GROWTH AND MORTALITY OF BIGTOOTH ASPEN TREES STRESSED BY DEFOLIATION

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ABSTRACT.—A survey conducted by the authors in 1993 in six stands within an area of declining aspen revealed that aspen mortality ranged from 25 to 67 percent per stand. Tree-ring analyses revealed that trees dead at time of sampling in 1993 had been growing slower in four of the six stands during the previous decade than were the surviving trees. However growth declines had also occurred in trees that were alive in 1993. The greatest mortality of bigtooth aspen trees occurred in 1992, following 2 consecutive years of severe gypsy moth defoliations. Based on basal area decline and stand deterioration in response to defoliation, we recommend harvesting bigtooth aspen stands in this area well prior to 70 years of age.

Bigtooth aspen (*Populus grandidentata* Michx.) is an important tree species managed for wildlife within even-aged, mixed-hardwood forests of northern Pennsylvania. However, local forestry personnel reported that canopy aspen trees in this area had suddenly declined in the early 1990s, a condition interfering with wildlife management plans. Following several field trips to the area and conversations with local forestry personnel, we theorized that the current decline was related to past stresses. Although aspen stands generally begin to deteriorate at 40 to 45 years on poor sites, they can be maintained for 60 to 70 years on good sites before deterioration and root rot becomes a serious problem (Laidly 1990).

The onset of mortality in the stands in question, which were of unknown age, was quite sudden. The temporal onset of such stresses may be inferred retrospectively by using tree-ring analyses (Fritts 1976, Cook and Kairiukstis 1989, McClenahen 1995, LeBlanc 1996) including the use of cross-dating (Stokes and Smiley 1968, Phipps 1985, Hart 1989), a procedure used to assign an exact year to a specified ring. Comparison of growth trends of healthy vs. declining populations of trees may provide insight as to when a current decline was initiated and possible causes (Tainter and others 1990). The objective of this investigation was to compare growth patterns of aspen that were live vs. dead at time of sampling.

METHODS

This study was conducted within even-aged, mixed-hardwood stands in the Tioga State Forest of northern Pennsylvania. Six stands, each of which contained at least 40 percent basal area of bigtooth aspen, previously had been selected to study the relationship between *Armillaria* (*sensu lato*) and dead and dying aspen (Frontz 1997, Frontz and others 1998). A 100 percent survey of bigtooth aspen trees within each of the six stands was conducted and the percentage of aspen mortality determined. Fifteen live and 15 dead bigtooth aspen trees within each of the six stands (n = 180) were randomly selected and felled in early May 1993 for tree-ring analysis. All sample trees were in the dominant or codominant crown class.

Stem sections, 20 cm in length and centered at 1.4 m above ground (breast height – BH), were removed from each sample tree. To minimize cracking, sections were air-dried for 5 weeks and then kiln-dried at progressively higher temperatures from 32 to 49 C for 7 weeks, at which time the stem sections had a moisture content of 8 percent. A 5-cm thick disk was cut from the center of each dry stem section, sanded with progressively finer grit sandpaper, and polished with lamb's wool to enhance ring boundaries.

Four radii, spaced approximately 90° apart, were penciled from the pith to the bark on each

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cross-sectional disk. Each disk was inspected along the marked surface for ring clarity, decay, cracks, discontinuous rings, and other obvious problem areas. The two radii judged to be least problematic were selected for ring-width measurements from the pith to the outside of the most recent growth ring. All individual tree-ring series were visually cross-dated (Stokes and Smiley 1968, Holmes 1983, Phipps 1985) and the entire circumference of every tenth ring was circumscribed on each disk to minimize measurement errors associated with discontinuous rings. Ring-widths were measured to the nearest 0.01 mm using a Bannister Incremental Measuring Machine (Fred C. Henson Co., Mission Viejo, CA) interfaced with the microcomputer program TRIMS (Tree Ring Incremental Measuring System) developed by Madera Software (Tucson, AZ).

Data were examined with the quality-control program COFECHA (Holmes 1985) to aid matching each ring to the correct year. Any chronologies that did not cross-date were eliminated from subsequent data analyses. Ten percent of the acceptable series were selected randomly for remeasurement. Any error between the original and remeasured series was compared, and if the error was greater than acceptable limit (Phipps 1985), the source of the error was located and corrected by re-measuring. This process was continued until measurements were within prescribed acceptable limits. Mean age was determined for each stand using only cross-dated series.

Linear ring-width and radius measurements for each tree were converted to basal area increment (BAI), the cross-sectional area (sq cm) of annual xylem produced per tree (Phipps and Field 1988). Annual values for individual trees in each stand were averaged to create a stand-average BAI, which was plotted and examined visually for relationship to known stress events. The relation of the growth series among the six stands was calculated using average series intercorrelation (Cook and Kairiukstis 1989).

Initial results from the tree-ring analysis indicated that radial growth in some stands had started to decline during the late 1960s. Therefore, the mean total BAI from 1968 to 1989 was calculated per stand and compared to determine if there were significant differences in total growth among stands during this period. Data were examined using analysis of variance and mean separation tests based on Tukey's pairwise comparisons ($P < 0.01$) (Phipps and Field 1988).

To aid in management decisions, the percentage of total BAI accumulated at various ages was compared among the six sites to help determine optimal harvest age. Also, the year in which each tree died was determined by noting the last year of growth on trees that were dead at time of sampling; year-of-death values were expressed as relative frequencies (Frontz 1997). In order to compare the growth of live vs. dead trees (at time of sampling), ratios of growth data were constructed and plotted for each year. The horizontal line indicates years in which both sets of trees were growing at the same rate. Values above the horizontal line (greater than "1") indicate that the trees that ultimately died were actually growing greater than the trees that were alive at time of felling.

RESULTS

Based on visual examination and COFECHA analysis, 84 percent of the tree-ring series could be cross-dated and therefore were used in further analyses. Growth patterns of both live ($n = 81$) and dead at time of sampling ($n = 71$) aspen trees generally exhibited synchronous variation. This finding indicated that events that resulted in wide or narrow growth rings were generally reflected in the growth patterns of both live and dead (at time of sampling) aspen trees in all six stands (fig. 1). Average series intercorrelation among the six sites was 0.59, being greatest at the Cushman site (0.69) and least at the Arnot 6 site (0.55).

Bigtooth aspen trees at the Deer Fence site were the youngest, averaging 69 years at BH. Trees in the Arnot 5, Arnot 6, Butler Hollow, and Cushman sites averaged 77 to 80 years. Aspen trees at the Seaman's Trail site were the oldest, having a mean age of 86 years. The incidence of tree mortality was greatest at the Arnot 5 site (67 percent) and least at the Seamans Trail site (25 percent). Approximately 90 percent of the dead sample trees had died between 1990 and 1992, and 50 percent of the dead trees had died during a single year, 1992.

Aspen trees in all six stands exhibited declining growth patterns in BAI during their last 25 to 40 years of growth, regardless of final state of health (fig. 2). In general, most trees in the Arnot 6 and Deer Fence stands started to decline in the mid-1970s, whereas trees in the other stands started a general decline in the early 1950s. Aspen trees that were dead at time of sampling in four stands (Arnot 6, Cushman, Deer Fence, and Seamans Trail) generally grew slower during the last *ca* 20 years of their lives

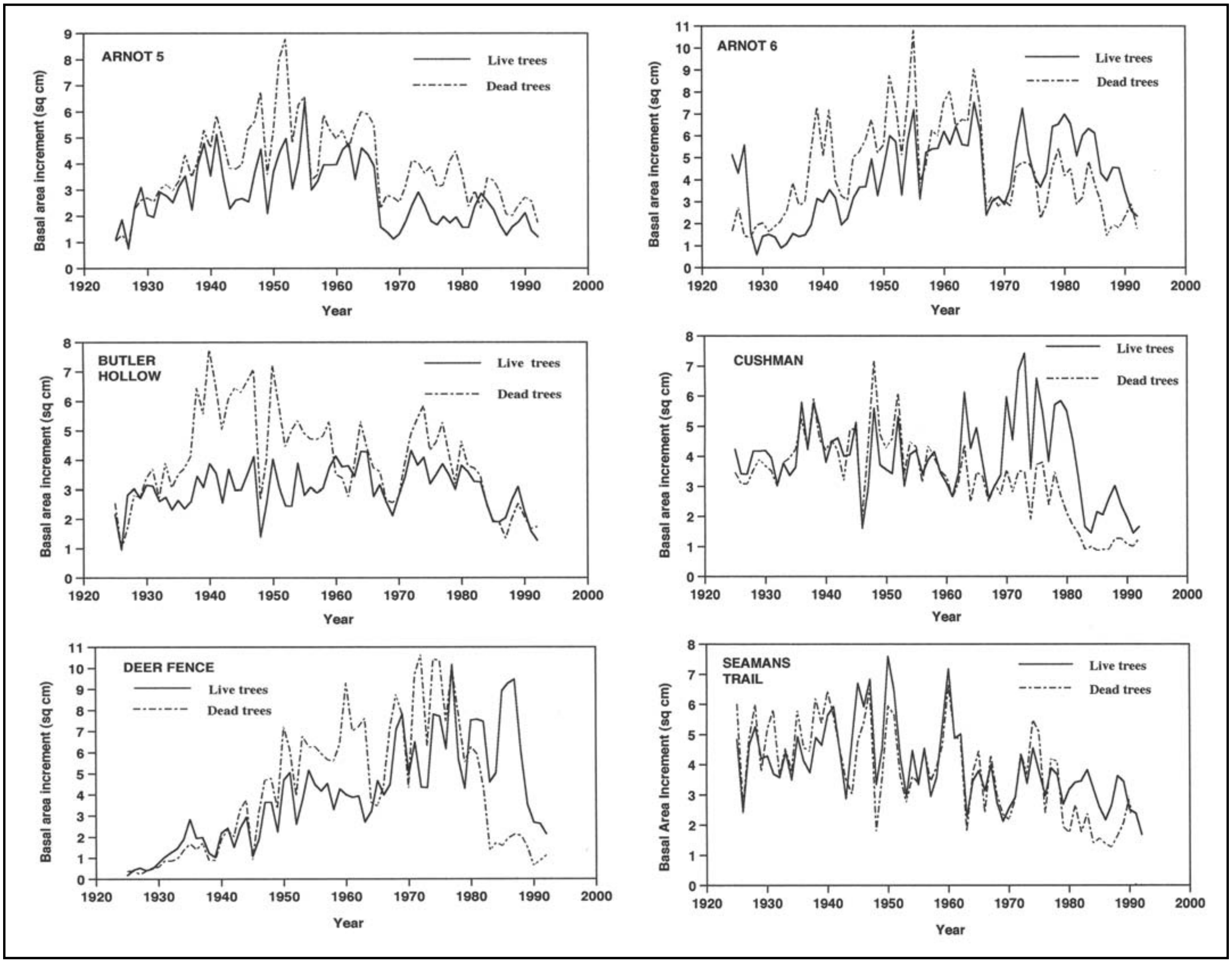

Figure 1.—*Solid lines indicate growth patterns of trees that were alive at time of felling and sampling in 1993. Dashed lines represent growth patterns of trees that were dead at time of felling in six stands in northern Pennsylvania.*

as compared to those trees that were alive at time of sampling. The growth rate displayed by aspen trees in Arnot 5 and Butler Hollow prior to dying often exceeded that of the trees that were alive at time of sampling. Trees that ultimately died in Arnot 5, Arnot 6, Butler Hollow, and Deer Fence stands often had greater growth rates in their early years than did those trees that were alive when sampled.

Trees that died in the Arnot 6 and Cushman stands exhibited declining growth beginning *ca* 1970 and generally continued to decline in growth until death. Trees that died in the Deer Fence and Semans Trail stands had a greater growth rate than the stand average until the mid-1970s and then declined until death.

Mean total BAI of sampled trees from 1968 to 1989 at the Deer Fence site (141.4 sq cm) and the Arnot 6 site (117.5 sq cm) were not statistically different, and were significantly greater than the mean total BAI of trees from the other four sites ($P < 0.01$). The mean total BAI of trees from the Arnot 5 (78.7 sq cm), Butler Hollow (80.2 sq cm), Cushman (78.7 sq cm), and Seamans Trail (80.6 sq cm) sites were not significantly different from each other ($P < 0.01$). Approximately 60, 75, and 92 percent of the total BAI from all six sites was produced in trees 50, 60, and 70 years of age, respectively.

DISCUSSION AND CONCLUSIONS

Tree-ring analyses were utilized in this study to investigate tree decline (McClenahen 1995, LeBlanc 1996). However, it has been our experience that bigtooth aspen often contains discontinuous rings, making it more useful to fell trees and take disks, as opposed to using increment borers (Trujillo 1975). Trees that were dead at

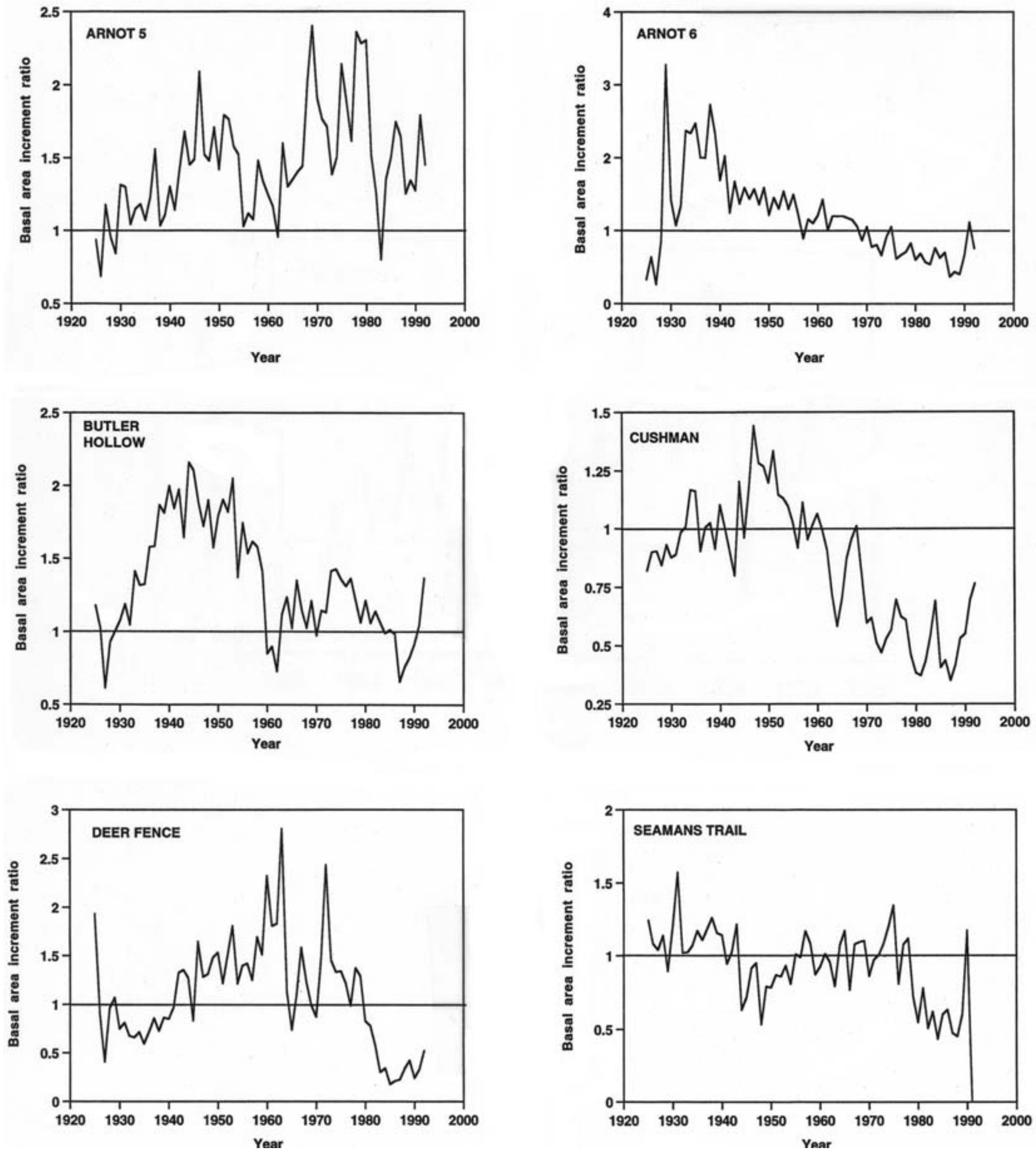

Figure 2.—*Ratio of Basal Area Increment (BAI) growth (sq cm) of bigtooth aspen trees in six stands in north-central Pennsylvania: The horizontal line at "1" indicates the value derived if the annual growth of the trees that were dead at time of felling equaled the annual growth of live trees (growth of dead trees/growth of live trees = 1). On the curve, values less than 1 indicate that the trees that were dead at time of harvest had been growing less than those trees that were alive at felling.*

time of felling in 1993 showed persistent patterns of growth decline in the decade prior to death in four of the six stands (fig. 1). Root excavations revealed *Armillaria* species associated with roots of dead and dying aspens (Frontz 1997, Frontz and others 1998).

In four of the six stands, trees that ultimately died were actually growing better in their early years than were trees that ultimately survived. This latter finding is similar to that reported by Jenkins and Pallardy (1995) for oak trees on relatively good sites, suggesting that rapid early growth rates may predispose trees to early death under certain conditions. Other studies have also reported that declines may follow periods of unusually high growth (Tainter and others 1984, VanDeusen and Snow 1991, Biocca and others 1993). Although faster growing trees have larger stem diameters, they may allocate less carbon to their roots, making them more susceptible to root diseases (Waring 1987, Jenkins and Pallardy 1995) such as Armillaria root rot (Wargo and Harrington 1991), or they may allocate less carbon to chemical defenses against insect attack (Waring 1987).

Bigtooth aspen is a preferred host for gypsy moth (Chilcote and others 1992). Unpublished PA Bureau of Forestry records indicate that severe insect defoliation events occurred on hardwoods in the study area in 1966-1967 and 1971-1972, followed by severe defoliation from gypsy moth (*Lymantria dispar* L.) during 1982-1983 and 1990-1991. Hart (1989) reported that aspen trees in Michigan that had suffered severe gypsy moth defoliations in 1986 died in 1987-1988 due to Armillaria root rot infections.

Different clones may respond differently to defoliation (Wall 1971, Barnes 1989, Chilcote and others 1992). Clonal differences, as well as site differences, may have influenced the differences in growth among the six stands. Both the live and dead (at time of sampling) trees in most stands exhibited reduced growth pulses, possibly related to insect defoliation (fig.1). In addition, the year-of-death peaked in 1992, immediately following severe defoliation by gypsy moth in 1990-1991. Again, the differential susceptibility of different aspen clones to stress may be responsible for the differences in mortality among the six stands.

Mean total BAI of sampled trees from 1968-1989 of trees within the Deer Fence and Arnot 6 stands were greater than that of the other stands. During related studies, Frontz (1997) noted that there were differences among stands in site factors such as soil stoniness and stand density. These were not quantified, but such differences, along with the clonal influences, may help explain differences in total growth among stands. Five of the six stands examined in this study were greater than 70 years old. Aspen trees at the Seamans Trail site were the oldest, averaging 86 years; however, stand mortality was the least (25 percent) at this site, indicating that mortality in these stands was not related to tree age. Nevertheless, 25 percent is still an unacceptable level of mortality.

In our study, 92 percent of the average total BAI for bigtooth aspen trees in the six stands had been achieved by age 70. This finding, along with the fact that aspen mortality in the six study stands ranged from 25-67 percent, allows us to recommend harvesting aspen stands in this area well prior to 70 years of age, perhaps even as early as 50 years.

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