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Abstract— After decades of multiyear defoliation episodes in southern New England, *Lymantria dispar dispar* (LDD; previously gypsy moth) populations collapsed with the appearance of the LDD fungus in 1989. Multiyear defoliations did not occur again until 2015-2018. To assess the impact of the return of multiyear defoliations, we examined 3095 oaks on 29 permanent study areas in Connecticut and Rhode Island that were established at least eleven years before the latest outbreaks. Pre-defoliation stand level oak mortality averaged 2% (three-year basis). Post-defoliation mortality did not differ between managed and unmanaged stands, but was much higher in severely defoliated stands (36%) than in stands with moderate (7%) or low-no defoliation (1%). Pre-defoliation mortality of individual trees differed among species, was lower for larger diameter trees and on unmanaged than managed stands. Post-defoliation mortality on plots with no to moderate defoliation was similar to pre-defoliation mortality levels. Following multiyear defoliations, white oak mortality was higher than for northern red and black oak. There was weak evidence that mortality was elevated on stands with higher basal area following severe defoliation. Natural resource managers should not assume that oaks that survived earlier multiyear defoliations episodes will survive future multiyear outbreaks, possibly because trees are older.

Keywords: *Quercus*, disturbance, gypsy moth, *Lymantria dispar*, drought

INTRODUCTION

Since its escape in eastern Massachusetts in the 1860s, *Lymantria dispar dispar* L. (LDD; formerly known as European gypsy moth) has spread to nineteen US states and five Canadian provinces (APHIS 2020). LDD defoliated over 7.0 million hectares between 2000-2019 in the United States (USDA Forest Service 2021). Although the rate of expansion has been slowed by the national "Slow the Spread" program, it is likely that the range of LDD will continue to expand. Because oaks (*Quercus* spp.) are a preferred host species, elevated mortality of oaks after repeated defoliations are accelerating the loss of these keystone species in eastern North America (Morin and Liebhold 2016).

In Connecticut, LDD was first seen in 1905, with the first large-scale, leading-edge defoliations (sensu Davidson et al. 1999) that caused notable mortality occurring in the 1960s. Subsequent large-scale defoliations occurred periodically through the late 1980s. Gypsy moth populations vary tremendously from year to year, with large-scale defoliations often occurring at five to ten-year intervals (Johnson et al. 2006, Bjørnstad et al. 2010). Mortality of upper canopy oaks was highly elevated following multiyear, but not single year, defoliation episodes during this period (Ward 2007). Other studies have noted mortality is elevated by multiyear events, especially compared to single year (Fosbroke and Hicks 1989, Morin and Liebhold 2016)

Collapses of LDD outbreak populations prior to 1990 were often caused by parasitoids and diseases including "wilt" disease caused by nucleopolyhedrosis virus (Podgwaite et al. 1979). The unexpected appearance in New England in 1989 of the east Asia LDD fungus

(*Entomophaga maimaiga*) caused a regional collapse of LDD populations (Andreadis and Weseloh 1990). High humidity is required for discharge of the conidial spores responsible for widespread caterpillar infection during a given year and resting spore germination is higher when watered in the field (Hajek 1999); i.e., periods of average to above average precipitation during late spring/early summer (Andreadis and Weseloh 1990, but see Elkinton et al. 2019).

In areas where the LDD fungus is established, outbreaks likely require not only low pupae predator populations, primarily small rodents (Grushecky et al. 1998), but possibly dry springs which are not conducive to widespread infection of caterpillars by the fungus. This dual set of conditions could in part explain the nearly thirty-five year gap between the regional outbreaks in 1981 and those of 2015-2018 (Fig. 1). There was a limited outbreak in 2005-2006, but at most 8K ha had 50% or greater defoliation both years in Connecticut and there were no reports of widespread oak mortality. The extended period without significant oak mortality induced by multiyear defoliation episodes lulled foresters and natural resource managers in southern New England to believe that multiyear defoliation episodes would no longer occur. This belief was shattered by the defoliations of 2015 (132K ha), 2016 (325K ha), 2017 (825K ha), and 2018 (132K ha) in southern New England (USDA Forest Service 2021).

Elevated individual tree mortality following defoliation has been associated with trees in the lower canopy position, low tree (crown) vigor, repeated and more severe defoliation, and higher oak abundance in stand (Campbell and Sloan 1977, Herrick and Gansner 1987, Fosbroke and Hicks 1989, Gottschalk et al. 1998, Davidson et al. 1999). It should be noted that vulnerability among oak species differs among studies (Ward 2007) and may be related to species-site interaction (Davidson et al 1999). Commonly identified risk factors for higher stand mortality include increased duration and intensity of defoliation, increased amount or proportion of preferred species in stand, and low quality sites (Bess et al. 1947, Fosbroke and Hicks 1989). Increased mortality has also been reported on high quality sites during periods of drought (Davidson et al. 1999).

Objectives

After a second year of defoliation in southern New England, extensive areas with high mortality developed which required emergency responses by state and municipal officials to remove dead trees from roadsides, parks, hiking trails, and near structures, and to capture some volume by harvesting dead trees while they remained salvageable. Therefore, the objectives of this study were to (1) document the effects of most recent multiyear defoliations on stand and individual tree mortality and (2) compare predictive factors of mortality risk of the recent multiyear defoliations with those factors in the literature. It is hoped this information would be of interest to foresters and other natural resource managers who are responsible for mature hardwood stands that had not experienced repeated, severe defoliation for several decades.

STUDY AREAS

Because both the spatial and temporal occurrence of multiyear regional defoliation events are unpredictable, we examined the impacts of defoliation on stand level mortality and individual tree mortality and diameter growth using pre-existing study areas located in Connecticut and eastern Rhode Island (Table 1). Study areas had different sampling schemes as they were part of several different studies. A summary of the sampling scheme used at each study area can be found in Appendix 1. Trees on all study areas had been monitored since 2004 or earlier. These data sets provided a baseline of pre-defoliation mortality and growth.

Typical of most southern New England forests, the study areas were second-growth forests that originated in the early 1900s following a century or more of pasture, cultivation, and/or repeated cutting for charcoal and other wood products. Upper canopies were predominately upland oaks with admixtures of white pine (*Pinus strobus* L.)/black birch (*Betula lenta* L.) on drier sites and red maple (*Acer rubrum* L.)/American beech (*Fagus grandifolia* Ehrh.)/northern hardwoods on more mesic sites. With the possible exception of a few smaller trees, the oaks included in this study were survivors of several periods of regionwide defoliations between 1961-1982 (Fig. 1) and initiation of another widespread defoliation in 1989 that was suppressed by the initial appearance of LDD fungus in North America (Andreadis and Weseloh 1990). There was a single year of defoliation in 2006, but we observed little, if any, increase in mortality on monitored plots.

Southern New England is in the northern temperate climate zone. Average annual precipitation evenly distributed over all months and varies from 1350 mm in northwest Connecticut and Rhode Island to 1160 in central Connecticut (NOAA 2020). The region experienced a period of moderate to severe growing season drought between 2015-2017 (Fig. 2). Mean monthly temperature range from -6.2C in January and 20.0C in July in northwest Connecticut to -3.2C in January and 23.1C in July in central Connecticut. There is an average of 176 frost free days per year. The topography is gently rolling with plot elevations ranging from 50 to 350 m MSL. Soils were Inceptisols derived from granite, gneiss, and schist which included Typic and Lithic Dystrudepts ablation (meltout) tills and Oxyaquic and Aquic Dystrudepts ablation tills over basal (lodgment) tills (Table 1). The basal till layers restricts root growth and creates a seasonally perched water table. Soil descriptions are from SoilWeb (O'Geen et al. 2017).

METHODS

Field Measurements

In 2018 and 2019, diameter and canopy position (upper – dominant or codominant, lower – intermediate or suppressed) were noted for all live trees. An estimate of mortality year was recorded for dead trees (details below), except for the crop tree study where exact year of mortality was known. While all species were included in measurements, only four species of oaks were included in this analysis: northern red oak (*Quercus rubra* L.), black oak (*Q. velutina* Lam.), white oak (*Q. alb*a L.), and chestnut oak (*Q. montana* Willd.). Only oaks with an initial (pre-defoliation) diameter of 10 cm or greater in 2004 were included in the analysis. Measurements were taken during the growing season when surviving trees still had green leaves. Mortality estimates were as follows: died current year (attached brown leaves throughout crown), died previous year (few if any attached dead leaves, fine twigs remaining throughout crown), died two years previously (many fine twigs broken off, first order branches still attached), died earlier (most fine twigs gone, many branches broken, or fungus fruiting through bark). These estimates were informed by the authors' decades of experience noting mortality on annually monitored plots. At least one of the authors was responsible for all mortality estimates.

As with all post hoc observational studies, there were limits to the design and some measurements. Ideally, plots would have been randomly established across the landscape at least several years before defoliations in areas that would have then experienced a range of intra- and inter-year defoliation intensities. In lieu of this idealized design, we utilized study areas with individual tree measurements that had been established at least eleven years prior to the latest period of defoliation. While acknowledging that these limitations increase the data uncertainty, we believe that the general conclusions are fairly robust because of a large data set in terms of the number of study areas (n=29) and individual trees (n=3095) examined.

Another limitation is that actual defoliation intensity and duration at individual study plots was not explicitly noted until the 2018 and 2019 surveys. However, the authors visited most Connecticut plots annually to either complete diameter measurements or to insure there has been no disturbance and thus were able to provide a qualitative assessment of defoliation in earlier years. For plots not visited, local foresters provided an assessment of general defoliation intensity in the area in previous years. Gottschalk et al. (1998) reported models of individual tree mortality were improved with the addition of the highest amount of defoliation observed in any year. However, they acknowledged that their approach did not include the effect of multiyear defoliations found important in other studies (Morin and Liebhold 2016). Therefore, we initially categorized defoliation severity into levels based on the observations of the authors or local foresters: none (no or light defoliation), moderate (single year or less than 50% defoliation), and severe defoliations (two or more years of 50% defoliation).

Lastly, we note that the short-term nature of this study will not capture all of the mortality initiated by the recent defoliations as some weakened trees still alive during our survey will succumb to secondary stressors such as twolined chestnut borer (*Agrilus bilineatus* Weber) and Armillaria (*Armillaria mellea* Vahl:Fr.). It is probable that oak mortality will remain elevated in defoliated areas for at least several more years (Muzika et al. 2000).

Data Analysis

Stand level

Because pre-defoliation mortality values were measured over different intervals (Appendix), they were converted to a common 3-year basis that also allowed direct comparisons with the observed three-year post-defoliation interval (Table 2). A logit transformation of mortality values was completed to improve normality prior to analyses (Warton and Hui 2011). Using only study areas with a management contrast, i.e. both managed and unmanaged plots were present, separate analysis of pre- and post-defoliation stand mortality rates (dependent variables) were completed using SYSTAT 13.2 Linear Mixed Model subroutines with TREAT (managed, unmanaged), DEFOL (none, moderate, severe), and TREAT × DEFOL interaction as fixed factors and study area as the random effect. Tukey's HSD test was used to test differences among defoliation levels in this and subsequent analyses. Differences were considered significant at $P < 0.05$. When initial analyses found stand pre- and post-defoliation mortality rates were independent of both TREAT and TREAT × DEFOL effects (See Results), all study areas were used to examine pre- and post-defoliation stand mortality rates with DEFOL as a fixed factor, initial stand oak basal area (BA) and density (DEN) as fixed covariates, and study area as the random effect. While full models and subsets were examined, only parsimonious models with the lowest Akaike's Information Criterion (AIC_c) including significant parameters for all variables are presented in Results (Burnham and Anderson 2002). Simple linear regression was then used to examine whether pre-defoliation stand mortality was correlated with post-defoliation mortality with each study area as a replicate.

Individual tree level

Differences in mortality rates among each pair of oak species were tested both pre- and post-defoliation using a 2X2 contingency table analysis as outlined in Zar (2010, p 549-550). Pre-defoliation mortality occurred over a 12-19 year period while post-defoliation mortality was for the two or three year period (depending on sample year of each plot). Differences were judged significant at $P < 0.05$ using Bonferroni adjusted probabilities. For example, we tested the difference between white and black oak mortality rates for the period before and a separate analysis for the period after defoliation. Preliminary analysis indicated that post-defoliation mortality rates differed among oak species (see Results). However, logistic regression analysis was only completed on combined oak species because classification tree analysis indicated no nodes separating species and small sample size of individual species.

We used classification tree analysis to identify those factors and variables that best predicted mortality (Herrick and Gansner 1987, Gottschalk et al. 1998). Separate analyses were completed for pre- and post-defoliation mortality. Half of stems (individual trees) were randomly assigned to the model building data subset with the independent variables species, DEN, BA, TREAT, together with DBH (initial stem diameter) and GROW (pre-defoliation diameter growth). Pre-defoliation canopy position data were not available for all sites and small sample size at the remaining sites precluded including it in the model; there were only 116 lower canopy trees alive prior to defoliation. Because we did not have pre-defoliation crown vigor estimates that have been found predictive in earlier models (Herrick and Gansner 1987, Gottschalk et al. 1998), we used GROW as a surrogate metric of tree health with the assumption that faster growing trees were healthier. Remaining stems were used for model validation. Analyses of both pre- and post-defoliation mortality were conducted in the SYSTAT 13.2 TREES module using classification tree analysis with phi coefficient loss function. Minimum split index and minimum improvement in PRE (proportional reduction in error) values were set at 0.05. Binary classification test statistics sensitivity, specificity, PPV, and NPV were calculated for both model building and validation data sets.

As shown in Results, we observed that the binary breakpoints in classification trees did not accurately represent the continuous response curve between mortality and independent variables. Therefore, logistic regression (SYSTAT 13.2 BLOGIT subroutine) was also used to evaluate the factors contributing to individual tree mortality, with separate models for pre- and post-defoliation mortality (Eisenbies et al 2007). Using the model building data subset, the full logistic regression model examined for pre-defoliation mortality (M_{pre}) was:

$$(1) \qquad M_{pre} = 1/(1 + \exp(\beta_0 + \beta_1 * SIZE_i + \beta_j * FACTOR_j + \ldots + \beta_k * FACTOR_k)) + \varepsilon$$

where β_0 was the estimated intercept, β_1·- β_j were the estimated parameters; $SIZE_i$ were independent continuous independent variables DBH and GROW; $FACTOR_j$ were TREAT, DEN (pre-defoliation oak stand density), and BA (pre-defoliation oak stand basal area); and ε was the residual error term. Variables not significant in full models were removed and the resulting simpler model was tested with the validation data set.. Area under ROC curve (AUC) values are presented for full and final logistic models. AUC is a metric of classification accuracy that ranges from 0.5-1.0; with values < 0.7 indicating poor discrimination, 0.7-0.8 indicating acceptable discrimination, and 0.8-0.9 indicating excellent discrimination (Hosmer et al. 2013).

The validation data subset was used to examine parsimonious models with similar minimal Akaike's Information Criterion (AICc). Root mean square errors (RMSE) were calculated for parsimonious models to examine fit of validation data mortality with model estimated mortality using 2 cm diameter classes. The final logistic model had the lowest RMSE and all included variables having significant parameter estimates. Using 2 cm diameter classes, we also estimated the Pearson correlation coefficient (PCC) between observed mortality of validation data subset and estimated mortality developed with model building data subset.

Post-defoliation mortality (M_{post}) models were as above but also included the categorical factor DEFOL. Initial classification tree analysis at both stand and tree levels and logistic analysis at individual tree levels indicated mortality did not differ between plots with no-little and moderate defoliation intensities, but mortality on both differed from that observed on stands with severe defoliation. Therefore, separate analyses were completed for plots with severe defoliation intensity and for plots with minor defoliation (i.e., plots that had no, little, or moderate defoliation).

RESULTS

Stand level mortality

There were seven study areas that experienced little or no defoliation, seven with moderate defoliation and fifteen with severe defoliation. Mean pre-defoliation mortality (3-year basis) was 1.9 ± 0.3%. For those study areas that had both unmanaged and unmanaged plots, pre-defoliation mortality did not differ between TREAT (managed vs. unmanaged) ($F_{(1,13)} = 0.22$, $P = 0.6491$), or DEFOL (future defoliation intensity levels) ($F_{(2,13)} = 0.13$, $P = 0.8784$), or the TREAT × DEFOL interaction ($F_{(2,13)} = 2.25$, $P = 0.1453$). For this paper, the best model is the model that had the lowest AIC_c with all estimated variable parameters significant. Expanding analysis to include plots on all study areas, the best pre-defoliation mortality model included both DEN ($F_{(1,10)} = 22.03$, $P < 0.0001$) and BA ($F_{(1,10)} = 16.67$, $P < 0.0001$), but not their interaction ($F_{(1,9)} = 0.57$, $P = 0.4677$) or future defoliation intensity levels ($F_{(2,10)} = 1.25$, $P = 0.3268$). The model with both DEN and BA [$\ln(M_{pre}) = -3.6641 + 0.0084*DEN - 0.0899*BA$] indicated that pre-defoliation mortality increased with increasing density while decreasing with increasing basal area. In single factor models, mortality was independent of BA ($F_{(1,11)} = 1.34$, $P = 0.2718$) but not DEN ($F_{(1,11)} = 5.22$, $P = 0.0432$). However, the model with both factors had a lower AIC_c than the model with only DEN, 85.9 and 94.0 respectively.

Not unexpectedly, post-defoliation mortality differed by defoliation severity levels ($F_{(2,9)} = 44.70$, $P < 0.0001$) (Fig. 3). Stands with severe defoliations experienced higher oak mortality (36 ± 4%) than stands with moderate defoliations (7 ± 2%) which in turn had higher mortality than areas with little or no defoliation (1 ± 0.5%). Mortality did not differ by TREAT ($F_{(1,9)} = 0.0001$,

$P = 0.9935$) or DEN ($F_{(1,9)} = 0.44$, $P = 0.5244$). The best model included both defoliation severity ($F_{(2,11)} = 63.36$, $P < 0.0001$) and BA ($F_{(1,11)} = 17.86$, $P = 0.0014$) [$\ln(M_{post}) = -4.6696 + 0.0681*BA + 1.3489*DEFOL_{mod} + 3.7252*DEFOL_{sev}$; where $DEFOL_{mod}=1$ for stands with moderate defoliation and $DEFOL_{sev}=1$ for stands with severe defoliations]. Post-defoliation oak mortality increased with both initial stand oak basal area and with increasing defoliation intensity (Fig. 4).

Individual tree mortality – pre-defoliation

A total of 3095 oaks with diameters of at least 10 cm were included in the study (Table 3). Using contingency table analysis (Zar 2010), pre-defoliation mortality over 12-19 years (not standardized to a 3-year period) of northern red oak (5%) differed from white oak (9%) and black oak (12%) which differed from chestnut oak (17%). However, classification tree analysis using the model building data set indicated only one node with higher mortality at DBH < 21.1 cm with no separation among oak species or by TREAT, GROW, BA, or DEN. Proportional reduction in error was modest (0.1464) with low sensitivity and high specificity (Table 4).

Similarly, logistic regression found pre-defoliation mortality of combined oak species decreased with increasing DBH ($Z = -10.0$, $P < 0.0001$). The initial model for estimating pre-defoliation mortality of combined oak species included all variables, but only TREAT, DBH, and DEN were in models examined with validation data.(Table 5). Comparison of models using validation data indicated that a more parsimonious model with only DBH had a lower RMSE (3.8%) than the complex model (7.4%). Both the model and validation data sets indicated that pre-defoliation mortality could be described by as continuous curvilinear function of decreasing mortality with increased diameter (Fig. 5a). The final model with only DBH was in close agreement with mortality values of validation data (Pearson correlation coefficient [PCC] = 95%).

Individual tree mortality – post-defoliation

A direct comparison among species mortality using contingency tables (Zar 2010) found individual tree post-defoliation mortality of northern red oak (9%) and chestnut oak (14%) differed from black oak (27%) which differed from white oak (34%). Classification tree analysis using the model building data set indicated no separation among oak species and a single node between severely defoliated plots and those plots that had no, little, or moderate defoliation. As noted above, further analyses were then completed using combined oak species Logistic regression of post-defoliation mortality of combined oak species also found individual tree post-defoliation mortality on plots with no or low defoliation differed from plots with severe ($Z = 9.7$, $P < 0.0001$), but not moderate defoliation ($Z = -1.4$, $P = 0.1676$). Because of these findings, defoliation intensity on plots that had no, little, or moderate defoliation were combined for further analyses and were referenced as minor defoliation. Separate analyses were completed for trees on stands following minor defoliation and for trees on stands following severe defoliation. .

Classification tree analysis indicated no nodes for post-defoliation mortality of combined oaks on plots following minor defoliation. In contrast, logistic regression indicated both TREAT and DBH influenced mortality (Table 6). Post-defoliation mortality decreased with increasing diameter and was higher on unmanaged than managed areas following minor defoliation. Comparison of models using validation data found the parsimonious model with only DBH as a factor had a lower RMSE (4.27%) than models with only TREAT and those with both TREAT and DBH (7.69% and 4.32% respectively). Agreement of validation data with estimated model was good (Fig. 5b, PCC = 88%). Although the region experienced a period of drought, a comparison of pre-defoliation models and validation data with post-defoliation for areas with minor defoliation showed minimal differences in mortality between the periods (Fig. 5).

On severely defoliated plots, classification tree analysis of individual tree mortality indicated a single node of decreased mortality at BA < 16.8 m^2/ha with low sensitivity and high specificity (Table 4). Logistic regression likewise found mortality was higher in stands with higher basal area, but additionally included TREAT and DEN (decreased mortality at higher densities). In contrast with areas that experienced minor defoliation, mortality following severe defoliation was higher on managed than unmanaged areas (Table 7). A comparison of models with validation data found the simpler model with only BA and DEN had the lowest RMSE (15.2%) compared with 23.5% for model with only BA and 15.6% for model with all three factors. There is modest confidence in this model as the model had wide confidence intervals (Fig 6), low AUC indicating poor discrimination (Table 7), and PCC = 55%.

DISCUSSION

Our observations indicate that many of the oaks that had survived earlier multiyear defoliation episodes during the 1960s-1980s did not fare well in the recent multiyear defoliations that occurred from 2015-2018. Many factors found predicative for increased mortality risk were similar for both earlier and recent multiyear defoliations including defoliation intensity and oak stand basal area. One constant across all studies including ours is that mortality increases with defoliation severity and duration (Baker 1941, Campbell and Sloan 1977, Gottschalk et al. 1998). Similar to other studies, oak mortality rates slightly increased with a single year of defoliation, but increased greatly with multiple years of defoliation (Fosbroke and Hicks 1989, Morin and Liebhold 2016).

While most studies have reported that post-defoliation mortality differed among species, there is little consistency in which oak species have higher mortality following defoliation. Our observation of higher mortality for black and white oak than for northern red oak is similar to some studies (Campbell and Sloan 1977, Herrick and Gansner 1987), but not others (Stalter and Serrao 1983). A difficulty in comparing among studies is that confounding and sometimes correlated variables of crown class, vigor, tree age, and other factors are often not accounted for in earlier studies. When they are included they can greatly influence patterns among species. To wit, differences in mortality rates among oak species interacted with defoliation intensity, vigor, and crown class in Pennsylvania (Gottschalk et al. 1998).

Our observations of higher mortality in stands with higher oak basal area is not unique. Estimated three-year mortality ranged from 9% in stands with less than twenty percent oak basal area to 35% mortality in stands with over seventy percent black and chestnut oak basal area in Pennsylvania (Gansner et al. 1987). A later Pennsylvania study indicated expected mortality would steadily increase above a threshold of oak constituting sixty percent stand basal area (Fosbroke and Hicks 1989). Defoliation levels increased with increasing basal area of susceptible species in Maryland (Davidson et al. 2001). An outlier, mortality decreased with an increasing proportion of stand basal area in susceptible species in Virginia/Maryland (Eisenbies et al. 2007). We also found that mortality increased in stands with higher oak density, even though the opposite pattern was found for basal area. This suggests that stand structure may play an important role.

In stands that experienced minor defoliation, we noted that mortality rates for individual trees did not differ between the pre-defoliation and post-defoliation periods. For both periods, our analysis indicated that mortality decreased with increasing diameter. Larger trees generally have a smaller ratio of leaf area to sapwood area which ameliorates hydraulic stress. However, this also means that there are fewer leaves producing carbohydrates to produce defensive compounds and support woody stem tissues. Mortality following LDD defoliation was higher for larger, older northern red oaks in New Jersey (Stalter and Serrao 1983). Larger, presumptively older oaks were predicted to have higher mortality than smaller, younger oaks in Pennsylvania (Gottschalk et al. 1998). In contrast, addition of stand age did not improve mortality models that included crown vigor as a parameter (Gansner et al. 1978, Herrick and Gansner 1987). While we did not see higher mortality in larger oaks following severe defoliation, the pre-defoliation pattern of higher mortality in smaller oaks disappeared. Given that pre-defoliation mortality of small trees could be as much as 2-4 times the mortality of larger ones (Figure 5), this may suggest increased defoliation related mortality was higher in larger trees but counteracted by higher mortality from other causes in small trees.

Contrary to our expectations, our metric of individual tree vigor (pre-defoliation diameter growth) was not correlated with post-defoliation mortality. The usefulness of vigor as a predictor of post-defoliation oak mortality has varied among studies. After defoliation in eastern Pennsylvania in the 1970s, mortality increased with the proportion of trees with poor crown vigor (Gansner et al. 1978). Inclusion of other factors did not improve mortality estimates. Crown vigor was also retained in decision tree models of post-defoliation mortality following initial defoliation episodes in central Pennsylvania in the 1980s (Herrick and Gansner 1987, Gottschalk et al. 1998). Following multiyear defoliations in the 1960s, mortality rates decreased with increasing pre-defoliation diameter growth for red oaks, but not white oaks in Connecticut (Ward 2007). However other studies, questioned the usefulness of this approach because they reported pre-defoliation tree diameter growth was not predictive of defoliation levels (Muzika and Liebhold 2000).

Management of forest stands has often been recommended to reduce both the susceptibility of stands to defoliation (e.g. by reducing the proportion of species preferred by LDD) and the vulnerability of trees once defoliation occurs (e.g. by removing less vigorous trees; Gottschalk 1993). We did not examine the effects of management on stand susceptibility; defoliation ranged from severe to none on both unmanaged and managed stands in our study. Evidence is mixed that management can reduce stand susceptibility to defoliation (Muzika and Liebhold 2000). Over 50% defoliation was observed for two consecutive years in some stands in West Virginia that had been recently thinned to reduce stand susceptibility to defoliation (Muzika and Twery 1995). Another West Virginia study, reported that thinning had no predictable impact on LDD densities (Liebhold et al. 1998) or defoliation intensity (Muzika and Liebhold 2000). However, outside of eastern North American deciduous forests, abundance of leaf chewing insects declined with a metric of management intensity in central Europe (Leidinger et al. 2019). Research in conifer stands found that the response to thinning on subsequent defoliation intensity differed among species and site classes in part because of differential production of secondary metabolites that can inhibit herbivory (Bauce and Fuentealba 2013).

Similarly, studies show mixed effects of management on post-defoliation mortality (vulnerability). We observed that mortality following minor defoliation was lower in managed than unmanaged stands; but the converse was observed in stands after severe, multiyear defoliations where mortality was higher in managed stands. Anecdotal reports of Pennsylvania foresters indicated defoliation induced mortality was higher in managed than unmanaged stands, as suggested by our results (Gottschalk 1989). To test these observations, he compared post-defoliation mortality rates in seventeen thinned to three unmanaged stands in central Pennsylvania. He reported that mortality rates did not differ by management history. In contrast, several West Virginia studies suggest management may be beneficial. In one study, total oak basal area loss (harvest plus mortality) in defoliated stands did not differ between thinned and unthinned stands – averaging 74% (Muzika and Twery 1995). By comparison in undefoliated stands, harvesting reduced oak basal area by 33% while oak basal area increased by 3% in unmanaged stands. Thus, while post-defoliation stand structure did not differ between thinned and unthinned stands, the harvests did capture volume otherwise lost to defoliation initiated mortality. Another study reported that basal area loss in unmanaged stands after defoliation (approximately 16 m^2 per ha), was actually greater than basal area decreases from combined harvested and defoliation in managed stands (approximately 12 m^2 per ha, Muzika et al. 1998).

Even if mortality following severe defoliation is higher on managed compared to unmanaged stands, we do not suggest a strategy of delaying planned harvest activity because of the potential of a near-term, future multiyear defoliation episode. Such a strategy would be difficult to implement at the correct time, would reduce income, and may lead to increased levels of hazard trees. First, while dry springs may be linked to non-activation of the *Entomophaga maimaiga* spores that control LDD (Andreadis and Weseloh 1990, Despland 2018), predicting these periods is both chancy and not always linked to LDD outbreaks. This can be seen by examining the drought indices and area defoliated between 1970-1973 (Figs. 1 and 2). It is very difficult to predict multiyear gypsy outbreaks. Second, stumpage paid for live trees is typically higher than for recent mortality and is certainly higher than for trees that have been dead for two or more years. This means that a strategy of delaying harvest could potentially reduce wood quality and income. Lastly, removing trees killed by severe defoliation or secondary organisms can be an expense rather than a profitable or break-even operation in parks or along public right-of-ways (e.g., roads, trails).

We were not able to separate the effects of drought and defoliation on mortality as all sites experienced droughts. Sites varied in defoliation intensity, but no sites had defoliation concurrent with normal precipitation. Our study found that drought by itself was not associated with elevated oak mortality levels as mortality rates were relatively stable on stands that did not have severe defoliations. An earlier Connecticut study that included several of the sites used in the current study, also concluded that repeated defoliation, but not drought, was associated with increased mortality (Stephens and Hill 1971). Drought by itself did not increase mortality, but drought may have exacerbated mortality levels of trees also stressed by repeated defoliations.

It is possible that an extended period of drought could also be an factor for initiating LDD outbreak episodes in addition to collapse of pupae predator populations (Grushecky et al. 1998). The regional absence of multiyear outbreaks in southern New England continued for decades (Morin and Liebhold 2016) until LDD populations surged in 2016 (Despland 2018), a period which coincided with severe late spring regional droughts. It is worth noting that earlier observations linked LDD outbreaks to two or more consecutive years with drought, especially spring droughts (Baker 1941, Bess et al. 1947) and that there were thirty year gaps with little or no statewide defoliation observed in several New England states.

While speculative, we suggest that tree age accounts for some of the differences in the relative importance of various tree and stand characteristics for predicting mortality between previous and more recent multiyear defoliation episodes. With a few exceptions, the oaks we measured were survivors of the multiyear defoliations in the 1960s and later. Hence, they were thirty-five years older and had grown larger since the last major outbreak in 1981. As noted earlier, the mixed oak forests in eastern Connecticut were highly resistant to defoliation when the stands were less than fifty years old in the mid-1940s (Bess et al. 1947). However, many stands in eastern Connecticut were among those most heavily defoliated in the most recent outbreaks (Pasquarella et al. 2018) and experienced heavy mortality. The difference? Trees in these stands included in this study were eighty years older than in the 1940s and were thirty-five years older than when they survived during the last widespread multiyear outbreak. Anecdotally, we observed little or no mortality of oaks in 10 and 40-year-old stands adjacent to mature stands that experienced heavy oak mortality.

Summary

This study found that post-defoliation mortality differed by defoliation severity, differed among species, and often but not consistently, varied with stand oak basal area. Consistent with previous studies, high levels of defoliation across multiple years greatly increased mortality. This study confirmed that mortality patterns are species specific, as northern red oak had lower mortality than white and black oak across all defoliation levels. However, comparison with other studies demonstrates that species susceptibility to LDD mortality can vary across time and space, so managers cannot assume that the species with the highest mortality in previous events will have the highest mortality in future defoliations. Effects of stand oak basal area and density, tree diameter, and management were much less consistent, suggesting the importance of site specific factors. Despite some indication of higher mortality in managed sites, forgoing management to reduce potential mortality is not recommended due to the difficulty in predicting outbreaks, potential loss of income, and the increased risk of hazard trees following severe defoliation in unmanaged stands.

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Table 1. Description of study areas used to examine defoliation mortality in southern New England. Management contrast – study area with both managed and unmanaged plots (yes) or only unmanaged plots (none); crown class – crown classes recorded prior to defoliation episodes (yes) or not recorded (no); Sample area (ha). See text for description of defoliation intensity.

Study Plot name	Management contrast	Crown Class	Defoliation intensity	Sample area	Stand age	Location	Soils[‡]
Blue Ribbon							
Ashford	none	yes	none-low	0.4	138	41.879,-72.199	Woodbr
Hawes	none	yes	severe	0.4	148	41.820,-72.092	Can-Cha
Pikes	none	yes	severe	0.4	128	41.821,-72.079	Woodbr
PinBlu	none	yes	severe	0.2	133	41.788,-72.096	Woodbr
PinYel	none	yes	severe	0.2	133	41.789,-72.098	Woodbr
Connecticut College							
ConCol	none	no	moderate	0.8	89	41.379,-72.115	Hol-Cha
Cutting methods							
Morris	yes	yes	none-low	n/a[*]	120	41.706,-73.169	Hol-Cha
NorMad	yes	yes	severe	n/a[*]	130	41.395,-72.648	Hol-Cha
Maramos crop tree							
BearPole	yes	yes	severe	n/a[†]	105	41.522,-72.586	Hol-Cha
BearSaw	yes	yes	severe	n/a[†]	116	41.524,-72.583	Cha-Cha
ChinaPole	yes	yes	severe	n/a[†]	98	41.522,-72.575	Hol-Cha
RockSaw	yes	yes	severe	n/a[†]	118	41.518,-72.580	Cha-Cha
Mature oak							
Ham	yes	yes	moderate	0.8	108	41.457,-72.936	Yalesv
MDC	yes	yes	none-low	0.8	124	41.815,-72.788	Holy
TuD	yes	yes	none-low	0.8	97	42.001,-72.888	Cha-Cha
TuN	yes	yes	none-low	0.8	139	42.007,-72.875	Cha-Cha
TWC	yes	yes	none-low	0.8	106	41.885,-73.181	Pax-Mon
Win	yes	yes	none-low	0.8	94	41.941,-73.103	Cha-Cha

New Series							
GayCity	none	yes	moderate	0.4	114	41.719,-72.468	Hol-Cha
Natchaug	none	yes	moderate	0.2	124	41.85,-72.0564	Woodbr
Old-Series							
Turkey	none	yes	severe	2.2	116	41.431,-72.538	Cha-Cha
Cox	none	yes	moderate	2.8	116	41.610,-72.559	Can-Cha
Reeve	none	yes	moderate	2.2	116	41.624,-72.572	Can-Cha
Cabin	none	yes	moderate	2.4	116	41.617,-72.551	Woodbr
TurBurn	none	yes	severe	1.5	87	41.430,-72.532	Pax-Mon
Providence Water							
PW00	yes	no	severe	0.3	n/a	41.785,-71.632	Can-Cha
PW01	yes	no	severe	0.3	n/a	41.775,-71.663	Can-Cha
PW02	yes	no	severe	1.5	n/a	41.785,-71.626	Can-Cha
PW03	yes	no	severe	0.5	n/a	41.815,-71.647	Can-Cha
Total				21.2			

* sample completed with prism plots;

† plot less study areas;

‡ Soil descriptions: Can-Cha (Canton-Charlton, Typic Dystrudepts); Cha-Cha (Charlton-Chatfield, Typic Dystrudepts); Hol-Cha (Hollis-Chatfield, Lithic Dystrudepts); Holy (Holyoke, Lithic Dystrudepts); Pax-Mon (Paxton-Montauk, Oxyaquic Dystrudepts); Woodbr (Woodbridge, Aquic Dystrudepts); Yalesv (Yalesville, Typic Dystrudepts).

Table 2. Sample size, density (n/ha), and basal area (m^2/ha) of oaks on study areas used to examine defoliation mortality in southern New England. Mortality estimates (%) are on a three-year basis.

Study Plot name	Oak sample size	Initial oak density	Initial oak basal area	Pre-defoliation mortality (%)	Post-defoliation mortality (%)
Blue Ribbon					
Ashford	28	69.2	8.6	0.7%	0.0%
Hawes	22	54.4	6.6	0.9%	33.3%
Pikes	34	84.0	12.3	1.1%	59.4%
PinBlu	43	212.5	17.7	4.3%	79.4%
PinYel	36	177.9	16.9	1.6%	78.8%
Connecticut College					
ConCol	137	171.0	11.8	3.3%	10.4%
Cutting methods*					
Morris	218	n/a[1]	n/a[1]	0.7%	2.4%
NorMad	150	n/a[1]	n/a[1]	1.8%	59.9%
Maramos crop tree†					
BearPole	60	n/a[2]	n/a[2]	0.0%	23.3%
BearSaw	58	n/a[2]	n/a[2]	0.0%	29.3%
ChinaPole	59	n/a[2]	n/a[2]	1.8%	31.5%
RockSaw	59	n/a[2]	n/a[2]	0.0%	35.6%
Mature oak					
Ham	144	102.7	14.3	1.1%	3.6%
MDC	134	85.3	13.2	1.7%	1.6%
TuD	140	101.3	15.1	0.9%	0.7%
TuN	119	69.3	15.3	2.2%	0.9%
TWC	111	58.7	11.0	0.5%	0.0%
Win	116	88.0	15.1	0.9%	0.0%
Old-Series					
Turkey	22	10.2	0.8	2.3%	20.5%

Cox	282	99.5	14.6	0.4%	11.4%
Reeve	219	98.4	14.3	0.4%	8.5%
Cabin	156	64.2	9.7	0.1%	2.4%
TurBurn	189	128.0	8.9	3.0%	15.8%
New Series					
GayCity	25	69.4	5.6	0.8%	0.0%
Natchaug	24	100.0	13.6	2.5%	9.5%
Providence Water					
PW00	18	55.6	6.1	2.2%	24.5%
PW01	90	278.0	16.0	3.8%	43.0%
PW02	315	216.2	12.7	5.2%	22.0%
PW03	87	179.1	10.0	6.5%	21.6%
Mean		111.9	11.7	1.7%	21.7%

* sample completed with prism plots;

† plot less study areas

Table 3. Initial sample size of oaks by species and defoliation intensity used to examine defoliation mortality in southern New England.

	Defoliation intensity			
Species	None	Moderate	Severe	Total
Northern red oak	665	511	402	1578
Black oak	102	374	455	931
White oak	40	96	300	436
Chestnut oak	31	34	85	150
All oaks	838	1015	1242	3095

Table 4. Classification tree statistics for model building and validation data sets of pre- and post-defoliation mortality in southern New England. PPV – positive predictive value, NPV – negative predictive value, PRE – proportional reduction in error

Period/data subset	Sensitivity	Specificity	PPV	NPV	PRE
Pre-defoliation					
Model building	0.5809	0.8913	0.3347	0.9576	0.1464
Validation	0.5081	0.8921	0.2958	0.9531	
Post-defoliation - minor					
Model building	no variable reduced PRE by at least 0.05				
Validation					
Post-defoliation - severe					
Model building	0.2632	0.9113	0.6716	0.6420	0.0578
Validation	0.2848	0.9098	0.6618	0.6725	

Table 5 – Pre-defoliation logistic mortality models for upland oaks (n=1581, 8.6% mortality)* with estimated parameters and statistics developed with model building data set. A negative b_i parameter indicates decreasing mortality with factor; b_o is the intercept and b_x are factors not included in final model. Factors: TREAT (managed vs. unmanaged), DBH (initial stem diameter), GROW (pre-defoliation diameter growth), DEN (pre-defoliation oak stand density, and BA (pre-defoliation oak stand basal area). AUC is the area under the ROC.

Species	Estimate	SE	Z	P	AUC
Full model					
b_0 – Constant	1.1202	0.3890	2.88	0.0040	0.8173
b_1 – TREAT	-0.9919	0.2266	-4.38	<0.0001	
b_2 – DBH	-0.0794	0.0107	-7.44	<0.0001	
b_x – DEN	0.0040	0.0020	2.00	0.0455	
b_x – BA	-0.0488	0.0338	-1.44	0.1486	
b_x – GROW	-0.6100	0.5525	-1.10	0.2696	
Final model					
b_0 – Constant	1.3184	0.2922	4.51	<0.0001	0.8118
b_1 – TREAT	-0.9555	0.1976	-4.83	<0.0001	
b_2 – DBH	-0.0979	0.0090	-10.93	<0.0001	

* Sample size only includes trees in model building data set . Mortality over a 12-19 year period depending on plot.

Table 6 – Post-defoliation logistic mortality models for upland oaks (n=914, 5.4% mortality)* on plots with no to moderate defoliation with estimated parameters and statistics developed with model building data set. A negative b_i parameter indicates decreasing mortality with factor; b_o is the intercept and b_x are factors not included in model. Factors: TREAT (managed vs. unmanaged), DBH (initial stem diameter), GROW (pre-defoliation diameter growth), DEN (pre-defoliation oak stand density, and BA (pre-defoliation oak stand basal area). AUC is the area under the ROC.

Species	Estimate	SE	Z	P	AUC
Full model					
b_0 – Constant	-3.2815	1.2364	-2.65	0.0080	0.7853
b_1 – DBH	-0.0669	0.0159	-4.22	<0.0001	
b_2 – TREAT	3.1410	1.0622	2.96	0.0031	
b_x – DEN	-0.0093	0.0054	-1.72	0.0849	
b_x – GROW	0.0731	0.0556	1.31	0.1888	
b_x – BA	0.6103	0.8682	0.70	0.4821	
Final model					
b_0 – Constant	-3.3362	1.1234	-2.97	0.0030	0.7812
b_1 – DBH	-0.0524	0.0127	-4.13	<0.0001	
b_2 – TREAT	2.8521	1.0162	2.81	0.0050	

* Sample size only includes trees in model building data set. Mortality rates on a two or three year basis depending on plot.

Table 7 – Post-defoliation logistic mortality models for upland oaks (n=531, 38.6% mortality)* on severely defoliated plots with estimated parameters and statistics developed with model building data set. A negative b_i parameter indicates decreasing mortality with factor; b_o is the intercept and b_x are factors not included in model. Factors: TREAT (managed vs. unmanaged), DBH (initial stem diameter), GROW (pre-defoliation diameter growth), DEN (pre-defoliation oak stand density, and BA (pre-defoliation oak stand basal area). AUC is the area under the ROC.

Species	Estimate	SE	Z	P	AUC
Full model					
b_0 – Constant	-0.7090	0.4204	-1.69	0.0917	0.6799
b_1 – TREAT	-0.9732	0.2736	-3.56	0.0004	
b_2 – DEN	-0.0096	0.0030	-3.21	0.0013	
b_3 – BA	0.2268	0.0540	4.20	0.0000	
b_x – GROW	0.7960	0.6591	1.21	0.2272	
b_x – DBH	-0.0048	0.0103	-0.46	0.6426	
Final model					
b_0 – Constant	-0.6871	0.2351	-2.92	0.0035	0.6850
b_1 – TREAT	-0.8867	0.2559	-3.46	0.0005	
b_2 – DEN	-0.0117	0.0026	-4.51	< 0.0001	
b_3 – BA	0.2619	0.0459	5.71	< 0.0001	

* Sample size only includes trees in model building data set. Mortality rates on a two or three year basis depending on plot..

Figure Captions

Figure 1. Estimated area (ha) defoliated by LDD in Connecticut and Rhode Island (Source: USDA Forest Service 2020).

Figure 2. Palmer drought severity index during the past 100 years in Connecticut (source: NOAA 2020).

Figure 3 – Pre- and post-defoliation stand level mortality of combined oaks by defoliation severity.

Figure 4. Stand level post-defoliation mortality by defoliation severity and oak stand basal area.

Figure 5. Comparison of (a) pre- and (b) post-defoliation models and validation data for stands with no to moderate defoliation in southern New England. Model means and CI based on logistic regression parameters estimates found in Tables 5 and 6.

Figure 6. Post-defoliation mortality model estimates compared with validation data for stands following severe defoliation in southern New England. Graphs based on logistic regression parameters estimates found in Table 7.

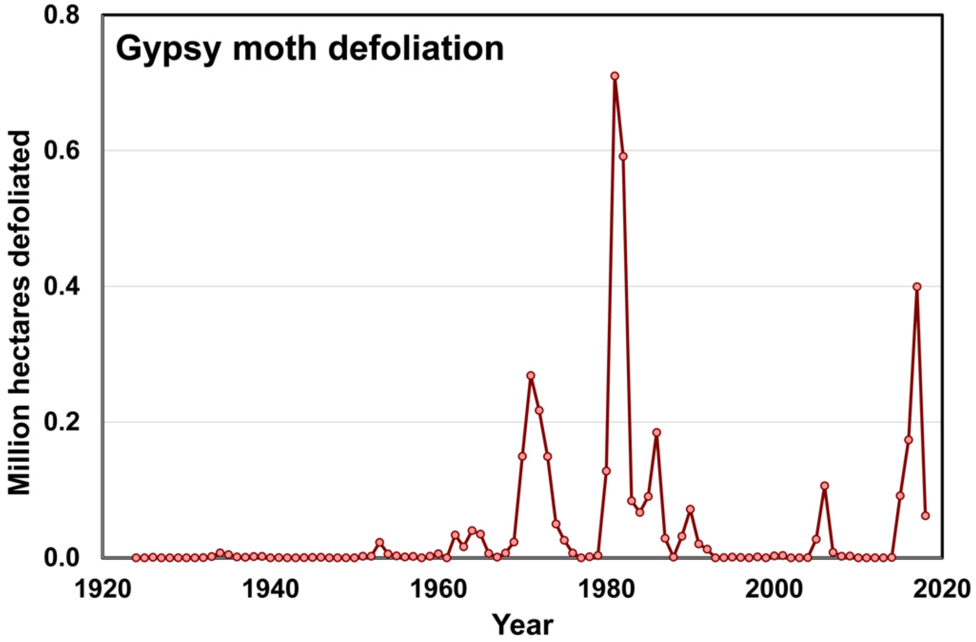

Figure 1. Estimated area (ha) defoliated by gypsy moth in Connecticut and Rhode Island (Source: USDA Forest Service 2020).

88x60mm (300 x 300 DPI)

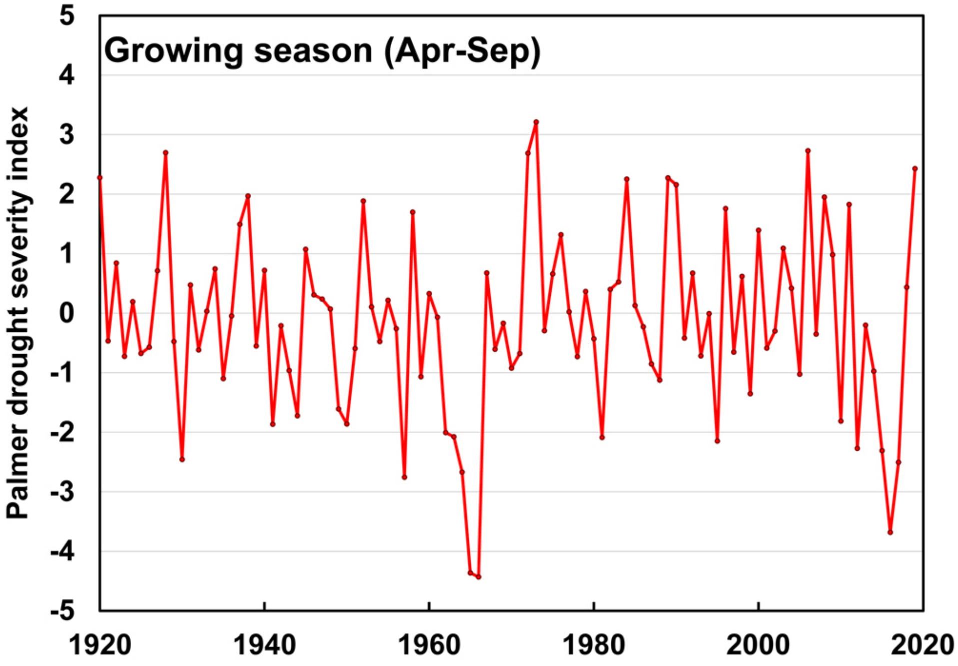

Figure 2. Palmer drought severity index during the past 100 years in Connecticut (source: NOAA 2020)

88x63mm (300 x 300 DPI)

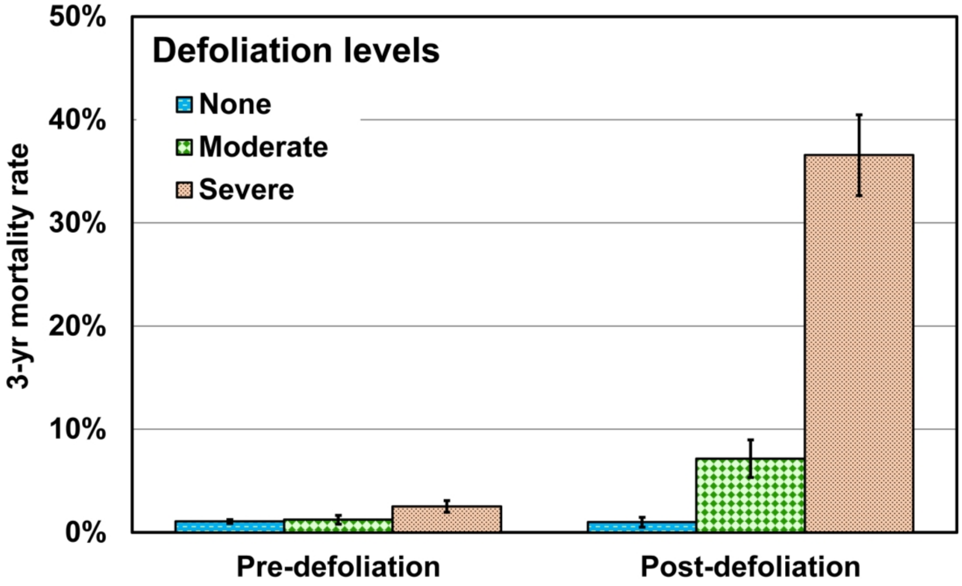

Figure 3 – Pre- and post-defoliation stand level mortality of combined oaks by defoliation severity.

165x100mm (300 x 300 DPI)

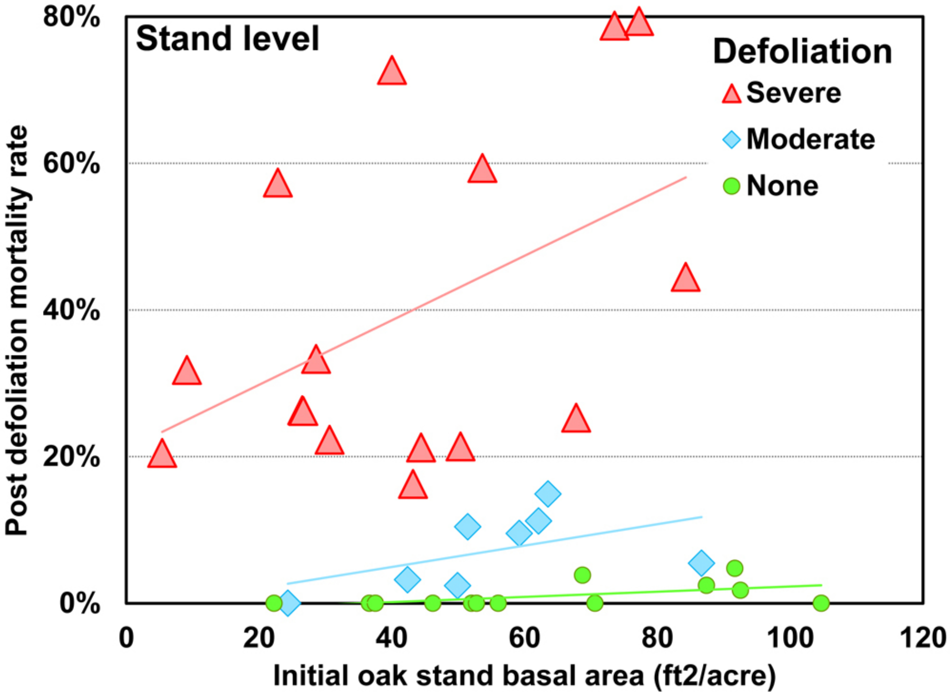

Figure 4. Stand level post-defoliation mortality by defoliation severity and oak stand basal area.

88x64mm (300 x 300 DPI)

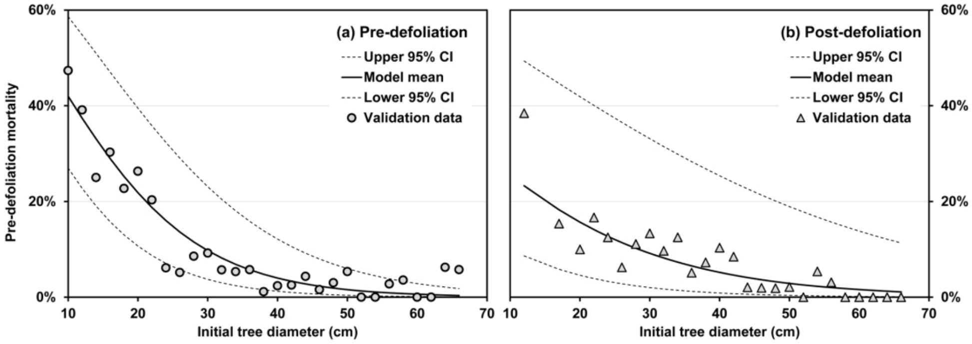

Figure 5. Comparison of (a) pre- and (b) post-defoliation models and validation data for stands with no to moderate defoliation in southern New England. Model means and CI based on logistic regression parameters estimates found in Tables 5 and 6.

182x63mm (300 x 300 DPI)

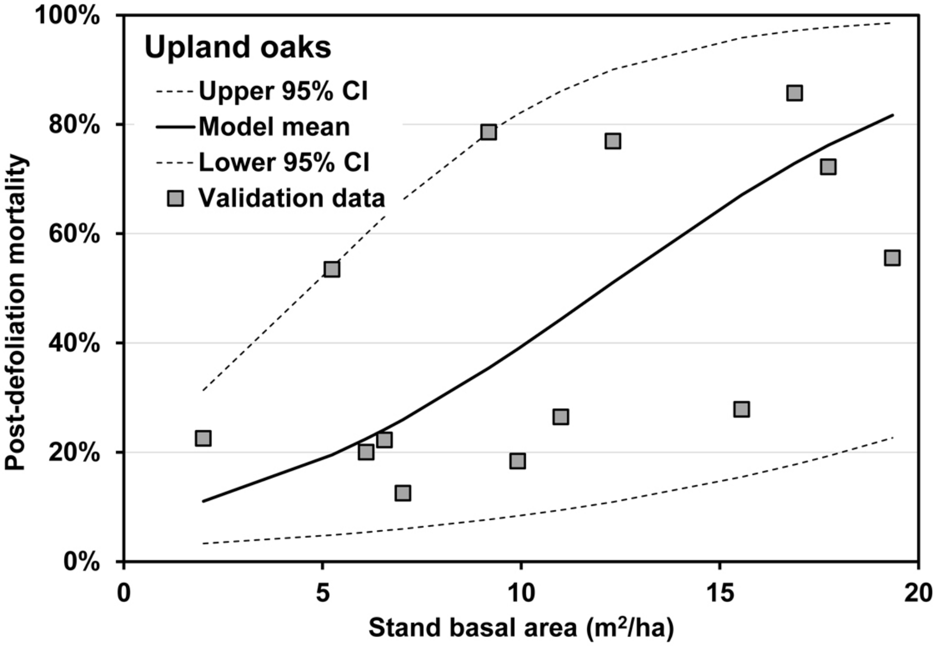

Figure 6. Post-defoliation mortality model estimates compared with validation data for stands following severe defoliation in southern New England. Graphs based on logistic regression parameters estimates found in Table 7.

101x69mm (300 x 300 DPI)

Appendix

While some studies measured trees with diameters less than 10 cm, only trees with diameters of at least 10 cm were included in this analysis.

Blue Ribbon (Ashford, Hawes, Pikes, PinBlu, PinYel). Collaborative study with CT DEEP. Plots were established in 1930s and relocated in late 1990s. There has been no management except limited firewood salvage in early 1980s. Plot sizes were 0.4 ha, except PinBlu and PinYel which were 0.2 ha. Diameters and crown classes were measured in 2000. Gypsy moth assessments completed in October 2018.

Connecticut College (Bolles) Study established and maintained by Connecticut College. Diameters have been measured every ten years since 1952 with pre-defoliation measurements in 2002 and 2012. Stems mapped one four 6 m wide transects with a total length of 1342 m (0.8 ha). There has been no management. Gypsy moth assessments completed in July 2019. Further details can be found in Small et al. (2005).

Cutting methods (WMF, RWA) Collaborative study with SCC Regional Water Authority and White Memorial Foundation. Plots were established in earlier 1980s with a second cutting cycle in 2001. Pre-defoliations diameter and crown class measurements were completed in 2004 using permanently numbered trees on 10-factor (Imperial) prism plots. Gypsy moth assessments completed in October 2018. The third replicate of study not included because of extensive windstorm damage in May 2018. Further details can be found in Ward et al. (2005).

Maramos crop tree (BearPole, BearSaw, ChinaPole, RockSaw) Collaborative study with Eversource Energy and Ferrucci and Walicki, LLC. Trees in study areas established in 1994 were randomly assigned to complete release completed in 1995 or no release. Diameters were measured annually through 2012, crown classes in 1994 and 2011. Gypsy moth assessments completed in October 2018. Further details can be found in Ward (2008).

Mature Oak (Ham, MDC, TuD, TuN, TWC, Win) Collaborative study with CT DEEP, Metropolitan District Commission, and Torrington Water Company. Diameters and crown classes have been measured annually since 2004. Each study area had a 50x50 m unmanaged control and two 50x50 m plots where stocking had been reduced to 60%. Harvests were completed between 2003-2006. Gypsy moth assessments completed in autumn 2018. Further details can be found in Ward and Wikle (2019).

New-Series (Gay City, Natchaug) Collaborative study with CT DEEP. Diameters and crown classes have been measured every ten years since 1960 with pre-defoliation measurements in 2000 and 2010. Across all plots trees mapped on thirty-seven 10 m wide transects with a total length of 1,340 m (1.3 ha). There has been no management. Gypsy moth assessments completed in October 2018. Further details can be found in Ward (2005).

Old-Series (Turkey, Cox, Reeve, Cabin) Collaborative study with CT DEEP. Diameters and crown classes have been measured every ten years since 1927 with pre-defoliation measurements in 1997 and 2007. Across all plots trees mapped on thirty-six 10 m wide transects with a total length of 11,064 m (11.1 ha). There has been no management. Gypsy moth assessments completed in October 2019. Further details can be found in Ward et al. (2013).

Providence Water (PW00, PW01, PW02, PW03) Study established and maintained by Providence Water. A series of 0.08 ha plots with permanently identified trees. Diameters were measured at five year intervals. Because sample sizes of individual plots were small, all plots within a given sample year were pooled; i.e., PW00 contains all plots measured in 2000, 2005, 2010, and 2015. Gypsy moth assessments completed in August 2019. Some plots in each pool were thinned and others unmanaged.

Appendix References

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