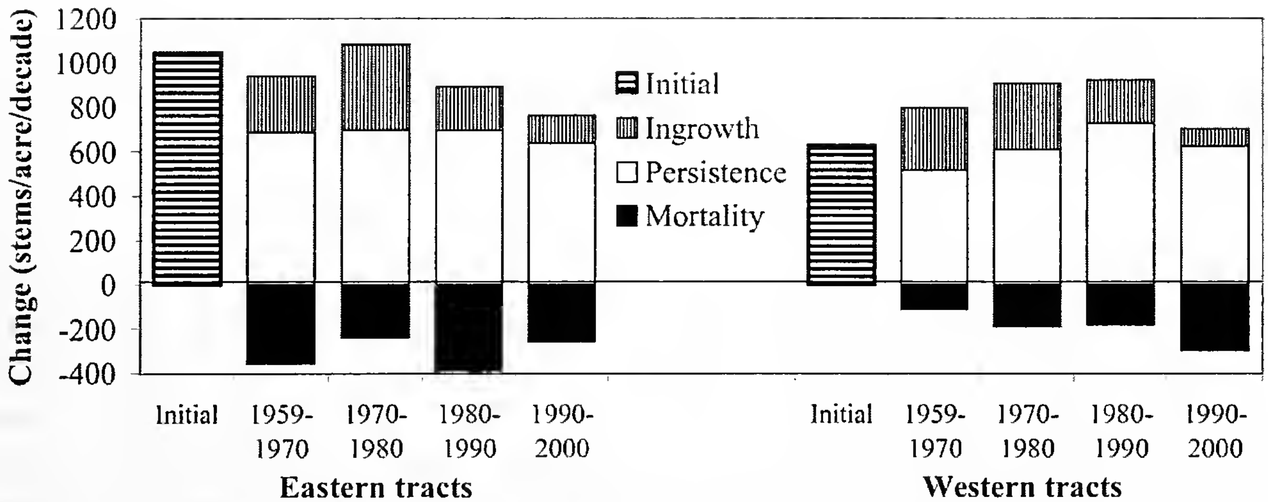

Figure 5. Components of total population dynamics by survey year for New-Series plots.

more tolerant species (Lamson and Smith 1991). These changes will affect not only the quality and makeup of forest products available to future generations, but will also affect the quality and variety of wildlife habitats (Scanlon 1992).

Total tree density decreased on the eastern tracts between 1959-70, rose between 1970-80, and has steadily decreased between 1980-2000 (Table 2, Fig. 4). This pattern is similar to that noted for the Old-Series tracts and was attributed to a lag response to the period of drought and defoliation during the early 1960's (Ward et al. 1999) that killed many of the upper canopy trees. Death of the upper canopy trees allowed increased sunlight to reach the forest floor – this resulted in an increase in regeneration. Increased populations of black birch and spicebush accounted for most of the increased density.

Density on the western tracts, in contrast, rose steadily from 1959-1990. These tracts experienced only minor defoliation over the past forty years. Eastern hemlock and American beech accounted for all of the increase. Density of every other species, except striped maple and elderberry, decreased during this period. The decrease of all species between 1990-2000 was probably due to self-thinning of the very dense stands, and not to an introduced insect. Hemlock woolly adelgid (*Adelges tsugae*) and elongate hemlock scale (*Fiorinia externa*) were observed in the western tracts in 2000, but had not caused any appreciable damage or mortality.

Minor species density peaked in 1980. American chestnut was the predominant Minor species in the eastern tracts, and striped maple in the western tracts. The most numerous Shrub species in both the eastern and western tracts was witchhazel. There was also a significant component of spicebush and elderberry in the eastern and western tracts, respectively.

Components of change

We examined the net changes in stem density from decade to decade in the preceding section. Decade-to-decade changes can be separated into three components (persistence, mortality, and ingrowth) to better understand the underlying dynamics affecting our forests (Fig. 5). Persistence is the number of stems that survive during a given time period. Persistence is important because it conveys a sense of the population stability. Mortality is the number of stems that die, and ingrowth is the number of new stems during a given period. Mortality measures disappearance from the forest. The net change in the population is determined by the balance between mortality and ingrowth. Population density can be stable under scenarios where mortality and ingrowth are both low, or where mortality and ingrowth are both high.

Persistence

The small decadal changes in density can be related to the high persistence of most species groups between the surveys (Fig. 6). Persistence peaked between 1970-1990 on the eastern tracts and between 1980-1990 on the western tracts. Persistence was similar on all tracts (~ 630 stems/acre) between the most recent surveys, 1990-2000. The number of stems that persisted exceeded the combined total of mortality and ingrowth for a given period.

There were differences in persistence among species groups. On the eastern tracts, Birch and Maple exhibited

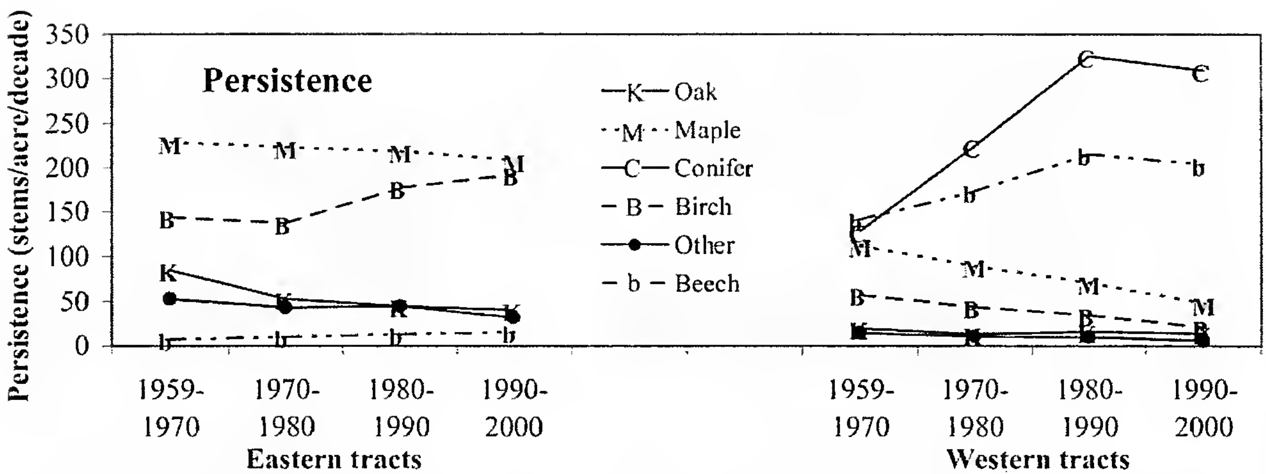

Figure 6. Persistence (stems/acre/decade) by species group and survey years for New-Series plots. Persistence includes stems that survived from one survey to the next.

higher persistence than Oak. Birch persistence increased from 1959-2000, while Maple persistence slightly decreased over the same period. Different patterns of persistence were noted for the western tracts. Conifer and Beech persistence dramatically increased from 1959-1990, while Maple and Birch persistence decreased steadily. It will take another 10-20 years to know if the drop in Conifer and Beech persistence between 1990-2000 is part of a long-term trend.

Mortality

As noted above, mortality is the loss of stems present at one inventory and absent on a subsequent inventory. The causes of mortality are varied. Large canopy trees usually die as a result of storm damage, disease, or declining vigor. As trees become larger and larger, more and more of the sugars produced by the tree are utilized to keep alive the massive support structure (trunk and branches) that lift the leaves above competing trees. Therefore, less energy can be allocated to defense against insect and disease attacks. Thus, as an aging tree becomes larger, it becomes more likely to succumb to an infestation. Competition for light, water and nutrients eliminates stems from the lower canopy and understory. Attack by insects and disease eliminates stems from all canopy strata. Some trees are broken by snow or ice, severe storms or other falling trees. Mortality can also occur on areas flooded by beaver impoundment.

For any given ten-year period, mortality varied from 238-385 stems/acre in the eastern tracts and 110-296 stems/acre in the western tracts (Table 3). Mortality generally increased over time for species groups with large numbers of stems in the subcanopy (e.g., Shrubs, Conifer, Beech). Species that were primarily in the upper canopy, such as Oak and Other, demonstrated a pattern of decreasing mortality over time. The mortality for a given decade was highly correlated (r^2 = 82%) with the density at the beginning of the period (Fig. 7). This was expected, given that trees are competing for limited resources (light, moisture, nutrients). More trees on a given acre means there are fewer resources per tree. For some trees this means death from competition.

Gross mortality numbers only tell how many stems have died, not how fast the stems are dying. For example, let us

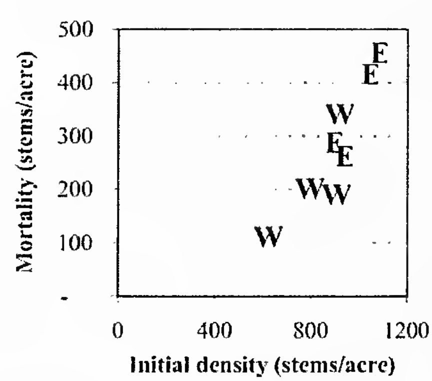

Figure 7. Relationship between initial density and mortality during the following decade for New Series plots.
E – eastern tracts, W – western tracts.

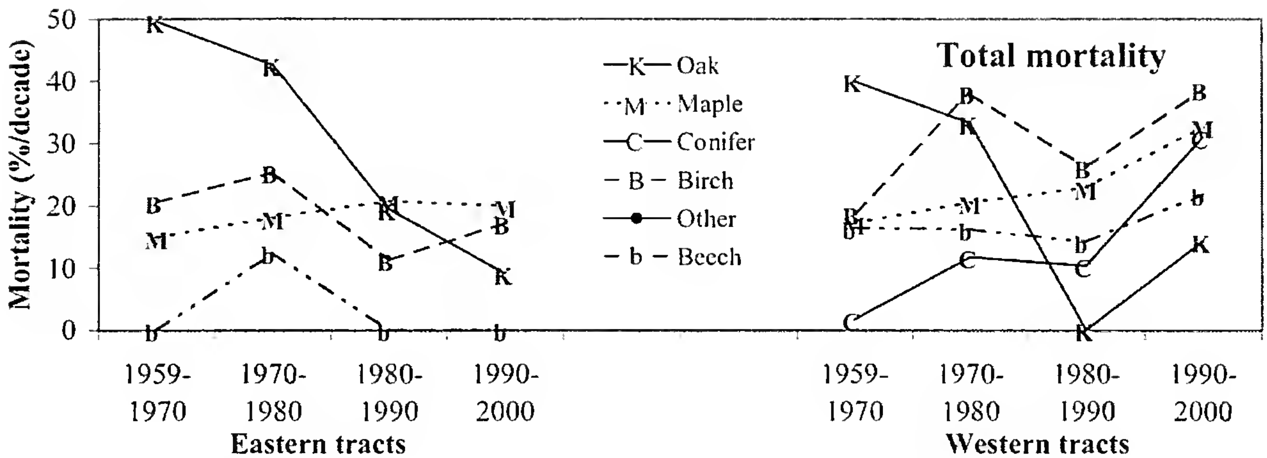

Figure 8. Mortality rate (%/decade) by species group and survey years for New-Series plots. Mortality rate is percent of stems that died between surveys.

imagine that the mortality of two species groups, A and B, was both 50 stems/acre/decade. If at the beginning of the period species group A had 100 stems and species group B had 1000 stems, then species group A would have a higher mortality rate (50%) than species group B (5%). These mortality rates (%/decade) are presented in Figure 8.

The mortality rate varied from decade-to-decade in both the eastern and western tracts. In all periods except 1990-2000, the mortality rate was higher in the eastern hardwood tracts, 29-36%, than in the western conifer tracts, 18-32% (Table 3). As noted above, much of this variation can be explained by the correlation with initial density and subsequent mortality.

Distinct patterns were noted for the different species groups. The mortality rate for Oak decreased over time on all tracts from a high of 48% between 1959-1970 to a low of 11% between 1990-2000. In contrast to the declining mortality rate exhibited by Oak over the past forty years, Maple mortality increased from 16% to 23%, and Conifer mortality increased from 2% to 31%. It is surprising that Beech mortality has increased only slightly over past forty years because 18% of trees were infected with beech bark disease (*Sirococcus clavigignenti-juglandacearum* / *Nectria coccinea* var. *faginata* or *N. galligena*). This disease complex has resulted in severe mortality (>50%) of upper canopy trees in other regions (Houston 1999).

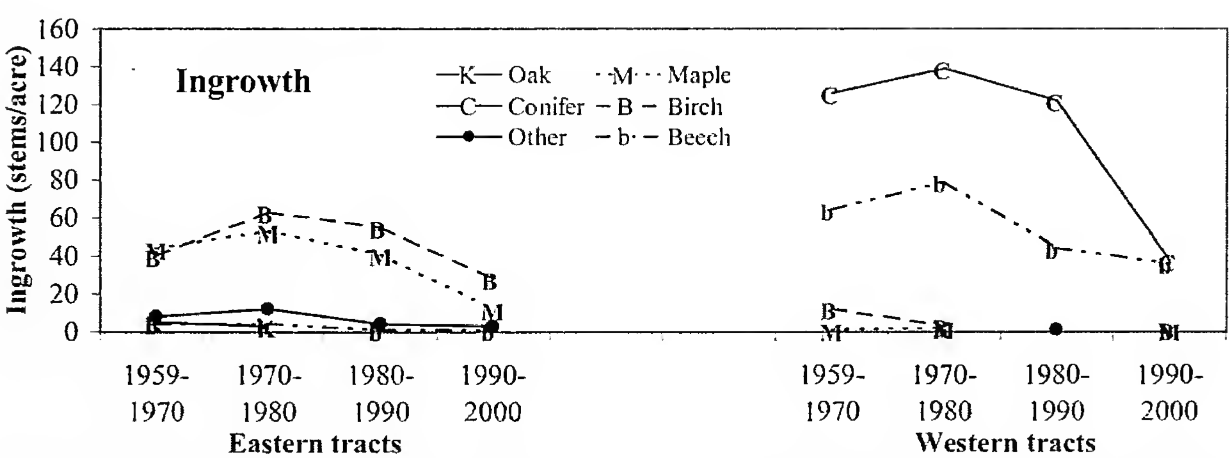

Figure 9. Ingrowth (stems/acre/decade) by species group and survey years for New-Series plots. Ingrowth includes stems that grew to threshold diameter between surveys.

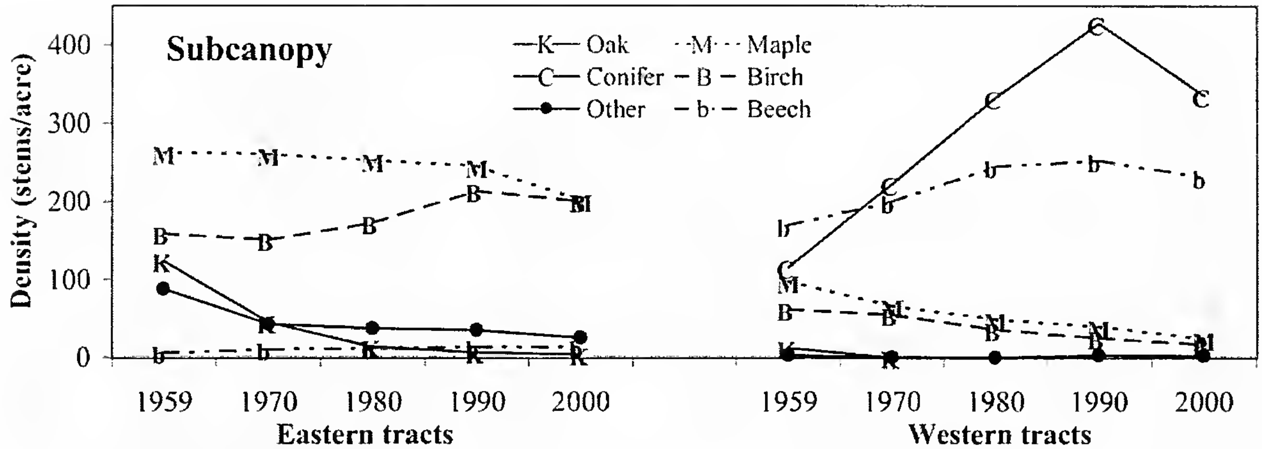

Figure 10. Subcanopy density (stems/acre) by species group and survey year for New-Series plots. Subcanopy includes trees in intermediate and suppressed classes.

Some species, such as gray birch and bigtooth aspen, are pioneer species that colonize recently disturbed areas, grow quickly, and die at a relatively young age (for trees). These species had very high mortality rates and have disappeared from these undisturbed forests. Mortality rates of Minor and Shrub species were generally higher, often much higher, than mortality rates for the other species rates.

Ingrowth

The growing space (and associated limited resources) that had been utilized by a tree becomes available when that tree dies. Some of the growing space is captured by the expanding root and crown systems of neighboring trees. Some of the growing space is colonized by new seedlings that may then grow large enough (0.5 inches dbh) to be included in our surveys. These new trees (ingrowth) are the pool of individuals that will form the future forest. Some of the ingrowth will survive and grow into the upper canopy with the passage of time. Examining the composition of the ingrowth provides us with clues as to the makeup of our future forests.

Ingrowth peaked between 1970-1980 in both the eastern and western tracts with 383 and 297 stems/acre, respectively (Table 4). This was probably a lag response to the periods of defoliations of the 1960's and 1970's. It can take 10-20 years for a seedling to grow large enough to be included in our surveys. Ingrowth densities decreased in each of the following decades with the absence of any addition disturbance.

Although a wide diversity of species was found on these tracts, almost all of the ingrowth was limited to several species. These species differed between the eastern and western tracts. There has been no oak or hickory ingrowth observed on these tracts since 1980. Among the species capable of growing into the upper canopy in these mature forests, Maple and Birch accounted for 83-95% of ingrowth on the eastern tracts (Fig. 9). On the western tracts, Beech and Conifer accounted for 94-99% of ingrowth.

Striking differences between the eastern and western tracts were also observed in the composition and density of Minor and Shrub ingrowth. Between 1980-2000, there were fewer than six stems/acre of Minor ingrowth in the western tracts, compared with 44 stems/acre in the eastern tracts. Most of this ingrowth was American chestnut and the deer resistant striped maple. Shrub ingrowth has been minimal on the western tracts, especially since 1980. In contrast, Shrub and Minor species have accounted for 49-65% of all ingrowth stems in the eastern tracts. American chestnut was the most common species, with some bluebeech and hophornbeam in recent years. Witchhazel and spicebush have been the dominant Shrub species.

SUBCANOPY TREES

In an unmanaged forest with a disturbance regime of single-tree or small group mortality, ingrowth trees (discussed above) form part of the subcanopy. Subcanopy trees are in the intermediate and suppressed crown classes under the upper canopy (Fig. 3). The more numerous suppressed trees live completely in the shade of lower trees, while intermediate trees receive sunlight on the top of their crowns. The subcanopy forms the pool of trees from which future upper canopy trees will emerge in a mature forest without major disturbance, such as the New-Series tract. However, most subcanopy trees grow and die before a

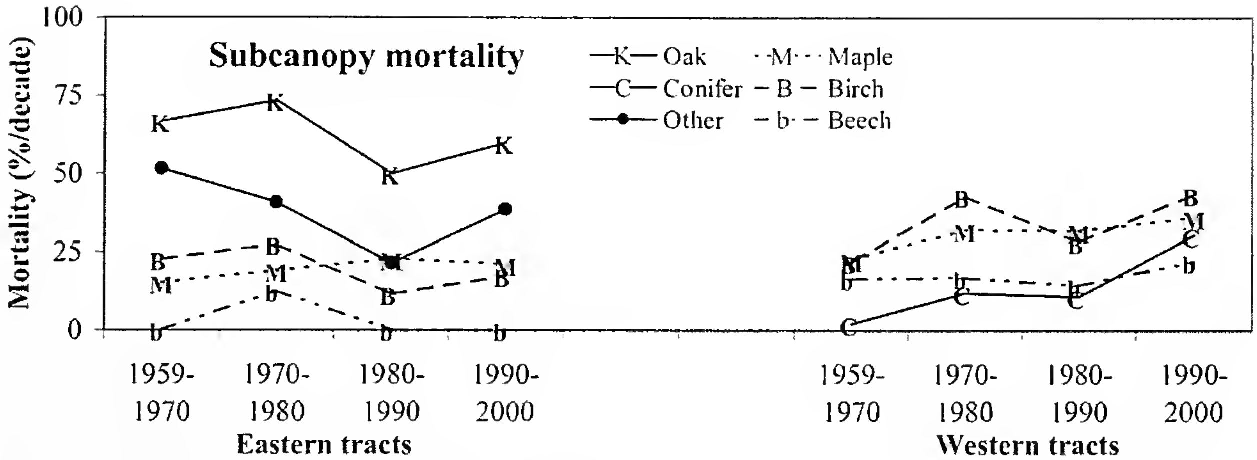

Figure 11. Subcanopy mortality (stems/acre/decade) by species group and survey year for New-Series plots.

canopy opening is created by the death of an adjacent upper canopy tree.

This environment where subcanopy trees grow is quite distinct from that of the upper canopy trees. Surviving and growing in this environment requires a different set of attributes from those best suited for growing in an open field, a recent clearcut, or a hurricane blowdown. Understory trees need to be able to produce sugars (photosynthesize) to survive and grow, albeit slowly, at low light levels. Light levels can be reduced by 90% or more, and the light that does get through is of a lower quality. One adaptation is that subcanopy trees often leaf out before the overstory trees. Some evergreen species have another adaptation. The maximum rates of photosynthate storage for hemlock occur on mild days during the winter and early spring before hardwood trees have formed new leaves (Hadley and Schedlbauer 2002).

Nutrient availability is also low in mature forests. Subcanopy trees have to be efficient scavengers of scarce mineral nutrients such as nitrogen, phosphorus, and iron. Humidity is generally higher, but obtaining soil moisture is constrained by the well established root systems of larger trees. Browse damage can be high, especially for the smaller saplings. Small trees can be crushed or damaged by falling branches and storm damaged trees.

Subcanopy trees have important ecological functions. Small mammals and birds consume the fruit of many subcanopy species such as spicebush, winterberry, and arrowwood. The preferred nesting site for some birds are the low branches of subcanopy trees. Subcanopy trees also provide cover for other animals. By filling the root gaps of larger trees, and by being efficient scavengers of nutrients, subcanopy trees recover nutrients that otherwise would be lost to natural leaching. This helps maintain site productivity and reduce mineral loss to adjacent wetlands and streams.

Density

As with total density (Table 2), subcanopy density decreased on the eastern tracts between 1959-70, rose between 1970-80, and has steadily decreased between 1980-2000 (Table 5, Fig. 10). Most of the increased density in the eastern tracts can be attributed to black birch and spicebush. As noted above, this pattern is similar to that noted for the Old-Series tracts and was probably a lag response to the period of defoliation during the 1960's and 1970's that caused high mortality of established trees. This mortality spike allowed increased sunlight to reach small seedlings and saplings.

Density on the western tracts rose steadily from 1959-1990 before decreasing by 23% between 1990-2000. Eastern hemlock and American beech accounted for nearly all of the increase. Density of every other species, except striped maple and elderberry, decreased during this period. This decrease was probably due to self-thinning of the very dense subcanopy stratum.

The density of most species groups has fallen during the past forty years. Between 1950-2000, the subcanopy density of Oak, Other, and Maple species decreased by 97%, 70%, and 39%, respectively. Oak has not been found in the subcanopy on the western tracts since 1960 and has virtually disappeared from eastern tracts by 2000. Some of the more shade intolerant species such as scarlet oak and black oak are no longer found in the subcanopy. While Birch declined by 73% on the western tracts to only 17 stems/acre, it increased by 26% to 200 stems per acre on the eastern tracts. The subcanopy density of the most shade tolerant species have exhibited an increase over the past forty years. Increases of eastern hemlock and American beech have been 190% and 39%, respectively.

Mortality

Trees in the subcanopy grow in a restricted resources environment with low light levels, low nutrient availability, limited available root space, etc. Small trees store the starch reserves needed to replace leaves or other parts destroyed by insects, disease, or browsing in these suboptimal conditions. Without these starch reserves, trees may be unable to recover from multiple episodes of damage and consequently, die. Subcanopy trees that develop in canopy gaps often decline and die when the gap is closed by lateral branch extension of surviving upper canopy trees. These scenarios and others (e.g., competition) contribute to the high levels of subcanopy mortality.

Subcanopy mortality, expressed as stems/acre/decade (S^{-A-D}), has fluctuated between 228-376 S^{-A-D} since 1959 on the eastern hardwood tracts (Table 6). Except for the period between 1959-70 when Oak mortality was high, Minor and Shrub species accounted for the largest share of mortality on the eastern hardwood tracts. Shrub species accounted nearly half of the mortality since 1980. The decrease in Oak mortality from a high of 83 S^{-A-D} between 1959-1970 to only 4 S^{-A-D} between 1990-2000 was related to a decrease in the number of subcanopy oaks, and not to increased survivorship as will be shown below.

In contrast, subcanopy mortality has steadily increased over time on the western conifer tracts, from 107 S^{-A-D} between 1959-1970 to 229 S^{-A-D} between 1990-2000. Subcanopy mortality for all species groups were relatively lower on the western conifer tracts until the 1990-2000 period. Eastern hemlock mortality increased from 2 S^{-A-D} between 1980-90 to 128 S^{-A-D} between 1990-2000. It is unclear whether this increased mortality is related to competition or to an alien insect (e.g., elongate hemlock scale). An analysis of mortality rates (i.e., the percent of stems that died on a per decade basis) reveals temporal patterns that were obscured by differences in initial densities (Fig. 11). Although the number of Oak subcanopy trees dying has steadily decreased since 1959-1970, the mortality rate has remained above 50% for the entire period between 1959-2000. The high mortality rate of this species group, coupled with the lack of ingrowth since 1980 (Table 4), suggests that Oak may not be present in the subcanopy within twenty years. This is important because in the absence of major disturbance, such as a hurricane, only trees in the subcanopy are able to grow into the upper

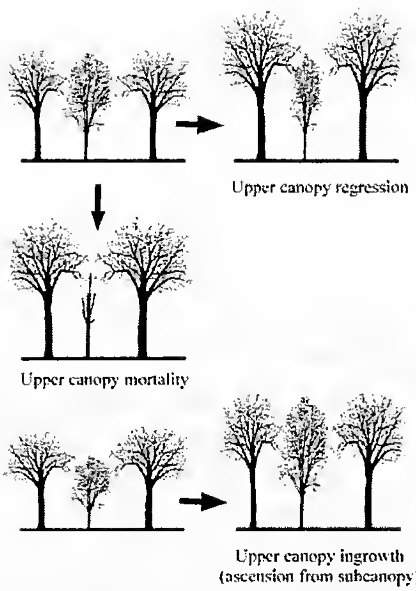

Figure 12. Schematic drawing showing upper canopy regression and ingrowth (ascension). Regression includes those trees that failed to grow fast enough to stay in the upper canopy (i.e., the tree had slower height growth than its neighbors). Upper canopy ingrowth (ascension) includes trees in the intermediate crown class that grew tall enough to form part of the upper canopy.

canopy. We may be witnessing the beginning of the loss of Oak from these stands.

Not only has absolute mortality increased on the western conifer tracts, as noted above, but the mortality rate has also increased – from 20% between 1959-70 to 32% between 1990-2000. Mortality rates on the western tracts have increased to levels higher than those observed on the eastern tracts. The mortality rate has increased for every species group, but most dramatically for Birch and Conifer. Comparing the 1959-1970 to 1990-2000 periods, Birch mortality has nearly doubled and Conifer mortality has increased 15-fold.

SUBCANOPY / UPPER CANOPY DYNAMICS

While most of the changes in subcanopy density can be explained by mortality and ingrowth (i.e., small trees growing large enough to be measured), there are other pathways, albeit smaller in scale. Subcanopy density is decreased by some trees growing into the upper canopy, and subcanopy density is increased by some canopy trees regressing into the subcanopy.

Occasionally, canopy gaps are large enough to allow a tree in the intermediate crown class to move into the upper canopy (Fig. 12). This is ascension, or ingrowth into the upper canopy from the subcanopy. Canopy gaps in unmanaged stands are commonly created in one of two ways: gradual tree mortality or severe weather.

Trees are not immortal. A healthy tree has one year's worth of starch reserves stored in the roots and above ground woody tissues. This reserve is used by the tree to recuperate from injuries caused by weather (broken branches, late spring freezes, drought), insects (gypsy moth, bronze birch borer), disease (anthracnose, Nectria canker), and fire. However, as trees become larger, more and more of the sugars produced by photosynthesis are used to feed the existing trunk, branch, and root systems. This leaves fewer sugars available to maintain the starch reserves and to produce the defensive compounds that protect a tree from injurious insects and disease. When a tree has low starch reserves, any moderate damage can cause the tree to enter a decline spiral and die – creating a canopy gap. Severe weather can also remove a tree from the upper canopy by causing massive damage to the uppermost branches, or in extreme cases, uprooting the tree or snapping off the trunk.

The reverse of ascension is regression. Regression in the movement of trees from an upper canopy position to the subcanopy. There are three common ways this can happen. First, a storm can break off the uppermost branches of a tree. Second, mortality of upper branches (dieback) may to sufficient that the tree is no longer in an upper canopy position. This may happen when the root system is damaged or reduced by competition. Lastly, regression includes those trees that failed to grow fast enough to remain in the upper canopy, i.e., the tree had slower height growth than its neighbors. For example, a 40-year-old upper canopy maple is 50 feet tall and surrounded by 50 foot tall oaks. Over the next 25 years the maple only grew nine feet taller, while the surrounding oaks grew 20 feet. Although the maple has increased its height, it has regressed into a lower canopy position because it was overtopped by the faster-growing neighboring oaks. Earlier studies have found that most of the larger maples and birch that are found under the upper canopy oaks are not younger than the oaks, just slower growing (Oliver 1978, Ward et al. 1999).

Upgrowth (Ascension)

Upgrowth, or upper canopy ascension, was much a more important process than regression between 1959-1970 (Fig 13). High upper canopy mortality during 1959-1970 increased the amount of growing space (light, nutrients, and moisture) available for lower canopy trees. This allowed some of them to grow sufficiently to move into the upper canopy (Table 7). Upgrowth on the eastern tracts averaged 31 stems/acre between 1959-60, and 42 stems/acre on the western tracts during the same period. This influx of new upper canopy trees precluded other lower canopy trees from ascending to a higher position in later years. Thus, upgrowth declined precipitously after 1980 to an average of only three stems/acre/decade. Because there were few, if any oaks in the subcanopy, most of the new upper canopy trees were species typical of the northern hardwood forest. Maple and Birch accounted for 73% of all upgrowth on the eastern tracts over the past forty years. Conifer (37%), Maple (28%), and Beech (21%) were the predominate species moving into the upper canopy on the western tracts.

Regression

For most periods examined, very few upper canopy trees regressed into the lower canopy (Fig 12). Regression

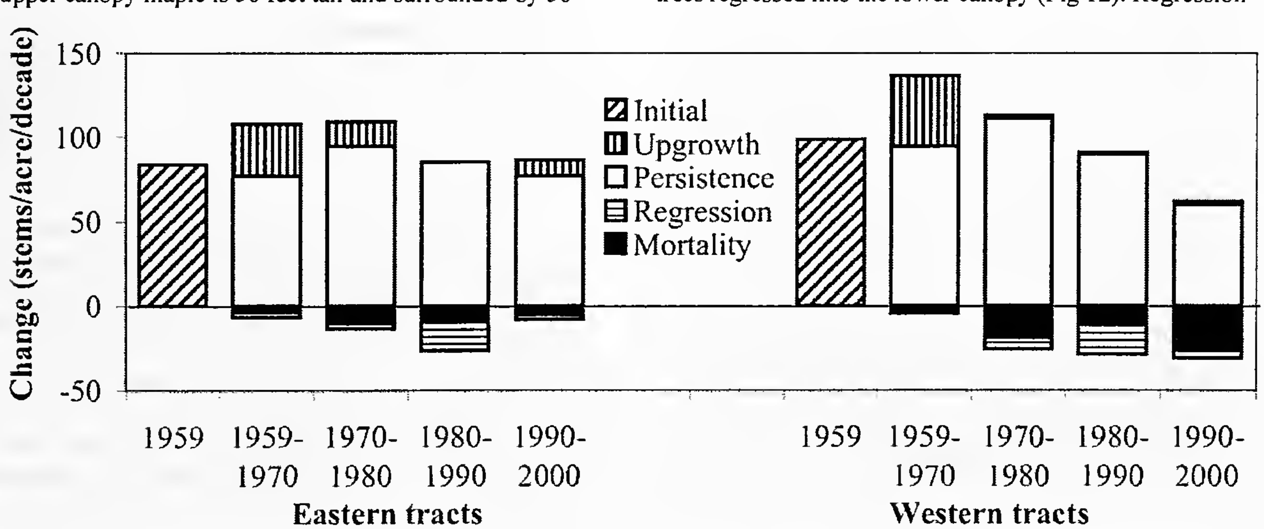

Figure 13. Components of upper canopy population dynamics by survey year for New-Series plots.

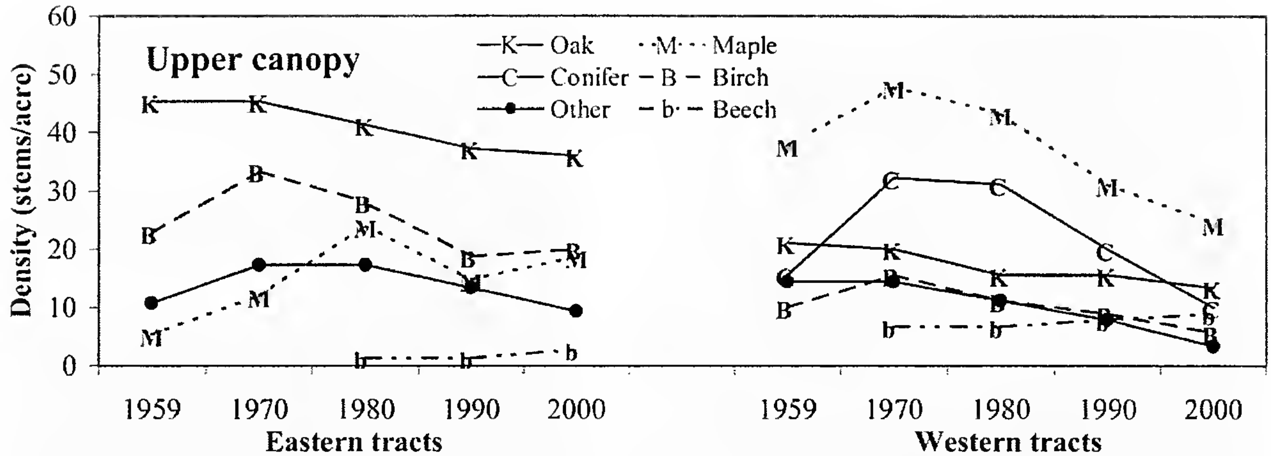

Figure 14. Upper canopy density (stems/acre) by species group and survey year for New-Series plots. Upper canopy includes trees in dominant and codominant crown classes.

averaged slightly less than three stems/acre (~ 3% of upper canopy stems) on the eastern hardwood tracts for all periods, except 1980-90 when over 17 stems/acre regressed into the lower canopy. Maple and Birch accounted for 68% of all regression. Regression on the western conifer tracts was also highest between 1980-90 when nearly 18 stems/ acre moved from the upper to lower canopy stratum. Conifer (37%) and Maple (37%) accounted for most the regression on the western tracts over the past forty years.

UPPER CANOPY TREES

From a distance the impression of a forest is gained only from those tree crowns that form the main canopy, the dominant and codominant trees. Trees and shrubs submerged in the lower canopy or in the understory remain unseen. As mentioned in the Methods section, upper canopy (or overstory) trees are those trees that have well developed crowns and receive direct sunlight from above and partly on the side. Forests are often typed, especially by the casual observer, by the composition of the upper canopy. Midslope forests with a northern red oak overstory, red maple subcanopy, and a mountain laurel shrub layer are most commonly categorized as red oak forests.

The composition of the upper canopy is important for several reasons. The composition of the upper canopy has a direct impact on seed production because there is a correlation between the amount of sunlight a tree receives and the amount of seeds produced. Thus, upper canopy composition affects both the makeup of the seedling strata and the wildlife species that live in the forest. Turkey, eastern white-tailed deer, and chipmunks are more common in oak forests, grouse in young aspen stands, and red squirrels in conifer forests.

Although 24 major, 7 minor, and 8 shrub species have been observed on these tracts, only 16 species appeared as dominant or codominant stems in the canopy during 1959-2000 (Table 8). Upper canopy stems were only a small fraction of all stems – 10% and 13% on the eastern hardwood and western conifer tracts, respectively. Only four species accounted for the majority of upper canopy in both the east and west. Eastern tracts were dominated by northern red oak, black birch, red maple, and scarlet oak. Western tracts were dominated by red maple, eastern hemlock, northern red oak, and sugar maple.

We commonly think of the forest as unchanging, especially for the large trees. The upper canopy is, in fact quite dynamic at time scales that span decades (Fig. 14). Nearly half of the original upper canopy trees found in 1959 had either died or regressed into the lower canopy by 2000. Indeed, a careful analysis (the details of which are beyond the scope of this bulletin) shows that the average sojourn of Oak in the upper canopy was 89 years, compared with only 65 years for Maple and 42 years for Birch.

As noted above, the Oaks are gradually being replaced by species typically found in the northern hardwood forests of central New England. Maple, Birch, and Beech have increased from one-third to more than one-half of the upper canopy trees on the eastern tracts over the past forty years. Over the same time period, the proportion of the upper canopy on the western tracts that is comprised of Conifer, Maple, and Beech has increased from 54% to 66%. Thus, in the absence of a major change in climate or disturbance, our children and grandchildren will know a very different forest than that which we are familiar with today – as we know a very different forest than our ancestors knew 100 years ago.

BASAL AREA

A decreasing number of trees is not necessarily indicative of a declining forest; but is usually a consequence of trees growing larger. Large trees need more resources (light, moisture, nutrients) than small trees. One or more resources becomes limiting as individual trees grow and utilize more and more resources. Mortality can be especially high for smaller trees growing under their larger neighbors. Because these smaller trees are more numerous, total forest density will decrease as part of natural stand development.

Another gauge of forest development and change is basal area. If you were to cut a tree at 4.5 feet aboveground and calculate the surface area of the cut, you would have determined the value that foresters refer to as the basal area of that tree. The basal area of a stand is simply the sum of the basal area value of all trees in that stand.

Basal area is an important measure as it is closely correlated with the bulk, or volume, of the forest. Because basal area is proportional to diameter squared it is easily seen that the basal area of many small trees is not great whereas the basal area of only a few trees of large diameter can be considerable. For example, 196 1-inch diameter trees have the same basal area as one 14-inch diameter tree. In general, basal area tends to increase with increasing stand age even though population decreases.

Unlike density, basal area has steadily increased over the past forty years, except between 1990-2000 on the western tracts (Table 9). The average annual basal area increase has been 1.1% and 0.5% on the eastern and western tracts, respectively. This indicates that although density has been generally declining since 1980 (Table 2), the forest is healthy and increasingly comprised of larger trees. Since 1959, the number of sawtimber trees (diameter $\geq$ 10.5 inches) has more than doubled on the eastern tracts and increased by 19% on the western tracts (Table 10). It is especially striking the density of trees with diameters larger than 20 inches has nearly tripled over the past forty years.

Basal area has also increased for most species groups over the past forty years (Fig. 15). Oak basal area increased on both the western and eastern tracts. It has remained near 25% of all basal area over the past forty years even as Oak density decreased from 12% to only 3% of stems. Beech increased on both the eastern and western tracts. Maple and Birch basal area increased on the eastern tracts, while declining on the western tracts. Conifer basal area increased by over 70% on the western tracts between 1959-1990 and then fell slightly in the following ten years.

SEEDLINGS AND SAPLINGS

Every tree species is adapted to thrive in a specific, optimal range of soil moisture, fertility, and climate; after all, oranges don't grow in New England. A large determinant of which species will be found in the seedling and sapling layer of unmanaged stands, such as those in this study, is the suite of adaptations that allow a seedling to grow in the shade of established trees and to exploit ephemeral canopy gaps created by dying trees. Species with these adaptations, such as American beech, eastern hemlock, sugar maple, and black birch, are flourishing in

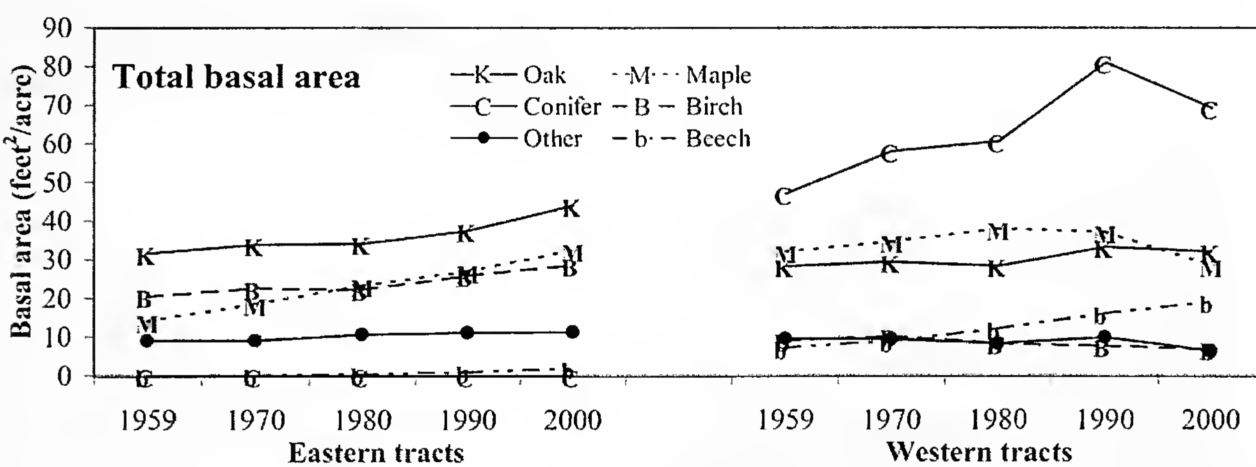

Figure 15. Stand basal area (ft²/acre) by species group and survey year for New-Series plots.

the New-Series stands. Without a change in the disturbance type or climate, it is likely that they will continue to increase and eventually dominate these stands. Species such as oak and aspen that require periodic disturbances (e.g., drought, fire) are slowly declining in these forests.

Seedlings populations are highly variable and can change rapidly over a period of several years. Seed production of different species is not synchronized. Beech, hemlock, birch, and maple produce some seed every year, with heavy production every several years. Other species including oak and hickory have large seed crops at longer intervals. Thus, in a given year, several species have high seed production, several species have intermediate production, and most species have very low seed production.

Seeds have innumerable hurdles to surpass in the process of germinating, surviving, and growing into the sapling size class. Most do not. Before a seed germinates, it must escape detection by a host of predators (weevils, mice, deer, etc.) that consume nearly every seed. For the few seeds that successfully escape detection and are able to germinate, most will begin life where chances of survival are minimal because of inadequate growing space (high competition), unfavorable soil/moisture environment, or recurring damage by deer browsing. Considering the host of tribulations that beset a seed before it can develop into a sapling, the natural regeneration of a forest is a remarkable process.

Seedlings

Seedling (<4 feet tall) densities were much higher than the combined density of saplings, subcanopy and upper canopy trees (Table 11). In 1980 there were nearly 12,000 seedlings/acre on the eastern tracts and over 8,600 seedlings/acre on the western tracts. There were a few trends for seedlings on the western tracts. Seedling densities increased for sugar maple, red maple, white ash, black oak, sassafras, and shadbush. Seedling density decreased for black birch, yellow birch, American beech, flowering dogwood, and bluebeech. Although yellow birch had the highest density in the sapling size class in 2000; red maple, white oak, white ash, and shadbush had higher seedling densities. Whether this is a harbinger of future changes in the composition of the sapling size class, or reflects the competitive superiority of yellow birch to develop into saplings, will require us to revisit these stands in future decades.

A different pattern was noted on the western conifer tracts where seedling density in 1990 was twice that of 1980, and triple that of 2000. The bulge of seedling density was largely explained by an increase of over 8000 stems/acre of eastern hemlock. Fewer than 700 of these seedlings were still alive ten years later. Seedling densities of two species, American beech and striped maple, increased between 1980 and 2000. Over the same time period, seedling densities of red maple, northern red oak, yellow birch, and shadbush declined. Interestingly, while eastern hemlock and American beech accounted for 87% of saplings on the western tracts in 2000; only 27% of the seedling population was comprised of these two species. Although nearly 40% of seedlings were red maple, no red maple saplings were found.

Saplings

For this section, saplings are defined as trees at least four feet tall with diameters less than one half inch. There is intense competition among the thousands of seedlings and fewer than ten percent grow large enough to become a sapling (Table 12). Sapling density doubled between 1980-2000 on the eastern hardwood tracts (Fig. 25). This increase was largely driven by an dramatic increases of highbush blueberry (1280%) and yellow birch (450%). Oak sapling density was relatively stable, while Maple sapling density actually declined. The complete loss of dogwood saplings after 1980 was probably related to dogwood anthracnose that was widespread in the region (Anagnostakis and Ward 1996).

In contrast, sapling density declined on the western conifer tracts between 1980-2000. Most of this decline was related to a decrease in eastern hemlock sapling density from 200 to 45 stems/acre. Many of the hemlock saplings were in "dog-hair" patches in canopy gaps created by the mortality of an upper canopy oak. The decrease in hemlock density was somewhat counterbalanced by an increase in American beech from 192 to 247 stems/acre. It is worth noting that two aforementioned species were the only tree species present in the sapling size class. This would suggest that these forests may be become less diverse with the passage of time.

THE FUTURE FOREST

Forty years of the research have shown that even our older forests are not static dioramas, but rather that they are dynamic and constantly changing as trees grow, die, and are replaced. Change will continue to be a characteristic of these and all of our forests. The research reported in this Bulletin suggests that two very different forests are developing.

On the warmer and drier tracts, oaks are not reproducing and are gradually being replaced by maple and birch. If this trend of the last forty years were to continue, scarcely ten percent of upper canopy trees will be oak in 100 years. The future is uncertain because of the potential effects of climate change, an alien insect that prefers maple (Asian longhorned beetle, *Anoplohora glabripennis*), and the potential reintroduction of blight resistant American chestnut (Anagnostakis 2001).

The cooler and moist tracts in western Connecticut have become increasingly dominated by northern hardwood species and eastern hemlock. The latest survey in 2000 found that nearly 90% of subcanopy trees were either eastern hemlock or American beech. However the fate of those species is uncertain because of the alien pests hemlock woolly adelgid and beech bark disease.

We will continue to monitor these tracts to more completely understand the processes that shape our forests. This will also allow us to gauge the any future impact to the forest caused by hurricanes, alien pests that are already in Connecticut (e.g., beech bark disease, hemlock woolly adelgid), and alien pests that may arrive within the next decade (e.g., Asian longhorned beetle, emerald ash borer (*Agrilus planipennis*)). The one lesson that we can take from this study of forest dynamics, and the history of the Connecticut forest, is that our forests are resilient and with careful conservation will continue to cloak our sea of hills with an ever changing kaleidoscope of species.

ACKNOWLEDGMENTS

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APPENDIX I

Common and scientific names of trees and shrubs mentioned in this Bulletin

Oak

White oak	*Quercus alba*
Scarlet oak	*Quercus coccinea*
Northern red oak	*Quercus rubra*
Black oak	*Quercus velutina*

Maple

Red maple	*Acer rubrum*
Sugar maple	*Acer saccharum*

Birch

Yellow birch	*Betula alleghaniensis*
Black birch	*Betula lenta*

Beech

American beech	*Fagus grandifolia*

Minor

Shadbush	*Amelanchier arborea*
Gray birch	*Betula populifolia*
Bluebeech	*Carpinus caroliniana*
American chestnut	*Castanea dentata*
Flowering dogwood	*Cornus florida*
Hophornbeam	*Ostrya virginiana*
Striped maple	*Acer pensylvanicum*

Conifer

Eastern white pine	*Pinus strobus*
Eastern hemlock	*Tsuga canadensis*

Other

Pignut hickory	*Carya glabra*
Shagbark hickory	*Carya ovata*
Mockernut hickory	*Carya tomentosa*
White ash	*Fraxinus americana*
Black ash	*Fraxinus nigra*
Tupelo	*Nyssa sylvatica*
Bigtooth aspen	*Populus grandidentata*
Black cherry	*Prunus serotina*
Black locust	*Robinia pseudoacacia*
Sassafras	*Sassafras albidum*
Basswood	*Tilia americana*
American elm	*Ulmus americana*
Slippery elm [A]	*Ulmus rubra*

Shrubs

Witchhazel	*Hamamelis virginiana*
Winterberry	*Ilex verticillata*
Spicebush	*Lindera benzoin*
Highbush blueberry	*Vaccinium corymbosum*
Hobblebush	*Viburnum alnifolium*
Arrowwood	*Viburnum dentatum*
Northern wild raisin	*Viburnum cassinoides*
Elderberry	*Sambucus canadensis*
Maleberry [B]	*Lyonia ligustrina*

[A] combined with American elm for analysis
[B] combined with highbush blueberry for analysis

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Table 1. Distribution of area (acres) by tract and soil moisture class of New-Series research plots.

	East		West		Combined plots		
	Gay City	Natchaug	Catlin Woods	Norfolk	East	West	Total
Wet	0.10	0.10	0.10	0.15	0.20	0.25	0.45
Medium	0.10	0.20	0.23	0.15	0.30	0.38	0.68
Dry	0.25	0.00	0.13	0.15	0.25	0.28	0.53
Total	0.45	0.30	0.45	0.45	0.75	0.90	1.65

Table 2. Stand density (stems/acre) during 1959-2000.

	Eastern plots					Western plots					Combined plots				
Species	1959	1970	1980	1990	2000	1959	1970	1980	1990	2000	1959	1970	1980	1990	2000
Eastern white pine	-	-	-	-	-	2	13	19	4	2	1	7	10	2	1
Eastern hemlock	-	-	-	-	-	129	241	344	443	343	70	132	188	242	187
Sugar maple	33	39	56	52	51	67	53	41	29	23	52	47	48	39	36
Red maple	235	233	220	208	169	69	60	51	42	26	144	139	128	118	91
Mockernut hickory	1	1	-	-	-	-	-	-	-	-	1	1	-	-	-
Pignut hickory	41	24	16	15	13	-	-	-	-	-	19	11	7	7	6
Shagbark hickory	7	4	4	4	3	-	-	-	-	-	3	2	2	2	1
Northern red oak	71	47	31	24	21	28	17	11	11	10	47	30	20	17	15
Black oak	9	5	4	3	3	-	-	1	1	1	4	2	2	2	2
Scarlet oak	11	11	11	9	8	-	-	-	-	-	5	5	5	4	4
White oak	79	28	9	8	8	6	3	3	3	2	39	15	6	5	5
Yellow birch	69	60	75	79	69	57	54	36	26	14	62	57	53	50	39
Black birch	109	123	125	153	151	14	16	11	9	8	58	64	63	75	73
American beech	7	11	13	15	16	169	206	251	260	240	95	117	143	148	138
White ash	23	12	12	9	5	10	9	8	8	3	16	10	10	8	4
Black ash	1	1	1	1	-	1	1	1	1	-	1	1	1	1	-
Basswood	4	1	1	-	-	-	-	-	-	-	2	1	1	-	-
American elm	4	4	3	3	3	-	-	-	-	-	2	2	1	1	1
Bigtooth aspen	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Tupelo	1	3	5	7	4	-	-	-	-	-	1	1	2	3	2
Black locust	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-
Black cherry	4	-	-	-	-	6	4	2	2	2	5	2	1	1	1
Sassafras	11	9	12	9	7	-	-	-	-	-	5	4	5	4	3
American chestnut	27	36	83	29	16	8	13	4	3	-	16	24	40	15	7
Gray birch	3	1	-	-	-	-	-	-	-	-	1	1	-	-	-
Flowering dogwood	33	41	39	3	-	-	-	-	-	-	15	19	18	1	-
Bluebeech	52	28	13	11	9	-	-	-	-	-	24	13	6	5	4
Shadbush	1	-	-	-	-	14	13	3	-	-	8	7	2	-	-
Hophornbeam	5	1	1	5	8	-	-	-	-	-	2	1	1	2	4
Striped maple	-	-	-	1	3	1	6	39	24	11	1	3	21	14	7
Witchhazel	171	124	171	123	121	41	73	63	27	8	100	96	112	70	59
Winterberry	16	9	16	15	24	-	-	1	1	1	7	4	8	7	12
Spicebush	7	69	129	77	36	-	-	-	-	-	3	32	59	35	16
Highbush blueberry	7	9	16	21	27	-	-	-	-	-	3	4	7	10	12
Hobblebush	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Arrowwood	-	1	15	9	-	-	-	-	-	-	-	1	7	4	-
Witherod	-	-	-	-	-	2	8	-	-	-	1	4	-	-	-
Elderberry	-	-	-	-	-	1	7	16	26	9	1	4	8	14	5
Combined species	1043	937	1081	893	775	626	798	907	921	706	815	861	986	908	737

Table 3. Periodic mortality (stems/acre/decade) during 1959-2000.

	Eastern plots				Western plots				Combined plots			
Species	1959 1970	1970 1980	1980 1990	1990 2000	1959 1970	1970 1980	1980 1990	1990 2000	1959 1970	1970 1980	1980 1990	1990 2000
Eastern white pine	-	-	-	-	0.0	1.1	14.4	2.2	0.0	0.6	7.9	1.2
Eastern hemlock	-	-	-	-	2.2	28.9	23.3	136.7	1.2	15.8	12.7	74.5
Sugar maple	2.7	5.3	12.0	5.3	13.3	13.3	12.2	6.7	8.5	9.7	12.1	6.1
Red maple	37.3	44.0	45.3	46.7	10.0	10.0	8.9	16.7	22.4	25.5	25.5	30.3
Mockernut hickory	0.0	1.3	-	-	-	-	-	-	0.0	0.6	-	-
Pignut hickory	20.0	9.3	1.3	2.7	-	-	-	-	9.1	4.2	0.6	1.2
Shagbark hickory	2.7	0.0	0.0	1.3	-	-	-	-	1.2	0.0	0.0	0.6
Northern red oak	28.0	17.3	6.7	2.7	11.1	6.7	0.0	1.1	18.8	11.5	3.0	1.8
Black oak	4.0	1.3	1.3	0.0	-	-	0.0	0.0	1.8	0.6	0.6	0.0
Scarlet oak	0.0	1.3	1.3	1.3	-	-	-	-	0.0	0.6	0.6	0.6
White oak	52.0	18.7	1.3	0.0	2.2	0.0	0.0	1.1	24.8	8.5	0.6	0.6
Yellow birch	18.7	13.3	12.0	14.7	12.2	21.1	10.0	12.2	15.2	17.6	10.9	13.3
Black birch	16.0	32.0	10.7	25.3	1.1	5.6	2.2	1.1	7.9	17.6	6.1	12.1
American beech	0.0	1.3	0.0	0.0	27.8	33.3	35.6	56.7	15.2	18.8	19.4	30.9
White ash	10.7	1.3	2.7	4.0	1.1	1.1	1.1	4.4	5.5	1.2	1.8	4.2
Black ash	0.0	0.0	0.0	1.3	0.0	0.0	0.0	1.1	0.0	0.0	0.0	1.2
Basswood	2.7	1.3	1.3	-	-	-	-	-	1.2	0.6	0.6	-
American elm	0.0	1.3	0.0	0.0	-	-	-	-	0.0	0.6	0.0	0.0
Bigtooth aspen	1.3	-	-	-	-	-	-	-	0.6	-	-	-
Tupelo	0.0	0.0	0.0	2.7	-	-	-	-	0.0	0.0	0.0	1.2
Black locust	-	-	-	-	1.1	-	-	-	0.6	-	-	-
Black cherry	4.0	-	-	-	1.1	2.2	0.0	0.0	2.4	1.2	0.0	0.0
Sassafras	5.3	2.7	5.3	4.0	-	-	-	-	2.4	1.2	2.4	1.8
American chestnut	21.3	13.3	74.7	26.7	3.3	10.0	2.2	3.3	11.5	11.5	35.2	13.9
Gray birch	2.7	1.3	-	-	-	-	-	-	1.2	0.6	-	-
Flowering dogwood	5.3	13.3	36.0	2.7	-	-	-	-	2.4	6.1	16.4	1.2
Bluebeech	30.7	17.3	5.3	4.0	-	-	-	-	13.9	7.9	2.4	1.8
Shadbush	1.3	-	-	-	5.6	10.0	3.3	-	3.6	5.5	1.8	-
Hophornbeam	4.0	0.0	0.0	0.0	-	-	-	-	1.8	0.0	0.0	0.0
Striped maple	-	-	-	0.0	0.0	1.1	18.9	13.3	0.0	0.6	10.3	7.3
Witchhazel	69.3	28.0	76.0	37.3	17.8	35.6	43.3	20.0	41.2	32.1	58.2	27.9
Winterberry	13.3	2.7	5.3	4.0	-	-	0.0	0.0	6.1	1.2	2.4	1.8
Spicebush	2.7	9.3	77.3	56.0	-	-	-	-	1.2	4.2	35.2	25.5
Highbush blueberry	0.0	0.0	4.0	4.0	-	-	-	-	0.0	0.0	1.8	1.8
Arrowwood	-	1.3	5.3	9.3	-	-	-	-	-	0.6	2.4	4.2
Witherod	-	-	-	-	0.0	7.8	-	-	0.0	4.2	-	-
Elderberry	-	-	-	-	0.0	0.0	4.4	18.9	0.0	0.0	2.4	10.3
Combined species	356.0	238.7	385.3	256.0	110.0	187.8	180.0	295.6	221.8	210.9	273.3	277.6

Table 4. Periodic ingrowth (stems/acre/decade) during 1959-2000.

Species	Eastern plots 1959-1970	Eastern plots 1970-1980	Eastern plots 1980-1990	Eastern plots 1990-2000	Western plots 1959-1970	Western plots 1970-1980	Western plots 1980-1990	Western plots 1990-2000	Combined plots 1959-1970	Combined plots 1970-1980	Combined plots 1980-1990	Combined plots 1990-2000
Eastern white pine	-	-	-	-	11	7	-	-	6	4	-	-
Eastern hemlock	-	-	-	-	114	132	122	37	62	72	67	20
Sugar maple	8	23	8	4	-	1	-	1	4	11	4	2
Red maple	36	31	33	8	1	1	-	-	17	15	15	4
Mockernut hickory	-	-	-	-	-	-	-	-	-	-	-	-
Pignut hickory	3	1	-	1	-	-	-	-	1	1	-	1
Shagbark hickory	-	-	-	-	-	-	-	-	-	-	-	-
Northern red oak	4	1	-	-	-	1	-	-	2	1	-	-
Black oak	-	-	-	-	-	1	-	-	-	1	-	-
Scarlet oak	-	1	-	-	-	-	-	-	-	1	-	-
White oak	1	-	-	-	-	-	-	-	1	-	-	-
Yellow birch	9	28	16	5	10	2	-	1	10	14	7	3
Black birch	29	35	39	23	2	1	-	-	15	16	18	10
American beech	4	4	1	1	64	79	44	36	37	45	25	20
White ash	-	1	-	-	-	-	1	-	-	1	1	-
Black ash	-	-	-	-	-	-	-	-	-	-	-	-
Basswood	-	1	-	-	-	-	-	-	-	1	-	-
American elm	-	-	-	-	-	-	-	-	-	-	-	-
Bigtooth aspen	-	-	-	-	-	-	-	-	-	-	-	-
Tupelo	1	3	1	-	-	-	-	-	1	1	1	-
Black locust	-	-	-	-	-	-	-	-	-	-	-	-
Black cherry	-	-	-	-	-	-	-	-	-	-	-	-
Sassafras	4	5	3	1	-	-	-	-	2	2	1	1
American chestnut	31	60	21	8	9	1	1	-	19	28	10	4
Gray birch	1	-	-	-	-	-	-	-	1	-	-	-
Flowering dogwood	13	11	-	-	-	-	-	-	6	5	-	-
Bluebeech	7	3	3	3	-	-	-	-	3	1	1	1
Shadbush	-	-	-	-	4	-	-	-	2	-	-	-
Hophornbeam	-	-	4	3	-	-	-	-	-	-	2	1
Striped maple	-	-	1	1	4	34	4	-	2	19	3	1
Witchhazel	23	75	28	35	50	26	7	1	38	48	16	16
Winterberry	7	9	4	13	-	1	-	-	3	5	2	6
Spicebush	65	69	25	11	-	-	-	-	30	32	12	5
Highbush blueberry	3	7	9	9	-	-	-	-	1	3	4	4
Hobblebush	-	-	-	-	-	-	-	1	-	-	-	1
Arrowwood	1	15	-	-	-	-	-	-	1	7	-	-
Witherod	-	-	-	-	6	-	-	-	3	-	-	-
Elderberry	-	-	-	-	6	9	14	2	3	5	8	1
Combined species	251	383	197	127	282	297	194	79	268	336	196	101

Table 5. Stand density (stems/acre) of subcanopy trees during 1959-2000.

	Eastern plots					Western plots					Combined plots				
Species	1959	1970	1980	1990	2000	1959	1970	1980	1990	2000	1959	1970	1980	1990	2000
Eastern white pine	-	-	-	-	-	-	11.1	16.7	2.2	-	-	6.1	9.1	1.2	-
Eastern hemlock	-	-	-	-	-	115.6	211.1	315.6	425.6	335.6	63.0	115.2	172.1	232.1	183.0
Sugar maple	32.0	37.3	54.7	52.0	49.3	55.6	36.7	25.6	20.0	12.2	44.8	37.0	38.8	34.5	29.1
Red maple	230.7	222.7	197.3	193.3	152.0	42.2	28.9	23.3	20.0	12.2	127.9	117.0	102.4	98.8	75.8
Mockernut hickory	1.3	1.3	-	-	-	-	-	-	-	-	0.6	0.6	-	-	-
Pignut hickory	37.3	20.0	10.7	10.7	9.3	-	-	-	-	-	17.0	9.1	4.8	4.8	4.2
Shagbark hickory	6.7	1.3	1.3	1.3	-	-	-	-	-	-	3.0	0.6	0.6	0.6	-
Northern red oak	46.7	24.0	9.3	2.7	1.3	10.0	-	-	-	-	26.7	10.9	4.2	1.2	0.6
Black oak	2.7	-	-	-	-	-	-	-	-	-	1.2	-	-	-	-
Scarlet oak	2.7	2.7	1.3	1.3	-	-	-	-	-	-	1.2	1.2	0.6	0.6	-
White oak	72.0	18.7	2.7	2.7	2.7	2.2	-	-	-	-	33.9	8.5	1.2	1.2	1.2
Yellow birch	61.3	50.7	66.7	73.3	62.7	47.8	42.2	27.8	20.0	11.1	53.9	46.1	45.5	44.2	34.5
Black birch	94.7	98.7	105.3	140.0	137.3	13.3	12.2	7.8	5.6	5.6	50.3	51.5	52.1	66.7	65.5
American beech	6.7	10.7	12.0	13.3	13.3	168.9	198.9	244.4	252.2	231.1	95.2	113.3	138.8	143.6	132.1
White ash	16.0	1.3	2.7	2.7	2.7	2.2	-	-	3.3	1.1	8.5	0.6	1.2	3.0	1.8
Black ash	1.3	1.3	1.3	1.3	-	-	-	-	-	-	0.6	0.6	0.6	0.6	-
Basswood	4.0	1.3	1.3	-	-	-	-	-	-	-	1.8	0.6	0.6	-	-
American elm	4.0	4.0	2.7	2.7	2.7	-	-	-	-	-	1.8	1.8	1.2	1.2	1.2
Bigtooth aspen	1.3	-	-	-	-	-	-	-	-	-	0.6	-	-	-	-
Tupelo	1.3	2.7	5.3	6.7	4.0	-	-	-	-	-	0.6	1.2	2.4	3.0	1.8
Black locust	-	-	-	-	-	1.1	-	-	-	-	0.6	-	-	-	-
Black cherry	4.0	-	-	-	-	-	-	-	-	1.1	1.8	-	-	-	0.6
Sassafras	10.7	9.3	12.0	9.3	6.7	-	-	-	-	-	4.8	4.2	5.5	4.2	3.0
American chestnut	26.7	36.0	82.7	29.3	16.0	7.8	13.3	4.4	3.3	-	16.4	23.6	40.0	15.2	7.3
Gray birch	2.7	1.3	-	-	-	-	-	-	-	-	1.2	0.6	-	-	-
Flowering dogwood	33.3	41.3	38.7	2.7	-	-	-	-	-	-	15.2	18.8	17.6	1.2	-
Bluebeech	52.0	28.0	13.3	10.7	9.3	-	-	-	-	-	23.6	12.7	6.1	4.8	4.2
Shadbush	1.3	-	-	-	-	14.4	13.3	3.3	-	-	8.5	7.3	1.8	-	-
Hophornbeam	5.3	1.3	1.3	5.3	8.0	-	-	-	-	-	2.4	0.6	0.6	2.4	3.6
Striped maple	-	-	-	1.3	2.7	1.1	5.6	38.9	24.4	11.1	0.6	3.0	21.2	13.9	7.3
Witchhazel	170.7	124.0	170.7	122.7	121.3	41.1	73.3	63.3	26.7	7.8	100.0	96.4	112.1	70.3	59.4
Winterberry	16.0	9.3	16.0	14.7	24.0	-	-	1.1	1.1	1.1	7.3	4.2	7.9	7.3	11.5
Spicebush	6.7	69.3	129.3	77.3	36.0	-	-	-	-	-	3.0	31.5	58.8	35.2	16.4
Highbush blueberry	6.7	9.3	16.0	21.3	26.7	-	-	-	-	-	3.0	4.2	7.3	9.7	12.1
Hobblebush	-	-	-	-	-	-	-	-	-	1.1	-	-	-	-	0.6
Arrowwood	-	1.3	14.7	9.3	-	-	-	-	-	-	-	0.6	6.7	4.2	-
Witherod	-	-	-	-	-	2.2	7.8	-	-	-	1.2	4.2	-	-	-
Elderberry	-	-	-	-	-	1.1	6.7	15.6	25.6	8.9	0.6	3.6	8.5	13.9	4.8
Combined species	958.7	829.3	969.3	808.0	688.0	526.7	661.1	787.8	830.0	640.0	723.0	737.6	870.3	820.0	661.8

Table 6. Periodic mortality (stems/acre/decade) of subcanopy trees during 1959-2000.

Species	Eastern plots 1959-1970	Eastern plots 1970-1980	Eastern plots 1980-1990	Eastern plots 1990-2000	Western plots 1959-1970	Western plots 1970-1980	Western plots 1980-1990	Western plots 1990-2000	Combined plots 1959-1970	Combined plots 1970-1980	Combined plots 1980-1990	Combined plots 1990-2000
Eastern white pine	-	-	-	-	-	1.1	14.4	2.2	-	0.6	7.9	1.2
Eastern hemlock	-	-	-	-	2.2	25.6	21.1	127.8	1.2	13.9	11.5	69.7
Sugar maple	2.7	5.3	12.0	5.3	13.3	12.2	10.0	6.7	8.5	9.1	10.9	6.1
Red maple	37.3	44.0	45.3	46.7	8.9	8.9	5.6	7.8	21.8	24.8	23.6	25.5
Mockernut hickory	0.0	1.3	-	-	-	-	-	-	0.0	0.6	-	-
Pignut hickory	20.0	9.3	0.0	2.7	-	-	-	-	9.1	4.2	0.0	1.2
Shagbark hickory	2.7	0.0	0.0	1.3	-	-	-	-	1.2	0.0	0.0	0.6
Northern red oak	28.0	16.0	6.7	2.7	10.0	-	-	-	18.2	7.3	3.0	1.2
Black oak	2.7	-	-	-	-	-	-	-	1.2	-	-	-
Scarlet oak	0.0	1.3	0.0	1.3	-	-	-	-	0.0	0.6	0.0	0.6
White oak	52.0	16.0	0.0	0.0	2.2	-	-	-	24.8	7.3	0.0	0.0
Yellow birch	18.7	12.0	10.7	14.7	12.2	17.8	7.8	10.0	15.2	15.2	9.1	12.1
Black birch	14.7	28.0	9.3	22.7	1.1	5.6	2.2	1.1	7.3	15.8	5.5	10.9
American beech	0.0	1.3	0.0	0.0	27.8	33.3	35.6	55.6	15.2	18.8	19.4	30.3
White ash	9.3	1.3	1.3	1.3	1.1	-	-	2.2	4.8	0.6	0.6	1.8
Black ash	0.0	0.0	0.0	1.3	-	-	-	-	0.0	0.0	0.0	0.6
Basswood	2.7	1.3	1.3	-	-	-	-	-	1.2	0.6	0.6	-
American elm	0.0	1.3	0.0	0.0	-	-	-	-	0.0	0.6	0.0	0.0
Bigtooth aspen	1.3	-	-	-	-	-	-	-	0.6	-	-	-
Tupelo	0.0	0.0	0.0	2.7	-	-	-	-	0.0	0.0	0.0	1.2
Black locust	-	-	-	-	1.1	-	-	-	0.6	-	-	-
Black cherry	4.0	-	-	-	-	-	-	-	1.8	-	-	-
Sassafras	5.3	2.7	5.3	4.0	-	-	-	-	2.4	1.2	2.4	1.8
American chestnut	21.3	13.3	74.7	26.7	3.3	10.0	2.2	3.3	11.5	11.5	35.2	13.9
Gray birch	2.7	1.3	-	-	-	-	-	-	1.2	0.6	-	-
Flowering dogwood	5.3	13.3	36.0	2.7	-	-	-	-	2.4	6.1	16.4	1.2
Bluebeech	30.7	17.3	5.3	4.0	-	-	-	-	13.9	7.9	2.4	1.8
Shadbush	1.3	-	-	-	5.6	10.0	3.3	-	3.6	5.5	1.8	-
Hophornbeam	4.0	0.0	0.0	0.0	-	-	-	-	1.8	0.0	0.0	0.0
Striped maple	-	-	-	0.0	0.0	1.1	18.9	13.3	0.0	0.6	10.3	7.3
Witchhazel	69.3	28.0	76.0	37.3	17.8	35.6	43.3	20.0	41.2	32.1	58.2	27.9
Winterberry	13.3	2.7	5.3	4.0	-	-	0.0	0.0	6.1	1.2	2.4	1.8
Spicebush	2.7	9.3	77.3	56.0	-	-	-	-	1.2	4.2	35.2	25.5
Highbush blueberry	0.0	0.0	4.0	4.0	-	-	-	-	0.0	0.0	1.8	1.8
Arrowwood	-	1.3	5.3	9.3	-	-	-	-	-	0.6	2.4	4.2
Witherod	-	-	-	-	0.0	7.8	-	-	0.0	4.2	-	-
Elderberry	-	-	-	-	0.0	0.0	4.4	18.9	0.0	0.0	2.4	10.3
Combined species	352.0	228.0	376.0	250.7	106.7	168.9	168.9	268.9	218.2	195.8	263.0	260.6

Table 7. Periodic ascension (stems/acre/decade) of trees that moved from lower to upper canopy position during 1959-2000. "n" indicates that subcanopy trees were present, but none moved into the upper canopy.

Species	Eastern plots				Western plots				Combined plots			
	1959 1970	1970 1980	1980 1990	1990 2000	1959 1970	1970 1980	1980 1990	1990 2000	1959 1970	1970 1980	1980 1990	1990 2000
Eastern white pine	-	-	-	-	-	n	n	n	-	n	n	n
Eastern hemlock	-	-	-	-	16.7	1.1	n	n	9.1	0.6	n	n
Sugar maple	n	n	n	1.3	5.6	n	n	1.1	3.0	n	n	1.2
Red maple	6.7	12.0	n	2.7	6.7	n	n	n	6.7	5.5	n	1.2
Mockernut hickory	n	n	-	-	-	-	-	-	n	n	-	-
Pignut hickory	n	1.3	n	n	-	-	-	-	n	0.6	n	n
Shagbark hickory	2.7	n	n	n	-	-	-	-	1.2	n	n	n
Northern red oak	n	n	n	n	n	-	-	-	n	n	n	n
Black oak	n	-	-	-	-	-	-	-	n	-	-	-
Scarlet oak	n	n	n	n	-	-	-	-	n	n	n	n
White oak	2.7	n	n	n	n	-	-	-	1.2	n	n	n
Yellow birch	2.7	n	n	1.3	3.3	n	n	n	3.0	n	n	0.6
Black birch	10.7	n	n	2.7	2.2	n	n	n	6.1	n	n	1.2
American beech	n	1.3	n	1.3	6.7	1.1	1.1	1.1	3.6	1.2	0.6	1.2
White ash	5.3	n	n	n	1.1	-	-	n	3.0	n	n	n
Black ash	n	n	n	n	-	-	-	-	n	n	n	n
Basswood	n	n	n	-	-	-	-	-	n	n	n	-
American elm	n	n	n	n	-	-	-	-	n	n	n	n
Bigtooth aspen	n	-	-	-	-	-	-	-	n	-	-	-
Tupelo	n	n	n	n	-	-	-	-	n	n	n	n
Black locust	-	-	-	-	n	-	-	-	n	-	-	-
Black cherry	n	-	-	-	-	-	-	-	n	-	-	-
Sassafras	n	n	n	n	-	-	-	-	n	n	n	n
Combined species	30.7	14.7	n	9.3	42.2	2.2	1.1	2.2	37.0	7.9	0.6	5.5

Table 8. Stand density (stems/acre) of upper canopy trees during 1959-2000.

	Eastern plots					Western plots					Combined plots				
Species	1959	1970	1980	1990	2000	1959	1970	1980	1990	2000	1959	1970	1980	1990	2000
Eastern white pine	-	-	-	-	-	2.2	2.2	2.2	2.2	2.2	1.2	1.2	1.2	1.2	1.2
Eastern hemlock	-	-	-	-	-	13.3	30.0	28.9	17.8	7.8	7.3	16.4	15.8	9.7	4.2
Sugar maple	1.3	1.3	1.3	-	1.3	11.1	16.7	15.6	8.9	11.1	6.7	9.7	9.1	4.8	6.7
Red maple	4.0	10.7	22.7	14.7	17.3	26.7	31.1	27.8	22.2	13.3	16.4	21.8	25.5	18.8	15.2
Pignut hickory	4.0	4.0	5.3	4.0	4.0	-	-	-	-	-	1.8	1.8	2.4	1.8	1.8
Shagbark hickory	-	2.7	2.7	2.7	2.7	-	-	-	-	-	-	1.2	1.2	1.2	1.2
Northern red oak	24.0	22.7	21.3	21.3	20.0	17.8	16.7	11.1	11.1	10.0	20.6	19.4	15.8	15.8	14.5
Black oak	6.7	5.3	4.0	2.7	2.7	-	-	1.1	1.1	1.1	3.0	2.4	2.4	1.8	1.8
Scarlet oak	8.0	8.0	9.3	8.0	8.0	-	-	-	-	-	3.6	3.6	4.2	3.6	3.6
White oak	6.7	9.3	6.7	5.3	5.3	3.3	3.3	3.3	3.3	2.2	4.8	6.1	4.8	4.2	3.6
Yellow birch	8.0	9.3	8.0	5.3	6.7	8.9	12.2	7.8	5.6	3.3	8.5	10.9	7.9	5.5	4.8
Black birch	14.7	24.0	20.0	13.3	13.3	1.1	3.3	3.3	3.3	2.2	7.3	12.7	10.9	7.9	7.3
American beech	-	-	1.3	1.3	2.7	-	6.7	6.7	7.8	8.9	-	3.6	4.2	4.8	6.1
White ash	6.7	10.7	9.3	6.7	2.7	7.8	8.9	7.8	4.4	2.2	7.3	9.7	8.5	5.5	2.4
Black ash	-	-	-	-	-	1.1	1.1	1.1	1.1	-	0.6	0.6	0.6	0.6	-
Black cherry	-	-	-	-	-	5.6	4.4	2.2	2.2	1.1	3.0	2.4	1.2	1.2	0.6
Combined species	84.0	108.0	112.0	85.3	86.7	98.9	136.7	118.9	91.1	65.6	92.1	123.6	115.8	88.5	75.2

Table 9. Stand basal area ($feet^2/acre$) during 1959-2000.

	Eastern plots					Western plots					Combined plots				
Species	1959	1970	1980	1990	2000	1959	1970	1980	1990	2000	1959	1970	1980	1990	2000
Eastern white pine	-	-	-	-	-	3.9	4.4	5.2	6.3	7.5	2.1	2.4	2.9	3.5	4.1
Eastern hemlock	-	-	-	-	-	43.1	53.6	55.2	74.7	61.7	23.5	29.2	30.1	40.7	33.7
Sugar maple	1.8	2.3	2.7	3.4	3.8	11.8	12.0	11.6	10.4	10.5	7.3	7.6	7.5	7.2	7.4
Red maple	12.4	16.3	20.7	23.6	28.7	20.3	22.6	26.3	26.8	18.0	16.7	19.7	23.8	25.3	22.9
Mockernut hickory	t	t	-	-	-	-	-	-	-	-	t	t	-	-	-
Pignut hickory	4.0	3.7	4.1	3.9	4.7	-	-	-	-	-	1.8	1.7	1.9	1.8	2.1
Shagbark hickory	1.0	1.0	1.2	1.4	1.4	-	-	-	-	-	0.5	0.5	0.5	0.6	0.6
Northern red oak	15.2	17.5	18.5	22.0	26.1	23.1	23.9	21.4	25.5	26.8	19.5	21.0	20.1	23.9	26.5
Black oak	2.0	2.0	2.2	2.3	2.9	-	-	0.9	1.3	1.7	0.9	0.9	1.5	1.7	2.2
Scarlet oak	4.6	5.4	7.0	7.3	7.9	-	-	-	-	-	2.1	2.5	3.2	3.3	3.6
White oak	9.6	8.8	6.4	5.9	7.0	5.1	5.4	5.9	6.4	3.6	7.2	7.0	6.1	6.2	5.2
Yellow birch	7.0	7.3	7.3	7.9	9.0	7.0	7.7	5.8	4.7	3.5	7.0	7.5	6.5	6.2	6.0
Black birch	13.4	15.2	14.9	17.9	19.6	2.0	2.4	2.4	2.9	3.3	7.2	8.2	8.1	9.7	10.7
American beech	t	0.2	0.5	1.0	1.9	7.1	8.9	12.0	16.0	19.0	3.9	4.9	6.8	9.2	11.2
White ash	3.3	3.8	4.8	5.1	4.4	5.0	5.2	5.2	5.9	2.4	4.2	4.5	5.0	5.5	3.3
Black ash	0.1	0.2	0.2	0.2	-	0.3	0.5	0.6	0.7	-	0.3	0.3	0.4	0.5	-
Basswood	t	t	t	-	-	-	-	-	-	-	t	t	t	-	-
American elm	0.2	0.3	0.2	0.2	0.3	-	-	-	-	-	t	0.1	t	0.1	0.2
Bigtooth aspen	0.2	-	-	-	-	-	-	-	-	-	t	-	-	-	-
Tupelo	t	t	t	0.1	0.1	-	-	-	-	-	t	t	t	t	t
Black locust	-	-	-	-	-	t	-	-	-	-	t	-	-	-	-
Black cherry	t	-	-	-	-	4.2	3.7	2.5	3.2	3.9	2.3	2.0	1.3	1.7	2.1
Sassafras	t	t	0.1	0.1	0.2	-	-	-	-	-	t	t	t	t	0.1
American chestnut	0.1	0.2	0.9	0.2	t	t	t	t	t	-	t	0.1	0.4	t	t
Gray birch	t	t	-	-	-	-	-	-	-	-	t	t	-	-	-
Flowering dogwood	0.6	0.7	0.8	0.2	-	-	-	-	-	-	0.3	0.3	0.4	t	-
Bluebeech	0.6	0.3	0.1	0.1	0.1	-	-	-	-	-	0.3	0.1	t	t	t
Shadbush	t	-	-	-	-	0.1	0.1	t	-	-	t	t	t	-	-
Hophornbeam	0.1	t	t	t	0.1	-	-	-	-	-	t	t	t	t	t
Striped maple	-	-	-	t	t	t	t	0.2	0.3	0.3	t	t	0.1	0.2	0.2
Witchhazel	1.0	0.9	1.1	0.8	0.9	0.1	0.2	0.2	0.2	t	0.5	0.5	0.6	0.5	0.4
Winterberry	t	t	t	t	0.1	-	-	t	t	t	t	t	t	t	t
Spicebush	t	0.2	0.8	0.6	0.2	-	-	-	-	-	t	t	0.4	0.3	0.1
Highbush blueberry	t	t	t	t	t	-	-	-	-	-	t	t	t	t	t
Hobblebush	-	-	-	-	-	-	-	-	-	t	-	-	-	-	t
Arrowwood	-	t	t	t	-	-	-	-	-	-	-	t	t	t	-
Witherod	-	-	-	-	-	t	t	-	-	-	t	t	-	-	-
Elderberry	-	-	-	-	-	t	t	t	t	t	t	t	t	t	t
Combined species	78.0	86.5	94.7	104.4	120.4	133.3	150.7	155.6	185.4	162.3	108.1	121.5	127.9	148.6	143.3

Table 10. Diameter distribution (stems/acre) during 1959-2000.

Diameter class	Eastern plots					Western plots					Combined plots				
(inches)	1959	1970	1980	1990	2000	1959	1970	1980	1990	2000	1959	1970	1980	1990	2000
0.5-2.4	737	649	797	619	496	266	457	569	583	434	480	544	673	599	462
2.5-4.4	133	112	116	99	99	143	118	113	107	98	139	115	115	103	98
4.5-6.4	71	68	63	55	55	73	66	68	77	53	72	67	65	67	54
6.5-8.4	43	41	35	44	32	51	41	34	31	32	47	41	35	37	32
8.5-10.4	33	32	25	28	35	36	48	46	31	20	35	41	36	30	27
10.5-12.4	15	15	19	17	16	22	26	30	34	19	19	21	25	27	18
12.5-14.4	7	11	15	17	19	10	16	18	22	13	8	13	16	20	16
14.5-16.4	3	5	4	4	8	6	4	7	10	9	4	5	5	7	8
16.5-18.4	-	3	5	4	7	6	9	8	6	8	3	6	7	5	7
18.5-20.4	1	1	1	3	4	6	1	4	7	3	4	1	3	5	4
20.5-22.4	-	-	1	4	4	3	8	4	2	3	2	4	3	3	4
>=22.5	-	-	-	-	1	4	6	6	11	12	2	3	3	6	7
Sapling	871	761	913	717	595	409	574	682	690	532	619	659	787	702	561
Poles	147	141	123	127	121	160	154	148	139	106	154	148	136	133	113
Sawtimber	25	35	45	49	59	57	69	77	92	68	42	53	62	73	64
Combined species	1043	937	1081	893	775	626	798	907	921	706	815	861	986	908	737

Table 11. Stand density (stems/acre) of seedlings (< 4 feet tall) during 1980-2000.

	Eastern plots			Western plots			Combined plots		
Species	1980	1990	2000	1980	1990	2000	1980	1990	2000
Eastern white pine	-	14	14	50	-	11	28	6	13
Eastern hemlock	-	-	-	1167	9499	686	656	5343	386
Sugar maple	96	289	491	-	169	11	42	221	221
Red maple	1436	1402	1648	4425	5340	2215	3117	3617	1967
Pignut hickory	214	275	332	-	-	-	94	120	145
Northern red oak	407	824	390	558	146	112	492	443	234
Black/scarlet oak	86	231	260	8	11	-	42	107	114
White oak	279	954	593	17	11	11	131	424	266
Yellow birch	643	87	491	1383	776	416	1059	474	449
Black birch	7318	275	58	42	11	-	3225	126	25
American beech	11	43	-	600	753	854	342	443	481
White ash	375	665	882	-	292	11	164	455	392
Slippery elm	32	-	29	-	-	-	14	-	13
Tupelo	-	58	14	-	11	-	-	32	6
Black cherry	-	-	145	100	22	461	56	13	322
American chestnut	75	318	101	25	112	-	47	202	44
Flowering dogwood	793	87	58	-	-	-	347	38	25
Bluebeech	64	14	14	-	-	-	28	6	6
Shadbush	86	14	564	92	34	45	89	25	272
Hophornbeam	-	43	145	-	-	-	-	19	63
Sassafras	64	130	159	-	-	-	28	57	70
Striped maple	-	43	14	142	124	776	80	89	443
Total	11979	5767	6403	8608	17312	5609	10083	12261	5956

Table 12. Stand density (stems/acre) of saplings (≥ 4 feet tall and < 0.5 inches dbh) during 1980-2000.

	Eastern plots			Western plots			Combined plots		
Species	1980	1990	2000	1980	1990	2000	1980	1990	2000
Eastern hemlock	-	-	-	200	157	45	113	89	25
Sugar maple	32	-	-	-	-	-	14	-	-
Red maple	21	14	14	-	-	-	9	6	6
Northern red oak	11	-	-	-	-	-	5	-	-
White oak	-	-	14	-	-	-	-	-	6
Yellow birch	21	43	116	-	-	-	9	19	51
Black birch	11	101	43	-	22	-	5	57	19
American beech	-	-	-	192	259	247	108	145	139
Sassafras	11	14	29	-	-	-	5	6	13
American chestnut	32	29	29	17	11	-	23	19	13
Flowering dogwood	54	-	-	-	-	-	23	-	-
Striped maple	-	-	-	17	-	-	9	-	-
Maple-leaf viburnum	-	116	14	-	-	-	-	51	6
Highbush blueberry	43	332	593	-	-	-	19	145	259
Witchhazel	32	14	130	42	11	11	38	13	63
Hobblebush	-	-	-	33	-	34	19	-	19
Spicebush	129	43	58	-	-	-	56	19	25
Beaked hazelnut	-	116	14	-	-	-	-	51	6
Arrowwood	193	-	-	-	-	-	84	-	-
Clethra	-	159	217	-	-	-	-	70	95
Winterberry	129	-	87	-	-	-	56	-	38
Azalea	-	43	101	-	-	-	-	19	44
Elderberry	-	-	-	-	45	-	-	25	-
Privet	-	-	14	-	-	-	-	-	6
Total	718	1026	1474	500	506	337	595	733	835