For. Sci. XX(XX):1–12
doi: 10.1093/forsci/fxy057
Published by Oxford University Press on behalf of the Society of American Foresters 2018.

entomology & pathology

The Frequency and Anatomical Characteristics of Anomalous Dark Rings in Black Cherry, and Their Relation to Cherry Scallop Shell Moth Defoliations

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Anomalous dark rings found in black cherry (*Prunus serotina* Ehrh.) sawlogs have been anecdotally related to defoliations from cherry scallop shell moth (CSSM) (*Hydria prunivorata* Ferguson). Using six timber harvest sites on the Allegheny National Forest and a thinning on the Kane Experimental Forest in northwestern Pennsylvania, we documented the occurrence of dark rings in the 1970s, 1980s, and 1990s, concurrent with historical CSSM defoliations. Thirty cross-sections sampled from six Allegheny National Forest sites showed that dark rings formed on 18 sections in the 1970s, 17 sections in the 1980s, and 5 sections in the 1990s. Fourteen cross-sections had multiple (2–4) dark rings. Anatomical studies show the dark rings formed in these three decades have similar characteristics: darkened and thinner (>50 percent) fiber cell walls than normal-colored fiber cell walls. A long-term Kane Experimental Forest study was thinned in 2011–12, and dark ring frequency on recently cut stumps ranged from 48 percent to 68 percent across three replications. Dark rings in 12 of 20 cross-sections were associated with a ≥50 percent growth reduction in mean ring width during 1982–84. These results show that dark rings are associated with CSSM defoliation and that growth may be significantly reduced by defoliation.

Keywords: wood anatomy, fiber cell walls, cherry scallop shell moth

Anomalous dark rings in sawlogs of black cherry (*Prunus serotina* Ehrh.) have been reported from timber harvests in northwestern Pennsylvania (Long et al. 2012). This defect can negatively affect black cherry value, especially for veneer products. Black cherry is among the most valuable timber species in its commercial range on the Allegheny Plateau in New York, Pennsylvania, and West Virginia (Marquis 1990). Black cherry produces high-value lumber and veneer products frequently used for cabinets and furniture. Additional black cherry wood products include paneling, interior trim, handles, crafts, and toys (US Department of Agriculture, NRCS 2018). Black cherry is also important for wildlife with the soft mast used by many birds and mammals, and leaves used by birds for nesting material (Uchytil 1991).

Land managers and timber buyers are uncertain about how common and widespread the black cherry dark rings are in the region. Dark rings are different from gum spots or gum rings that form in response to a traumatic injury and have been well described previously (Hough 1963, Kulman 1964, Rexrode and Baumgras 1980). Gum spots are frequently associated with overwintering niches created between the bark and cambium by the peach bark beetle, *Phloeotribus liminaris* (Harris), and result in a gum exudate and wood defect (Hanavan et al. 2012). These injuries are distinctly different from dark rings. Dark rings have a black, brown, or green appearance that, at the cellular level, is due to darkened fiber cell walls (Long et al. 2012). These anomalous rings, while unreported in the wood-products literature, have been known to timber buyers and loggers since at least the 1970s (D. Payne, personal communication). The rings have various names in the vernacular but most frequently are referred to as “defoliation rings,” “dry rings,” or “dead rings.” Neither the occurrence of dark rings in different black cherry stands nor the frequency of dark rings in individual trees

Manuscript received May 25, 2017; accepted October 30, 2018; published online XXXX XX, XXXX

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Acknowledgments: *We wish to thank the land managers, especially David Trimpey and Troy Firth, who provided insight and knowledge concerning the occurrence of these anomalous rings and their impact on marketing veneer products. Special thanks to Joshua Hanson and Scott Tepke, Allegheny National Forest, for their assistance with the sampling and evaluation of stumps in the thinning study at the Kane Experimental Forest. Thanks also to former Irvine Laboratory technicians, Ernie Wiltsie, Greg Sanford, Eric Baxter, and Mike Trisket for obtaining and preparing cross-sections for these analyses. Special thanks to Timothy Fox, Biological Technician, for help in cross-dating and measuring the cross-sections.*

within a stand is known. The causal mechanism of this darkening is unknown, but inferences from loggers and foresters have related it to defoliation events, most particularly, cherry scallop shell moth (CSSM) (*Hydria prunivorata* Ferguson) defoliations. In northwestern Pennsylvania, black cherry typically initiates growth and flowers about mid-May when the leaves are nearly fully expanded and reddish in color (Marquis 1990). Black cherry, a semi-ring porous to diffuse porous species (Wheeler 2011), forms earlywood, which transitions to latewood by midsummer after leaf expansion and maturation (Coder 2017, Meier 2018) when feeding injury from CSSM is first evident on black cherry foliage. CSSM defoliations also reduce the ring-width increment, resulting in less growth the year following the initial defoliation (Schultz and Allen 1977). If there are two successive years of defoliation, growth is reduced during the second year of defoliation and for the first year after defoliation has ended, but then will recover during the second year after defoliation has ended (Schultz and Allen 1977). Dark rings are frequently associated with these periods of reduced growth (Long et al. 2012).

CSSM overwinters as pupae in the litter, and adult moths emerge in the spring (Schultz and Allen 1975). Peak emergence on the Allegheny Nation Forest (ANF) is late May and early June. Adults lay eggs on the black cherry leaves about 23–26 days after they emerge, and eggs hatch beginning 4–6 days following oviposition (Schultz and Allen 1975). Larvae mature through four instars, and foliar injury usually is evident in mid to late July as brown leaves. The caterpillars feed gregariously, building a tube-like nest from the foliage and consuming the upper epidermis of the leaf (Allen 1993). The leaves turn brown, desiccate, and fall from the tree. Fourth-instar caterpillars move down the bole or spin down on a strand of silk to the litter beneath the crown and pupate (Schultz and Allen 1975). There is only one generation per year.

Outbreaks of CSSM were reported in Michigan and Wisconsin in the 1950s (Schultz and Allen 1975), and in the 1970s, both New York and Pennsylvania reported major outbreaks of CSSM resulting in significant black cherry defoliation (Anon. 1970, 1971, 1972, 1973, Nichols et al. 1972). Widespread outbreaks of CSSM were documented on the ANF during 1971–73, 1982–84, and 1994–96 (Bonstedt 1985, Morin et al. 2006). This latter defoliation affected over 250,000 acres (100,000 hectares) across the ANF (Bonstedt 1985, Morin et al. 2004). Other insect pests of black cherry include the early-season defoliator, eastern tent caterpillar, *Malacosoma americanum* Fabricius, but few widespread outbreaks have been reported on the ANF (Bonstedt 1985). More recently, the fall web worm, *Hyphantria cunea* (Drury), a late season defoliator with a broad host range, caused significant injury to black cherry during 2011 and 2012. Other early-season insect defoliators such as forest tent caterpillar, *Malacosoma disstria* Hübner, and elm spanworm, *Ennomos subsignaria* (Hübner), will feed on black cherry, but cherry is not usually the preferred host for these insects. During 1991–93, there was an unprecedented elm spanworm outbreak affecting about 340,000 acres (138,000 hectares) on the ANF, and the most severely affected species were red maple, *Acer rubrum* L., American beech, *Fagus grandifolia* Ehrh., sugar maple, *A. saccharum* Marsh., and black cherry (Morin et al. 2006). Historically, CSSM has caused the most severe and widespread injury to black cherry, starting in the 1970s and continuing at approximately 10-year intervals through 1996 (Morin et al. 2006). There was no significant CSSM outbreak in the first decade of the 2000s, but a new outbreak occurred in 2015 on the ANF.

Earlier work reported on dark rings in black cherry cross-sections from nine different stands owned or managed by Collins Pine Co., Kane Hardwood Division, Kane, Pennsylvania (Long et al. 2012). Nearly all of the dark rings in the examined 36 sections were formed in the 1990s, usually 1994 or 1995, a period coincident with the last major CSSM outbreak in northern Pennsylvania. Only four of the sections had dark rings in 1983, also a year during a CSSM outbreak (Bonstedt 1985). Kane Hardwood land managers and others have reported that dark rings were also observed in the 1970s (D. Payne, personal communications).

The objectives of this study were to: (1) determine whether the dark rings formed in the 1970s, 1980s, and 1990s are anatomically similar based on macro and microscopic examination; (2) determine the frequency of dark rings in recently thinned black cherry stands with a known defoliation history and assess growth impacts and potential interactions with drought; and (3) assess the incidence of dark ring formation in six additional stands in or adjacent to the ANF.

Methods

Anatomical Comparisons of Dark Rings Occurring in Different Decades

Wood cross-section samples with dark rings, 4–10 samples per site, were obtained from five locations in the ANF (Figure 1, sites 1–5) and one site on an adjacent private industrial forest (site 6). These sites were identified based on information from timber buyers, loggers, and land managers. In some instances, samples were taken from logs at the log landing while the sale was in progress. In other instances, samples were obtained from postharvest visits, and only the remaining tree tops and stumps were readily available

Management and Policy Implications

Anomalous dark rings in black cherry (*Prunus serotina* Ehrh.) were related to defoliations from cherry scallop shell moth (CSSM), *Hydria prunivorata* Ferguson, based on assessments of dark rings formed in the 1970s, 1980s, and 1990s, which coincided with known periods of CSSM defoliations. Black cherry wood quality and economic value can be negatively affected by dark rings, particularly veneer-quality trees after dark rings enter the heartwood. Dark rings are considered a defect for veneer products, and therefore potential veneer logs must be sold for lower-quality products. Although not all CSSM defoliated black cherry trees produced wood with dark rings, we found that dark rings occurred in 48–68 percent of surveyed stumps 28 years after a CSSM defoliation in 1983. We determined that the dark color in the growth rings was associated with the fiber cell walls, and these walls were about 50 percent thinner than normal-colored fiber cell walls. CSSM defoliation also reduced the growth of black cherry by as much as or more than 50 percent, usually in the year following the defoliation event. Foresters managing black cherry will need to consider the impact of CSSM defoliations on the value of potential veneer quality trees. For stands or forests nearing maturity and with a known CSSM defoliation history, an early harvest could prevent value loss if done before the dark ring advances well into the heartwood. Management activities to suppress outbreaks of CSSM could reduce their impact on black cherry limiting growth loss and inhibiting formation of dark rings.

for sampling. Stumps were sometimes too discolored and colonized by secondary organisms to identify dark rings, so the bases of the remaining tops were cut to obtain samples. Our observations, and reports from timber buyers and loggers, are that dark rings occur throughout the bole and are usually visible at both ends of the log (T. Firth, personal communication). All cross-sections were planed and sanded to enhance the appearance of ring boundaries and then cross-dated under a dissecting microscope using skeleton plots and the list method (Speer 2010). Dark rings were visually identified after wetting the cross-section with water. The year(s) associated with the dark rings were recorded for each cross-section.

To compare the anatomical features of dark rings observed in three different decades, we selected 12 partial cross-sections with dark rings in different decades for detailed examination at the US Forest Service, Forest Products Laboratory, Madison, Wisconsin. These 12 samples had one or more dark ring(s) that formed in the 1970s, 1980s, or 1990s. Not all samples had dark rings in each decade. Small wood samples with dark rings were excised and soaked in water. Unstained thin sections were cut using a scalpel and a microtome. Anatomical features of the dark rings that formed in the different decades were compared under low (40×) and high (100×) magnification using a compound light microscope, and higher magnification (300× to 1000×) using a scanning electron microscope (SEM). Digital color photos from the light microscope and micrographs from the SEM were used to compare and contrast xylem cellular features and color noting the anatomical differences and similarities in visual appearances of the rings, and the dark and normal-colored portions within a dark ring.

A preliminary assessment of potential differences in fiber cell wall thickness in dark and normal-colored rings was conducted using an SEM micrograph. Two lines were drawn across the micrograph perpendicular to the rays in the dark portion of the ring, and 10 double cell wall thicknesses were measured from cell lumen to cell lumen along each line for a total of 20 measurements. This was repeated in the normal-colored portion of the ring using two lines

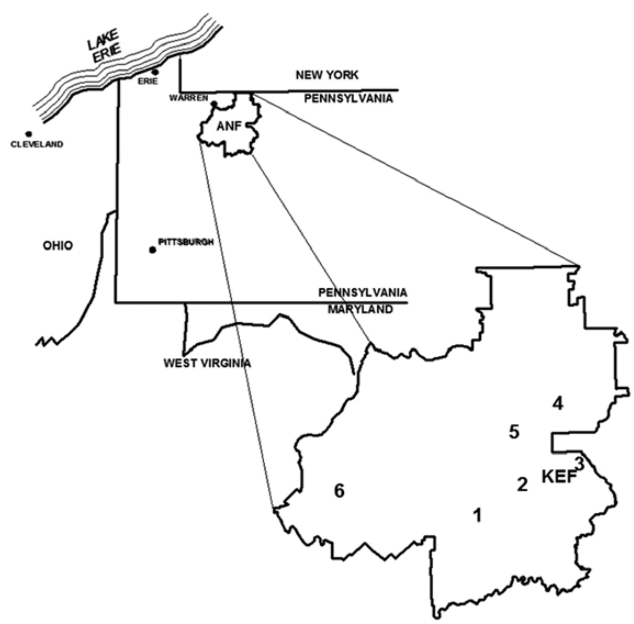

Figure 1. Locations of sites used for sampling to determine the presence of dark rings in black cherry. KEF, Kane Experimental Forest.

perpendicular to the rays. The 0.0012 inch (30 μm) scale bar in the micrograph was used to scale the measurement, and each measurement was divided by two to obtain the cell wall thickness (CWT). Cell wall thickness means were calculated from each set of 20 measurements, and *t*-tests were used to evaluate the CWT differences between the dark-colored and normal-colored cell walls.

Frequency of Dark Rings in Managed Forest Stands

A 2011–12 thinning in a long-term study located at the Kane Experimental Forest (KEF) permitted assessment of the frequency of dark ring occurrence in managed Allegheny Hardwood stands. These stands originated from chemical wood cuts in the early- to mid-1920s. Because black cherry is a fast-growing, shade-intolerant species, cherry quickly grows past tolerant competitors (Marquis 1981). Most of the black cherry in the thinning blocks were in dominant or codominant crown positions by the start of the study in the early 1970s. Crown position was evaluated in 1979, and 83 of these black cherry trees were cut in the 2011–12 thinning when dark rings were observed. This long-term thinning study was originally conceived to assess timber quality and quantity in stands cut to varying relative densities (see Nowak 1996 for more details). The third thinning in 2011–12 provided an unanticipated opportunity to assess dark ring formation in stands with a known defoliation history. We did not attempt to relate dark ring frequency to any thinning objectives.

To determine the frequency of dark rings in these managed stands, recently cut stumps were surveyed immediately following a timber harvest in three replications (blocks) of this thinning study at the KEF. These KEF stands are 0.6–29 miles (1–47 km) miles from the other stands used for sampling dark rings (Figure 1). Each thinning replication had 10 or 11 two-acre (0.8-hectare) plots, each treated with different thinning prescriptions including untreated control plots. The three replications were located along Forest Road 138 approximately 3 miles (5 km) south of Kane, Pennsylvania. Trees in the replications were 80–90 years old in 2011. The first and second thinning treatments were conducted in the dormant seasons of 1972–73 and 1988–89 for replication 1, dormant seasons of 1974–75 and 1990–91 for replication 2, and late winter 1976 and the dormant season of 1990–91 for replication 3. All three replications received a third thinning in December to March of 2011–12. During this harvest, incidences of dark rings were observed by research technicians while inspecting the harvest progress.

Each thinning treatment plot within a replication is a 2-acre (0.8-hectare) plot with an interior 0.6-acre (0.24-hectare) measurement plot surrounded by a 66-foot (20-m) buffer area (Nowak 1996). All trees are individually numbered in the measurement plots, but not in the buffer areas. The trees selected for cutting in the thinning operation were selected based on relative density objectives for each particular treatment, and trees were not cut with prior knowledge of dark ring presence or absence. The thinning prescription was unrelated to the dark ring study and required two-thirds of the cut basal area to be removed in trees below the average diameter and one-third from above the mean diameter until a desired relative density was obtained (Nowak 1996). We thus considered the stumps left after cutting as a random sample from the population of black cherry trees in a replication. The crown position of the trees was visually estimated in 1979.

Surveyed stumps included all the cut and numbered black cherry trees in research plots (0.6-acre interior of a treatment unit) and unnumbered trees in the buffer area that received the same treatment associated with the thinning study plot. The diameters of the cut black cherry trees ranged from 7.3 inches (18.5 cm) to 28.3 inches (71.9 cm) and averaged 15.9 inches (40.4 cm). The cut stumps were cleared of any chainsaw debris and sprayed with water to enhance the appearance of the dark rings. When dark rings were present, an estimate of the decade in which they occurred was made by counting the rings on the stump. The frequency of dark rings in the 1970s, 1980s, and 1990s was estimated in the field by ring counts on the fresh cut stumps. Dark rings were visually assessed by rating each ring as either uniformly dark around the circumference of the growth ring or variable, meaning faded and indistinct in places (Figure 2A).

During the 1980s, between the first and second thinnings, a severe outbreak of CSSM occurred and affected these trees. The relation of defoliation severity (light, moderate, or heavy) to thinning replication was assessed with individual tree defoliation ratings conducted in August 1983. All numbered black cherry trees (n = 991 in 1983) were evaluated in all three replications. Each numbered tree was given a rating (trees in the buffer areas were not rated) based on the amount of CSSM defoliation as lightly (≤30 percent), moderately (31 percent to 60 percent), or heavily (>60 percent) defoliated. These data were used to examine whether dark ring occurrence was related to defoliation severity for 83 numbered black cherry trees that were rated in 1983 and cut during the 2011–12 thinning.

To determine whether the proportion of stumps with dark rings was the same in all three thinned replications, we used contingency table analyses and Fisher's exact test of independence to assess these relations (McDonald 2014). A similar contingency table analysis was used to assess whether the proportions of trees in the three defoliation classes (trees assessed in 1983) were different among the three thinning replications. Because multiple comparisons were conducted, we used a Bonferroni correction to keep the familywise error at the .05 probability level (McDonald 2014). We used one overall test with all three replications and three pairwise comparisons of the replications, so the Bonferroni critical value was 0.05 / 4 = 0.012. McNemar's test (SAS Institute 2012) was used to assess whether the 1983 defoliation severity ratings were related to the presence of dark rings. This required combining light and moderately defoliated trees into one defoliation class and comparing these with heavily defoliated trees.

The relation of crown position to dark ring formation was assessed by using the 83 numbered black cherry trees with crown position data. Fisher's exact test of independence was used to test whether dark ring occurrence was related to the four different crown position classes (dominant, codominant, intermediate, suppressed). An additional test combined dominant and codominant trees into one class and intermediate and suppressed trees into a second class. These two classes were then used to determine whether dark ring occurrence was independent of crown class. Most of the thinned black cherry was in dominant or codominant crown classes, and the smaller trees cut in this third thinning were usually sugar maple, red maple, American beech, sweet birch, *Betula lenta* L., and other minor species.

Dating and Measuring of Cross-Sections from KEF

Twenty stumps with dark rings were randomly selected across the three thinning replications, and cross-sections were cut, surface prepared, and cross-dated. These trees had diameters at breast height (dbh) that ranged from 8.7 inches (22.1 cm) to 20.1 inches (51.0 cm) and averaged 15.2 inches (38.6 cm). Seven of these were numbered trees, six of the seven trees were in dominant or codominant crown classes, and one tree was intermediate. The remaining trees were cut from buffer areas, and dbh ranged from 15.1 (38.1 cm) to 22.4 (56.9 cm) inches with an average dbh of 17.7 inches (45 cm). No crown class data were available for these buffer trees, but they were likely in dominant and codominant crown classes. The Fire History Analysis Exploration System software (Grissino-Mayer 2001, Sutherland et al. 2015) was used to record the dark rings present in each section and to develop event history charts. The annual rings in the dated cross-sections from KEF were measured using Win-DENDRO (Regent Instruments, Quebec City, Canada). The quality control program, COFECHA (Holmes 1983), was used to validate the cross-dating and ring-width measurements.

The measured ring widths were standardized by fitting a negative exponential curve followed by a linear regression line and dividing the actual ring-width value by the curve-fitted value using the ARSTAN program (Cook and Holmes 1996). The ARSTAN program is a widely used flexible program for standardizing

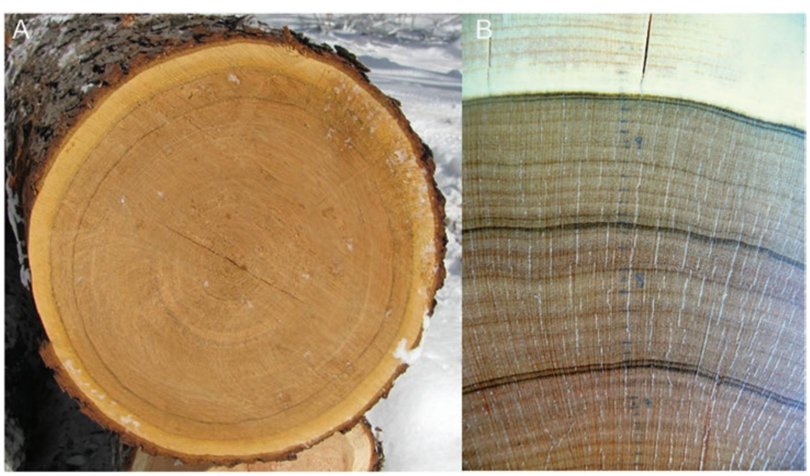

Figure 2. (A) View of a log end at a log landing on the Kane Experimental Forest; (B) close-up of a sanded and recently water-wetted cross-section with dark rings in 1973 and 1974, 1983 and 1994.

ring-width measurements with applications in ecology (Speer 2010, Clark et al. 2017) and dendroclimatology (Cook et al. 2004, Copenheaver et al. 2017). The primary purpose of standardization of ring-width measurements is to remove age-related growth trends and other long-term variability that can be considered noise (Speer 2010). Tree-ring width measurements are nonstationary and typically show a decreasing trend with tree age, and so measurements should not be averaged. Depending on the standardization method and study objectives, different frequencies are removed depending on the curve fit. Standardization produces dimensionless indices that can be averaged to produce a site or stand chronology. By averaging, common signals, usually associated with climate or a stand-wide disturbance, are more readily identified (Speer 2010).

Defoliation Effects on Growth

Dark rings that occur during these defoliations are frequently associated with reduced growth. The standardized ARSTAN chronologies and individual tree ring width measurements were used to assess the impact of defoliating insects, primarily CSSM, and the potential influence of drought on tree growth. The program JOLTS from the International Tree-Ring Data Bank Program Library (Holmes 1999) was used to identify growth suppressions that could be related to defoliations using the ring-width measurement series from each cross-section. The JOLTS program enables users to identify suppression periods in measured tree rings using specific user-defined criteria (Brose and Waldrop 2010, White et al. 2012). We used a 5-year running mean to locate suppression events in individual cross-sections and mean suppression factor at 50 percent of the running mean. The mean suppression factor is the magnitude of the suppression compared with the previous 5-year running growth mean (Holmes 1999). The minimum number of years between detected suppressions was set to 3 years. Coincidence of dark ring formation with growth reduction was also recorded.

Climatic Factors

The influence of drought on dark ring formation was assessed by using Palmer drought severity indices (PDSI) for Pennsylvania climate division 10 (National Oceanic and Atmospheric Administration 2011). For each year with a dark ring, monthly PDSI data from October, November, and December of the previous year through September of the year with a dark ring were examined. The number of months when the PDSI value was –1 or less (mild drought or more severe drought on the Palmer drought index scale) was tallied for each year, as was the cumulative number of dark rings recorded for that year. This included the years 1972–1976, 1982–1984, and 1994–1995. Fisher's exact test was used to assess whether dark ring frequency in a year was dependent on the number of drought months. In addition to the PDSI –1 or less threshold value, a similar test was used to evaluate whether just the growing season PDSI values (April through September; values ≤ –1.0) were related to dark ring frequency.

Dark Ring Occurrence in Stands Identified by Timber Buyers

The relation of CSSM defoliations to the formation of dark rings was also assessed with 30 samples obtained from six additional locations on or adjacent to the ANF where timber sales had occurred in the past 2 or 3 years (Figure 1). Samples from these sites and KEF were also used for anatomical study related to objective 1. At each site, cross-sections were obtained for identifying and dating dark rings. The Fire History Analysis Exploration System program (Grissino-Mayer 2001, Sutherland et al. 2015) was used to summarize the dark rings in a graphic event history chart similar to those used for recording fire scars (*sensu* Grissino-Mayer 2001). Cross-sections from two sites with the most samples, ANF3 (n = 6) and ANF6 (n = 10), were cross-dated and measured. The JOLTS program was used as described above to assess defoliation impact by identifying suppressions, and the ARSTAN program was used to develop mean site chronologies. Historical defoliation data were obtained from internal reports and a GIS defoliation layer developed from digitized aerial sketch mapping of defoliation events (GIS Defoliation Database 2014). These data were used to assess whether defoliations occurred in or near (≤0.62 mile or 1 km) the stands that currently have dark rings, and whether the dark ring years coincide with CSSM defoliation events or droughts.

Fisher's exact test was used to assess the hypothesis that defoliation and dark ring presence were independent (McDonald 2014). For this test, we used all the years from 1972 to 1996 and the data from all six sampled sites and the KEF. Each year was classified as having or not having a CSSM defoliation and then whether a dark ring was present or absent in that year.

Results

Anatomical Comparisons of Dark Rings in Different Decades

Black cherry with dark rings that formed in the 1970s, 1980s, and 1990s were readily evident in some cross-sections at log landings and at recent timber sale sites (Figure 2A and 2B). Microscopic wood anatomical comparisons of 12 sections with dark rings in one or more decade show no major differences among the anomalous dark rings formed in each decade (Figure 3). Five sections had dark rings in the 1990s, three sections in the 1980s, and two sections in the 1970s, and two sections had dark rings in both the 1970s and 1980s. The rings were characterized by darkened fiber cell walls. The darkening usually occurred after a period of normal cells formed as earlywood, and the darkened fibers likely formed midseason concurrent with CSSM defoliations.

The darkened fiber cell walls tended to be thinner than the normal-colored fiber cell walls based on a preliminary analysis (Figure 3). The change in fiber cell wall thickness (CWT) was more evident at higher magnification with the SEM (Figure 4). CWTs differ when comparing dark and normal-colored portions of the ring. Measurements taken on an SEM micrograph showed wall thicknesses of 0.00014–0.00018 inch (3.5–4.5 μm) for the normal-colored fibers at the top of the ring (Figure 4), but only 0.000079–0.00012 inch (2–3 μm) for the fibers at the bottom of the ring, which is the dark ring area. The thin-walled, dark-colored fibers averaged 0.000051 inch (standard error ± 0.0000031 inch) (1.3 μm; standard error ± 0.08 μm), and the thick-walled, normal-colored fibers averaged 0.00011 inch (standard error ± 0.0000055 inch) (2.7 μm; standard error ± 0.14 μm). A t-test showed that means for thick and thin-walled cells were different, t = –8.81, P < .001.

Viewed by the naked eye and under low-power magnification, the variation among the dark rings was primarily related to the thickness of the darkened zone within the annual ring and the intensity of the darkening around the circumference of the section.

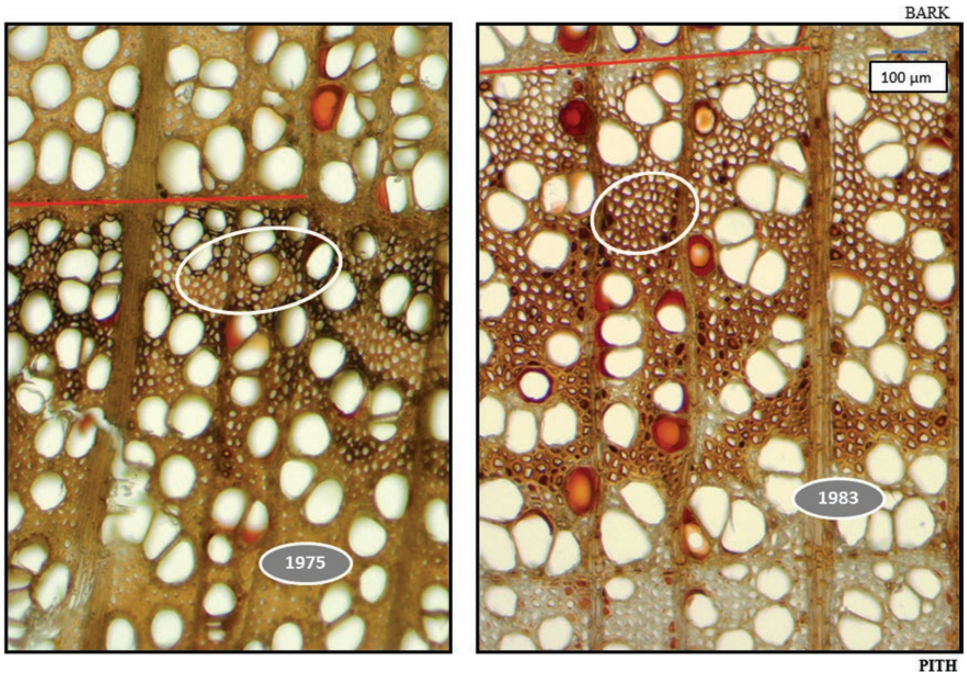

Figure 3. Dark rings formed in 1975 (left) and in 1983 (right), both taken at 100× magnification. The blue scale bar is 100 µm in length. These respective cross-sections are from different trees in different stands. White outlined ovals denote some of the cells within the dark rings that have thinner fiber cell walls than cells formed earlier in the growing season. The red line denotes the boundary between 1975 latewood and 1976 early wood (left panel) and between 1983 latewood and 1984 earlywood (right panel).

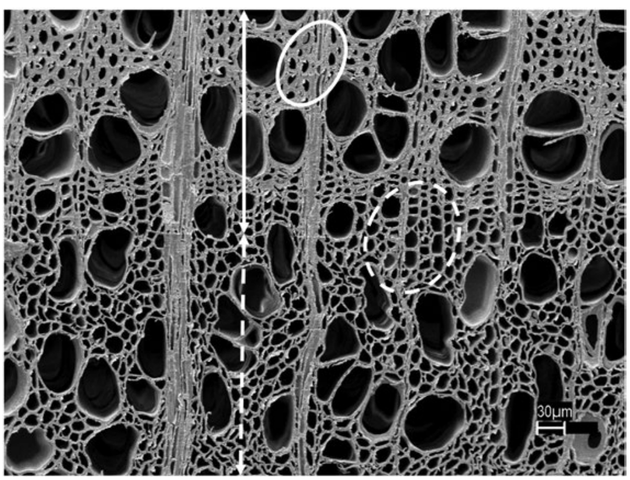

Figure 4. SEM micrograph showing the difference in fiber cell wall thickness between normal-colored portion of the ring (upper half with solid white circle and white arrow) and dark portion of the ring (center and lower half with dashed white circle and dashed white arrow).

Some rings were thin and not as dark as other rings, and some rings faded away and were barely perceptible in some areas of a cross-section. However, based on the microscopic comparison of the dark rings from all three decades (1970s, 1980s, and 1990s), there did not appear to be any major anatomical or morphological differences among the dark rings formed during these different years.

Dark Ring Frequency at the KEF

The long-term thinning study on the KEF provided an opportunity to assess the frequency of dark ring occurrence in managed stands known to have been defoliated by CSSM in the 1980s and 1990s. Three replications with varying treatment histories had a total of 232 black cherry stumps available for assessment after a thinning operation in the winter of 2011–12. Across all three replications, 62 percent of stumps had one or more dark rings. Replication 1 had the most black cherry stumps available for assessment. One hundred twenty-nine black cherry stumps were examined, and 69 percent contained one or more dark rings. Replications 2 and 3 had fewer black cherry stumps because of differences in species composition. The frequency of stumps with one or more dark rings was 54 percent in replication 2 and 48 percent in replication 3 (Figure 5A). Dark ring presence/absence was independent of replication (Fisher's $P = .032$, Bonferroni-adjusted critical value $P \leq .012$). Pairwise comparisons of replication 1, 69 percent dark ring frequency, with replication 3, 48 percent dark ring frequency, were also nonsignificant (Fisher's $P = .015$) based on the Bonferroni-adjusted probability critical value, $P \leq .012$.

Fifty percent of the stumps examined had only one dark ring (Figure 5A), whereas 11 percent had two dark rings present (Figure 5B). Of the 171 dark rings, 78 percent occurred in the 1980s, and 21 percent occurred in the 1990s. All three replications showed the same trend, with more than 70 percent of the dark rings occurring in the 1980s. Only one stump had a dark ring in the 1970s.

Of 171 dark rings examined, 64 percent were uniform on a stump. The dark color of the remaining rings faded in portions of the circumference around the stump (Figure 5C). Replications 1 and 3 had higher percentages of uniform rings than variable rings, whereas in replication 2, the numbers of uniform and variable dark rings were similar.

Defoliation severity estimated in 1983 was not independent of replication (Fisher's exact test $P < .001$, Bonferroni-adjusted critical value $P \leq .012$) (Table 1). Although more than 70 percent of the black cherry trees were heavily defoliated in all three replications, replication 2 had the highest proportion of trees heavily defoliated, 95 percent, compared with 75 percent and 79 percent in replications 1 and 3, respectively (Fisher's exact test $P < .001$ for both comparisons). For the 83 numbered trees defoliated in 1983 and cut in 2011–12, 61 percent had a dark ring(s) present; however, 39 percent, despite having been defoliated in 1983, did not have any dark rings in 2012. Heavily defoliated trees ($n = 69$) had a greater proportion of trees with dark rings, 64 percent, compared with lightly and moderately defoliated trees ($n = 14$, light and moderate classes were combined), in which 50 percent had dark rings (McNemar's $S = 10.12$, $P = .002$).

The relation of dark ring occurrence to crown position for these 83 trees was assessed using a contingency table and Fisher's exact test. Using all four crown position classes, dark ring occurrence was independent of crown position (Fisher's exact test $P = .11$). However, when trees were combined into two classes, dominant + codominant and intermediate + suppressed, there was a significant (Fisher's exact test $P = .035$) relation between crown class and dark ring occurrence. For dominant + codominant trees ($n = 63$) dark rings occurred in 68 percent (43/63) of the sampled trees; for intermediate and suppressed trees ($n = 20$) dark rings occurred in only 40 percent (8 trees) of the sampled trees. The influence of crown position on defoliation severity was similarly assessed. Ninety-two percent (58/63) of the dominant and codominant trees were severely defoliated in 1983, and defoliation severity was not independent of crown class (Fisher's exact test $P < .001$). Most of the black cherry in these stands were dominant or codominant trees, and most of these trees were heavily defoliated. All of the 20 intermediate and suppressed trees were defoliated in 1983. Eleven trees, three with dark rings, were heavily defoliated (>60 percent of foliage removed); seven trees, four with dark rings, were moderately defoliated (31–60 percent defoliation); and two trees, one with a dark ring, were lightly defoliated (≤30 percent defoliation).

Dated Cross-Sections from KEF

Dated cross-sections showed that dark ring occurrence was mostly synchronous on the KEF thinning replications (Figure 6A). Only one cross-section had a dark ring in the 1970s decade, in 1973. All of the cross-sections had dark rings in 1982 or 1983, and one tree had a dark ring in 1984. More detailed assessments of sampled cross-sections from KEF showed a 1982 dark ring in 75 percent of the sections; a 1983 dark ring in 60 percent of the sections and a 1984 dark ring in 5 percent of the sections. Seven trees, 35 percent, had dark rings in both 1982 and 1983, and 20 percent had dark rings in three years (1982, 1983, and 1994). Ten trees, 50 percent, had dark rings in the 1990s, all in 1994, coincident with a CSSM defoliation.

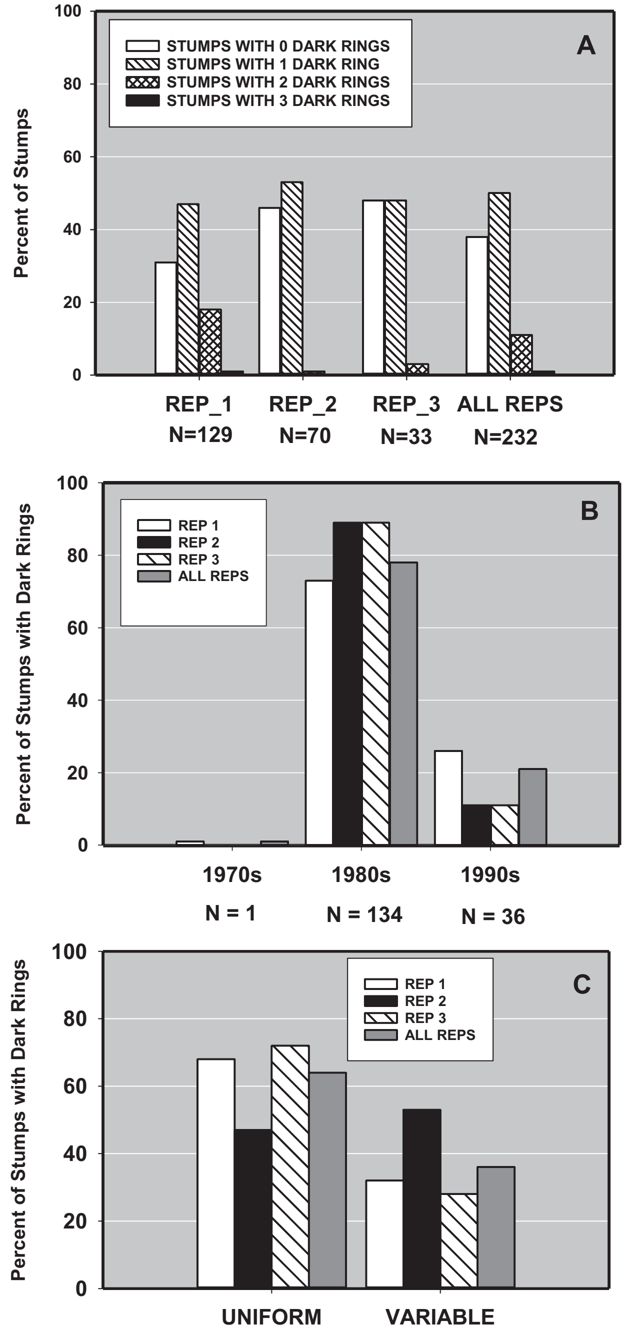

Figure 5. Summary of stumps with dark rings at Kane Experimental Forest: (A) numbers of dark rings in sampled stumps; (B) decades associated with the identified dark rings; (C) percentage of stumps with uniform or variable dark rings.

Dark Ring Occurrence in Stands Identified by Timber Buyers

Dark ring occurrence varied across the ANF, but was observed in the 1970s, 1980s, and 1990s on 30 cross-sections collected from six sites on or near the ANF (Figure 1). Site 3, only 0.6 mi (1 km) northeast of KEF thinning replications, had dark rings in 1982 and 1983, similar to the thinning replications (Figure 6B). However, at site 3, five of the six sections also had a dark ring in 1972, and one section (ANF3-4) had dark rings in 1972 and 1973. Sites 5 and 6 also had dark rings recorded in the 1970s. At site 5, dark rings were noted in 1973 and 1974, and additional dark rings were in the 1980s and 1990s from two cross-sections provided by loggers at a log landing. This was the only site with dark rings present in all three decades and coincident with known CSSM defoliations. At site 6, located 29 mi (46 km) southwest of the KEF, dark rings were only found in the 1970s, in 1974 and 1975. Site 2, about 2 miles (3.2 km) west of thinning replication 1 on the KEF, only had dark rings in the 1980s on the three cross-sections from this site, and site 1, 12 miles (19 km) southwest of KEF, only had dark rings in the 1990s.

Sites 3, 4, 5, and KEF have dark rings coincident with, or 1 year after, known defoliations by CSSM, based on digitized aerial sketch maps (Table 2). However, site 2 had major CSSM defoliations in the 1970s, and no dark rings were observed in this decade.

Conversely, site 6 had no record of CSSM defoliations, yet dark rings in the 1970s were prominent in the samples from this stand.

The association of dark rings and defoliation was assessed using the years 1972 through 1995, the period coincident with documented CSSM defoliations and dark rings. Combining the six stands identified by timber buyers and the thinning blocks at KEF, there were 10 years with dated dark rings, and 5 of these 10 years were associated with CSSM defoliations (1972, 1973, 1982, 1983, and 1994). The 5 years not associated with a CSSM defoliation were 1974, 1975, 1976, 1984, and 1995. In most cases, a dark ring was recorded for the year associated with a defoliation. Dark ring formation was dependent on defoliation during this 24-year period (Fisher's exact test $P = .006$).

Table 1. Number (percent) of black cherry trees with light, moderate, and heavy defoliation from cherry scallop shell moth in August 1983 in three thinning replications on the Kane Experimental Forest.

Replication	Light	Moderate	Heavy	Total
1	26 (7)	71 (18)	292 (75)	389 (39)
2	2 (<1)	16 (4)	375 (95)	393 (40)
3	11 (5)	33 (16)	165 (79)	209 (21)
Total	39 (4)	120 (12)	832 (84)	991 (100)

Defoliation Effects on Growth

Growth suppressions were identified in 36 measured cross-sections from three sites (KEF $n = 20$, ANF3 $n = 6$, and ANF6 $n = 10$) and provide additional evidence of insect defoliation impact. Despite the known CSSM defoliations in the 1970s, only one tree at ANF6 showed ≥50 percent reduced growth over a 3-year period, 1972–74, compared with the previous 5-year period using the program JOLTS running mean algorithm (Holmes 1999). Growth reductions associated with the 1980s defoliations were more acute and frequent, and 16 of the 36 (44 percent) cross-sections showed a ≥50 percent reduction in mean ring width in the period from 1982 to 1984, with most of the samples from KEF. All 16 cross-sections with suppressed growth had one or more dark rings in the period from 1982 to 1984. Three sections (8 percent) had growth suppression identified in the 1980s, but no dark rings present in that decade. These three sections had dark rings in 1974 or 1975, but there was no associated growth suppression. Seventeen cross-sections (47 percent) had dark rings in one or more of the 1970s, 1980s, or 1990s decades, but no major growth suppressions were detected by JOLTS.

For the KEF thinning replications, the ARSTAN standardized chronology, representing mean ring-width variation averaged across all measured samples at the site, showed a 1982 growth suppression of almost 60 percent starting in 1982. The other two chronologies were insufficiently replicated to assess stand-wide growth effects.

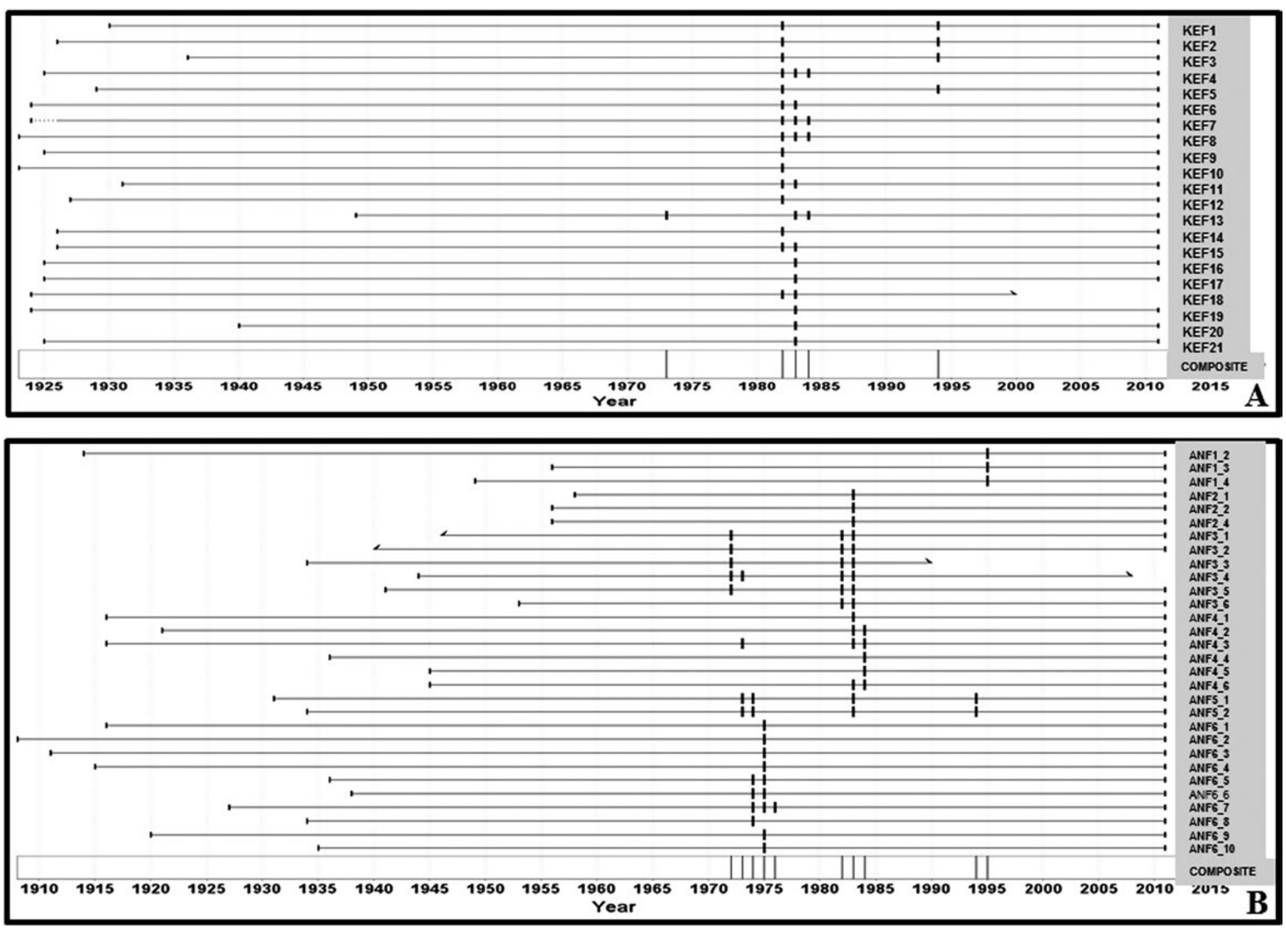

Figure 6. Event history charts produced from the Fire History Analysis Exploration System program (Sutherland et al. 2015) showing years with dark rings: (A) in 20 cross-sections from thinning replications at KEF; (B) in 30 cross-sections from six other sites on or adjacent to the ANF. ANF, Allegheny Nation Forest; KEF, Kane Experimental Forest.

Table 2. Sites and years with dark rings and associated defoliations derived from digitized sketch maps that include the insect defoliator and the severity of the defoliation in the mapped polygon.

Site	Dark ring year(s)	Defoliation year(s)	Defoliation agent	Defoliation severity
1	1995	1993	ESW	M
		1994	CSSM	H
2	1983	1972	CSSM	M
		1973	CSSM	H
		1974	CSSM	M
		1983	CSSM	H
3	1972	1972	CSSM	M
	1973	1973	CSSM	H
	1982	1974	CSSM	M
	1983	1983	CSSM	H
		1992	ESW	M
		1992	ESW	M
4	1983	1972	CSSM	M
	1984	1982	PT	H
		1993	ESW	M
		1994	FTC	M
5	1973	1972	CSSM	M
	1974	1983	CSSM	H
	1983			
	1994			
6	1974	1987	GM	M
	1975			
	1976			
KEF	1973	1972	CSSM	M
	1982	1973	CSSM	H
	1983	1974	CSSM	M
	1984	1983	CSSM	H
	1994	1992	ESW	M
		1993	ESW	H

Note: CSSM, cherry scallop shell moth; ESW, elm spanworm; FTC, forest tent caterpillar; GM, gypsy moth; H, heavy; M, moderate; PT, pear thrips, *Taeniothrips inconsequens* (Uzel).

Climatic Factors

The relation between the cumulative frequency of dark rings in a year with the number of months when PDSI values were ≤–1 was assessed using Fisher's exact test and showed that these were independent (P = .205). Other assessments using just the growing season April to October PDSI values showed no relation with number of drought months and frequency of dark rings (Fisher's exact test P = .481). A graphical comparison of the KEF standardized tree ring chronology and the mean April–September PDSIs shows no clear relation with drought (Figure 7). During the 1970s CSSM defoliation, seasonal PDSI values were positive, indicating adequate moisture, and ranged from 1.32 to 2.15, although a major drought preceded this period during the mid-1960s. During the CSSM defoliations in the 1980s, tree growth was sharply reduced with a minimum index value of 0.52 in 1983; however, this was a period of above-average moisture conditions with PDSI values from 0.66 to 2.41. Only in the 1990s were CSSM defoliation and dark ring occurrence coincident with a drought year. The mean April–October PDSI in 1995 was –1.61, five months had PDSI values ≤–1.5, and three dark rings were recorded in 1995. However, the mean 1994 April–October PDSI was 3.08, no PDSI values were negative, and 12 dark rings were recorded.

Discussion

There was clearly an association between dark ring formation and CSSM defoliations. However, there was no evident mechanism to explain the formation of these discolored rings based on the available data. Based on the KEF survey and data from six other stands, dark ring occurrence was dependent on defoliation (Fisher's exact test P = .006). We also observed a relation between the severity of defoliation and the proportion of trees having dark rings. McNemar's test with KEF thinning study trees defoliated in 1983 and harvested in 2011–12 indicates that severely defoliated trees had a significantly higher proportion of dark rings than lightly and moderately defoliated trees. It is important to note that the 1983 survey included just the numbered trees after the first thinning, but the cut trees we evaluated after the third thinning in all three replications included only a subset of these plus the additional stumps surveyed in the buffer areas around each treatment unit. These buffer trees were not rated in the 1983 crown assessments because they were outside the measurement plots.

In the early 1980s and 1990s, the ANF had a series of unprecedented and severe defoliations from three principal insect defoliators that included gypsy moth *Lymantria dispar* L., elm spanworm, and CSSM (Morin 2006). In the 16 years from 1984 to 1999, 85 percent of the ANF land area was defoliated at least once (Morin et al. 2004). Black cherry was infrequently defoliated by gypsy moth or elm spanworm, although spanworm would sometimes feed on black cherry after defoliating beech, red maple, and sugar maple (T. Hall, personal communication). The 1990s CSSM outbreak followed the year after the elm spanworm defoliations had ended. As shown in the KEF thinning replications, not all defoliated black cherry trees in the 1980s had cross-sections with dark rings from the 1980s. This might have been caused by several factors. Unlike the early season defoliators such as forest tent caterpillar defoliation or elm spanworm, CSSM is a mid- or late-season defoliator attacking trees after leaves have fully expanded, and growth has been initiated (Schultz and Allen 1975, Allen 1993). In some instances, defoliation by CSSM was followed by refoliation of the crown, or sometimes just the most severely defoliated portions of the canopy. Another factor potentially influencing dark ring formation was the effect of two successive years of defoliation. The CSSM defoliation ratings from 1983 were useful, but having 1982 and 1984 ratings might have improved the ability to predict dark ring formation, as would data regarding the degree of crown refoliation. Other factors that might account for the heterogeneity of dark ring formation across the landscape may be related to the size of insect defoliator populations and the frequency and severity of defoliation. At site 6, on the western portion of the ANF, black cherry was a small component, probably <10% of the stand basal area. Although dark rings were present in sampled cross-sections from this stand, they showed no relation with any mapped defoliations. Aerial sketch mapping has limitations and does not always accurately record defoliation because the affected area was either too small to map or not readily identifiable from the air. Other research has shown that errors associated with aerial sketch mapping are due to aerial underestimation of the degree of defoliation, especially for plots with <10 percent defoliation (MacLean and MacKinnon 1996). Even more problematic is the fact that midseason aerial surveys were not always feasible, so the aerial survey data are not comprehensive, and some records rely on ground-based observations.

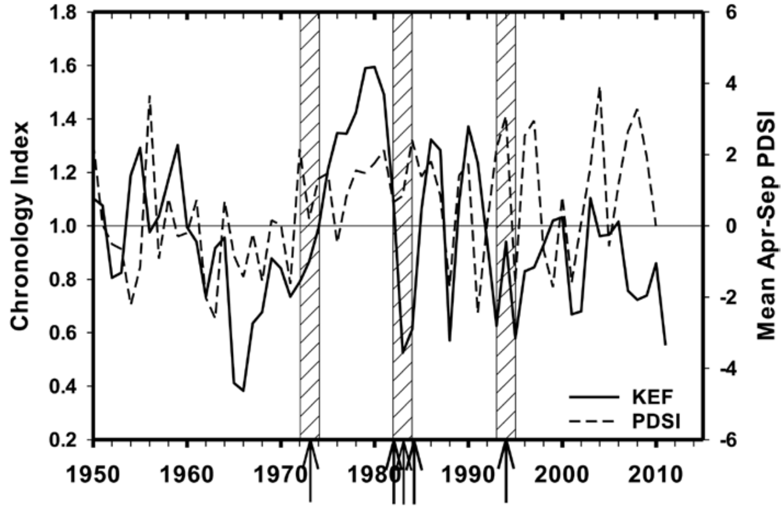

Figure 7. Standardized tree ring chronology from KEF with the Pennsylvania Division 10 mean April–September PDSI value for each year. Cross-hatched areas show the periods associated with cherry scallop shell moth defoliations in the 1970s, 1980s, and 1990s, and years with dark rings are noted by vertical arrows along the *x*-axis. KEF, Kane Experimental Forest; PDSI, Palmer drought severity indices.

Other research related to "white rings" in trembling aspen (*Populus tremuloides* Michx.) showed that the timing of the defoliation had some relation to the color of the growth ring. Trembling aspen and several other diffuse porous species form lighter-colored "white rings" in response to forest tent caterpillar defoliations (Sutton and Tardif 2005). White rings are characterized by thinner fiber wall thickness and a corresponding larger fiber cell lumen (Sutton and Tardif 2005). The fiber cell walls lack secondary thickening, possibly related to lignin content, and they have a uniform pale or white appearance to the naked eye (Hogg et al. 2002a). Possible mechanisms include defoliation effects on growth hormones and a reallocation of reserves to produce new foliage rather than cell wall thickening (Sutton and Tardif 2005). In artificial defoliation studies, Hogg et al. (2002b) showed that white rings formed in trembling aspen were most consistently associated with early June defoliation, similar to what occurs naturally with forest tent caterpillar defoliations, whereas July and August defoliations did not result in white ring formation. By July and August, aspen had already formed most of the growth ring, and this later defoliation mainly affected the ring width in the next year's growing season (Hogg et al. 2002b).

In our study, darkened fiber cell walls are evident after normal-colored cells are produced early in the growing season when viewed under magnification. However, there is considerable variation in the thickness of the dark ring band and the darkness of the fiber cell walls. Early-season fiber cell walls have normal coloration, and the darkened cell walls that form after these are likely coincident with the CSSM defoliation that typically occurs from mid-July to early August. Longitudinal variation of dark rings in sawlogs was not assessed in this study. Anecdotal evidence from loggers and our own observations indicates that dark rings are evident at both ends of a log. Whether the dark ring width and darkness intensity of a dark ring vary from the base of the tree to end of the first log has not been determined. A dark ring at either location will reduce the value of the log according to timber and veneer buyers. Rexrode and Baumgras (1980) found that the frequency of parenchyma fleck and gum spots caused by cambium miners increased with height in a tree. The same effect may occur with scallop shell moth, but more detailed research will be required. An artificial defoliation study could more definitively relate dark ring formation to timing of the defoliation, as was shown with trembling aspen (Hogg et al. 2002b). Sutton and Tardiff (2005) evaluated the influence of defoliation on diffuse porous species. It is possible that CSSM defoliation influences black cherry similarly, since annual growth rings may be either semi-ring porous or diffuse porous (Wheeler 2011, Coder 2017, Meier 2018).

Although anatomical features in black cherry dark rings provide few clues as to the causal mechanism of dark ring formation, the preliminary SEM analysis showed a major difference in fiber CWT. Fiber CWT for darkened cell walls, 0.00005 inch (1.30 μm), was less than half the CWT for normal-colored fiber cell walls, 0.00011 inch (2.75 μm). Black cherry fiber cell walls were thinner than reported for *Prunus domestica* L. which had cell walls 0.00016 inch (4.08 μm) thick (Kiaei et al. 2014). The thinner fiber cell walls in the darkened portion of the growth ring might affect black cherry mechanical properties, but these properties were not evaluated. We speculate that dark ring formation might result from the formation of secondary defensive compounds or other biochemical or hormonal changes formed in response to defoliation, and these changes might produce darkened fiber cell walls. It is uncertain when dark rings become visible in the wood. We suggest that because only a few dark rings have been observed in the black cherry sapwood, the rings might turn dark when the sapwood transitions to heartwood.

Most defects in black cherry wood are associated with insect attacks that cause gum spots or gum rings (Marquis 1990) and these should not be confused with dark rings. Trees weakened by defoliation and drought lack defensive energy to repel secondary invaders. Gum spots have been shown to be caused by larval feeding of the agromyzid cambium miner, *Phytobia pruni* (Grossenbacher), and they are found in the earlywood of black cherry (Hough 1963, Rexrode and Baumgras 1980). Other research has demonstrated the importance of injury by peach bark beetles, especially after trees are weakened by CSSM defoliations (Schultz and Allen 1977, Rexrode 1981). This injury might also cause abundant gummosis producing gum spots or a continuous ring of gum spots in the wood (Rexrode 1981). Macroscopically, a gum ring can resemble a dark ring, but on closer examination, it is easily distinguishable. Although we observed gum spots and gum rings in some of the cross-sections examined in this study, we saw no association of these injuries with dark rings.

Dark rings in black cherry observed in the 1970s, 1980s, and 1990s have a similar anatomy and morphology, hence indicating they are produced by similar processes. CSSM defoliation is coincident with the formation of these rings and likely causes some physiological change that subsequently affects the color and thickness of the fiber cell walls. Heavily defoliated trees are more likely to have dark rings. Regardless of the causal mechanism, CSSM appears to play a major role in formation of dark rings making outbreak suppression, if feasible, a tool to prevent their formation. Determining the mechanism of dark ring formation will require a long-term study and perhaps the use of artificial defoliation techniques. A new outbreak of CSSM on the Allegheny National Forest starting in 2015 may permit additional research to proceed in order to better understand this phenomenon and its effect on the color and quality of black cherry wood.

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