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THE INDIVIDUAL TREE AND FOREST STAND LEVEL IMPACTS OF WINTER MOTH DEFOLIATION IN EASTERN MASSACHUSETTS, USA

BY

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*To be co-authored with Thomas D. Lee[1], Mark J. Ducey[1], Joseph S. Elkinton[2], George H. Boettner[2], and Kevin J. Dodds[3] when submitted for publication.

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ABSTRACT

THE INDIVIDUAL TREE AND FOREST STAND LEVEL IMPACTS OF WINTER MOTH DEFOLIATION IN EASTERN MASSACHUSETTS, USA

by

Michael J. Simmons
University of New Hampshire, September, 2013

Winter moth is a non-native invasive defoliator in New England. This thesis related host tree radial growth of individual trees in eastern Massachusetts to winter moth defoliation intensity using tree core analysis. Further, tree core analysis was used to identify winter moth defoliation events in several forest stands in eastern Massachusetts and these events were used to relate winter moth to stand level tree mortality and understory woody plant density. *Quercus* radial growth from 2005-2010 was negatively related to winter moth defoliation. In addition, *Quercus* mortality in mixed – *Quercus* and *Quercus* - *P. strobus* forests in eastern Massachusetts was influenced by site productivity and winter moth defoliation, with mortality negatively associated with site index and positively associated with number of winter moth defoliation events. Understory woody plant density was positively associated with number of winter moth defoliation events.

CHAPTER I

INTRODUCTION

Winter moth, *Operophtera brumata* L. (Lepidoptera: Geometridae) is a polyphagous defoliator that acts as an eruptive species in its native Europe, with outbreaks occurring on an approximate 10 year cycle (Tenow et al. 2007). Invasions of winter moth occurred in Nova Scotia in the 1930s and in the Pacific Northwest in the 1950s (Roland 1988). Winter moth has recently invaded forests of New England. Widespread defoliation has been reported in eastern Massachusetts since the early 1990s and was originally attributed to the native fall cankerworm, *Alsophila pometaria* Harris (Lepidoptera: Geometridae). However, after defoliation did not decline after a few years (as was expected with fall cankerworm), larvae of the geometrid defoliator were examined and, in 2003, were identified as winter moth (Elkinton et al. 2010).

The effects of insect defoliation are well understood and have received great attention (Kulman 1971). Insect defoliation can lead to a reduction in radial growth and an increase in crown dieback and tree mortality (Kulman 1971), subsequently altering stand dynamics through canopy disturbance (Reinikainen et al. 2012). Canopy disturbance is an important factor of forest stand dynamics (Oliver and Larson 1996). In New England, both large and small-scale canopy disturbances influence species composition and structure (Oliver and Stephens 1977; McClure and Lee 1993). Canopy gaps created by dead trees can, through increased light and soil resources, increase understory plant establishment (McClure et al. 1993) and growth (McClure et al. 2000;

Runkle and Yetter 1987) and can increase crown expansion of bordering canopy trees (Runkle and Yetter 1987).

In its native and exotic ranges, winter moth has contributed to radial growth decline and mortality of host trees. As part of their seminal work on winter moth population ecology at Wytham Woods, Berkshire, England, Varley and Gradwell (1960) noted a reduction in the latewood growth of *Quercus robur* defoliated by winter moth and *Tortrix viridana*. In eastern Fennoscandia, Tikkanen and Roininen (2001) found a reduction in radial growth of *Prunus padus* L., *Sorbus aucuparia* L., and *Populus tremula* L. defoliated by winter moth. In Nova Scotia, winter moth defoliation contributed to radial growth decline and mortality of *Quercus rubra* (Cuming 1961; Embree 1967).

Although winter moth defoliation has been studied in its native and exotic ranges, to date, no studies have evaluated the individual tree and forest stand level impacts of winter moth defoliation in the recently invaded forests of New England. This thesis addresses the individual tree and forest stand level impacts of winter moth defoliation in eastern Massachusetts. This research was prompted by growing concern about winter moth defoliation in the forests of northeastern United States from forest health offices in New England states and the US Forest Service State and Private Forestry Forest Health Protection group in Durham, New Hampshire. The two chapters of this thesis are written as discreet manuscripts to be submitted to peer-reviewed journals. Chapter one relates percentages of winter moth defoliation, estimated by a previous University of Massachusetts-Amherst study, to the radial growth of individual *Quercus* spp. and *Acer* spp. trees. Chapter two characterizes the tree species composition and structure of forests of eastern Massachusetts invaded by winter moth and relates stand level *Quercus* spp. mortality estimates to winter moth defoliation and site characteristics.

Objectives

1) *Dendroecology*:

Use tree core analysis to determine the relationship between winter moth defoliation and host tree radial growth.

2a) *Winter Moth Stand Surveys*:

Develop a stand level description of forests in eastern Massachusetts invaded by winter moth.

2b) *Dendrochronology*:

Use tree core analysis to estimate duration of winter moth activity in forests of eastern Massachusetts and relate to mortality estimates and understory woody plant density.

Hypotheses

1) Host tree radial growth rate is negatively related to winter moth defoliation.

2) Stands with winter moth defoliation will demonstrate higher levels of tree mortality and understory plant density as duration (# of years) of winter moth activity increases.

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CHAPTER II

EFFECTS OF INVASIVE WINTER MOTH DEFOLIATION ON TREE RADIAL GROWTH IN EASTERN MASSACHUSETTS, USA

Abstract

Winter moth (*Operophtera brumata* L.) has been defoliating hardwood trees in eastern Massachusetts since the late 1990s. Native to Europe, winter moth has also been detected in Rhode Island, Connecticut, eastern Long Island (NY), New Hampshire, and Maine. Individual tree impacts of winter moth defoliation in New England are currently unknown. Using dendroecological techniques, this study related radial growth of individual host (*Quercus* spp. and *Acer* spp.) trees to defoliation estimates collected from a separate study. Winter moth defoliation was associated with up to a 68% reduction in annual radial growth of *Quercus rubra* L. trees. Latewood production was reduced by up to 93% in the same year as defoliation, while earlywood production was reduced by up to 79% in the following year. Winter moth defoliation was not a strong predictor of radial growth in *Acer* species. Radial growth of non-host *Pinus strobus* L. did not show an association with winter moth defoliation of *Quercus* species. Knowledge of these impacts is a critical first step when gauging the potential ecosystem-wide effects of novel invasions of winter moth.

Introduction

Winter moth, *Operophtera brumata* L. (Lepidoptera: Geometridae), has been responsible for widespread defoliation of trees in Massachusetts for over a decade. Native to Europe, winter moth was identified in southeastern Massachusetts in the late 1990s and has since been detected throughout much of eastern Massachusetts and portions of Rhode Island, Connecticut, eastern Long Island (NY), New Hampshire, and Maine (Elkinton et al. 2010). The distribution of winter moth in Massachusetts is expanding (Elkinton et al. 2010) and defoliation damage has reached historic levels (36,000 ha defoliated in 2011; USDA and MA DCR 2012). In portions of its range in New England, winter moth may dominate the spring defoliator guild that includes fall cankerworm (*Alsophila pometaria* Harr), Bruce spanworm, (*O. bruceata* Hulst), forest tent caterpillar (*Malacosoma disstria* Hübner), and European gypsy moth (*Lymantria dispar* L.).

Winter moth is an important and well-studied defoliator in European forests (e.g. Varley and Gradwell 1960; Feeny 1970; Tikkanen and Roininen 2001). While recently discovered in Massachusetts, winter moth has a history of invasion in North America with introductions in Nova Scotia in the early 1930s (Embree 1965) and the Pacific Northwest in the 1950s (Gillespie et al. 1978; Roland 1988). Winter moth feeds on a variety of hardwood trees and shrubs in its native and exotic ranges and can be a serious pest of orchards, landscape trees and deciduous forests (Wylie 1960; Embree 1965; Embree 1991). In Nova Scotia, winter moth defoliates *Malus* spp., *Quercus rubra*, *Ulmus americana* L., *Acer rubrum* L., *Tilia americana* L., and *Ostrya virginiana* (Mill.) K. Koch as well as other deciduous tree species (Cuming 1961). The species composition and climate of the deciduous forests of eastern North America offer ideal habitat for winter moth (MacPhee 1967; Elkinton et al. 2010). In addition, the native range of winter moth may be expanding due to global climate change (Jepsen et al. 2008).

Winter moth is an early-season defoliator that feeds in the expanding buds and leaves of its hardwood host (Feeny 1970). The life history of winter moth in New England is similar to that in Nova Scotia and Europe. Briefly, winter moth is a univoltine species that overwinters as an egg; larval eclosion typically occurs in April and larvae feed in the expanding buds and later on the foliage for approximately six weeks, with much of the damage often occurring inside the buds prior to leaf expansion. Pupation occurs in the soil beginning in mid- to late May. Adults emerge from the soil in late fall to early winter, when, upon mating, the flightless female lays eggs in bark crevices and branches of selected host trees (Cuming 1961; Varley et al. 1973). Host preference and the level of defoliation associated with winter moth larval feeding is largely determined by the degree of synchrony between budburst and larval eclosion (Feeny 1970; Tikkanen and Lyytikäinen-Saarenmaa 2002).

The population dynamics of winter moth have received great attention (e.g. Embree 1965; Varley et al. 1973; Holliday 1977). In its native range, winter moth occurs as an outbreak species responsible for elevated levels of defoliation on a cyclic basis (Varley et al. 1973 and Wesolowski and Rowinski 2006). The extent of damage associated with winter moth defoliation has also been reported. In Nova Scotia *Quercus rubra*, winter moth defoliation reduced radial growth and basal area (Embree 1967), and repeated defoliation caused decline and mortality (Cuming 1961). In addition, Varley and Gradwell (1960) and Tikkanen and Roininen (2001) found radial growth reductions in host trees defoliated by winter moth in European forests. Little is known of the individual tree impacts of winter moth defoliation in New England. Of interest here is the effect of winter moth defoliation on radial stem growth of host trees.

Dendroecology, the analysis of annual wood rings, is an effective tool used in the study of biological invasions (Burnham and Lee 2010; Dodds and Orwig 2011). Moreover, dendroecological techniques have been used to elucidate the effects of insect defoliation on tree radial growth. Several studies have shown a negative relationship between insect defoliation and radial growth of both hardwood and softwood host trees (Kulman 1971). Radial growth can be used as a predictor of tree mortality (Monserud 1976; Wyckoff and Clark 2000). Thus, measuring the effect of defoliation on radial growth of host trees is a logical step when gauging the potential ecosystem-wide impacts of novel invasions of forest defoliators.

Understanding the influence of winter moth defoliation intensity and duration on tree growth will provide important information on the threat of winter moth invasions in North American and European hardwood forests, while also providing guidance to pest management strategies. The objective of this study was to estimate the impact of winter moth defoliation intensity on the radial growth of defoliated host trees using analysis of tree cores. To meet this objective I took advantage of defoliation data collected from a previous study. Beginning in 2004 (Whited 2007), individual trees were selected to document the population ecology of winter moth throughout its burgeoning outbreak in Massachusetts. Among the data collected were estimates of defoliation (JS Elkinton unpublished data) attributable to winter moth and the availability of these data allowed the present study to proceed. In 2011, tree cores were extracted from the individual trees from which defoliation estimates were collected and radial growth patterns of these cores were related to the estimates of winter moth defoliation.

Methods

Winter Moth Defoliation Sampling

Annual levels of winter moth defoliation were quantified (percent leaf area removed by larval feeding) on selected *Quercus rubra*, *Quercus velutina* Lam., *Acer rubrum*, and *Acer saccharum* Marsh. trees from 2004 – 2010 at seven long-term winter moth study sites that spanned the area infested by winter moth in eastern Massachusetts (Table 1). The locations of the trees used for this study varied from private house lots with individual open-grown trees, to trees near the edge of forested tracts. Sites were selected by University of Massachusetts – Amherst (UMass) researchers in 2004, following the 2003 confirmation of winter moth in Massachusetts. Study sites were selected so as to 1) be spread out across the area infested by winter moth; 2) have *Acer rubrum*, *Q. rubra* or *Q. velutina* were present and, 3) have no prospect of pesticide application to control winter moth or any other defoliator. To my knowledge, trees were neither watered nor fertilized during the sample period. Trees were selected based on ease of access to crowns to facilitate successful winter moth life stage (including egg and larval counts) and defoliation sampling (access for pole pruners). Although tree sampling began in 2004, more trees (at other sites) were added as winter moth spread into new areas.

Each year in late May or early June when winter moth feeding had finished and the larvae had pupated, pole pruners were used to cut leaf clusters from throughout the canopy of each sample tree. An effort was made to sample leaves throughout the canopy to capture the overall level of defoliation. Thirty leaves were selected from the leaf clusters and these were dried and pressed for later analysis. Percent defoliation was estimated by visually rating each leaf on a 10 point scale (0-10%, 11-20%.... 91-100%) and averages were computed for the 30 leaves from each tree. Estimates of leaf re-flushing were not included in the study. While other defoliators, including gypsy moth and forest tent caterpillar, were present in the region during the early years (2004-6) of the population ecology study, these defoliators were never abundant on the sample trees and winter moth was invariably the most abundant defoliator during this time period.

Increment Core Collection

There were three categories of trees selected for increment core analysis, 1) defoliation trees, 2) cross-dating trees and, 3) control trees. Defoliation trees were the *same trees* on which defoliation levels were estimated during the UMass winter moth population ecology study (trees cored = 14). Two increment cores, separated by at least 60°, were extracted from each sample tree at breast height (1.4 m) using increment borers. Location of core extraction was based on tree bole orientation and growth form. In addition, to assist in cross-dating, each study tree was paired with a nearby tree of the same species from which two cores were also extracted. These 'cross-dating trees' (trees cored = 29) were selected in order to have a sufficient number of trees for legitimate cross-dating of radial growth trends. I used a control species to reinforce any radial growth trends demonstrated by a host species, as the lack of a response of a non-host species would indicate that winter moth defoliation was not correlated with any extraordinary environmental variables. Thus, two cores were also taken from two non-host *Pinus strobus* trees (herein referred to as *Pinus*) at each site to serve as controls (trees cored = 12). Cores were labeled in the field and returned to the lab for preparation and analysis. In total, 55 trees (including defoliation trees, cross-dating trees and control trees) were cored from the seven study sites.

Core Preparation and Analysis

Increment cores ($n = 110$; two cores per tree from 55 trees from seven sites) were stored in paper straws and allowed to dry. Cores were then glued to wooden mounts and sanded with progressively finer sandpaper, concluding with a 600-grit. Cores were aged using a dissecting microscope. A Velmex measurement system (Velmex, East Bloomfield, New York), in combination with Measure J2X software (VoorTech Consulting) was used to measure annual growth ring widths to the nearest 0.001 mm. Once measured, cores were visually cross-dated based on event years (i.e., years having low growth due to known drought, insect defoliation, etc.; Yamaguchi 1991; Tardif and Conciatori 2006) using scatterplots created in MS Excel. The program COFECHA (Holmes 1983) was used to verify cross-dating and to assess measurement error.

Once the entire collection of cores was cross-dated, the *Q. rubra* ($n = 10$ cores), *Q. velutina* ($n = 6$ cores), *A. rubrum* ($n = 10$ cores) and *A. saccharum* ($n = 2$ cores) cores from the defoliation trees (trees with quantified defoliation percentages) were used to evaluate defoliation impacts, as were the *Pinus* control cores ($n = 24$ cores). *Quercus rubra* and *Q. velutina* belong to the red oak group (*Erythrobalanus*) and were thus combined for analysis and are herein referred to as *Quercus*. *Acer saccharum* was combined with *A. rubrum* for analysis, and are herein referred to as *Acer*. In order to remove age-related growth trends, the raw ring width data of the study trees were detrended and converted to a dimensionless ring-width index (RWI) following procedures outlined by Bunn (2008). Using the dplR computer package (Bunn 2008) within the R statistical program (R Development Core Team 2009), a modified negative exponential curve was fit to the raw ring width data for each core; subsequently, these data were detrended within dplR by dividing the annual raw ring widths by the predicted values estimated by the fitted modified negative exponential curve. The detrended data for the two cores per tree were averaged and provided one average RWI per study tree. Therefore, a total of eight *Quercus* and six *Acer* trees were used to analyze defoliation impacts and 12 *Pinus* trees served as controls.

In addition to total annual ring widths, earlywood increment was measured for the *Quercus* study trees in years of known defoliation levels. *Quercus* are ring-porous tree species; thus, earlywood and latewood were identified based on changes in vessel size and wood color (Muzika and Liebhold 1999). Proportions of each ring that were earlywood and latewood were calculated. Detrended earlywood and latewood ring width indices (RWI) were calculated by multiplying the proportions by the total RWI.

Statistical Analysis

Statistical analyses were performed using the JMP 9.0 software (SAS, Cary, NC). Using simple linear regression, the ring width index (RWI) of each tree species group was regressed on tree age to evaluate the effectiveness of the detrending technique; the correlation between the two variables was assessed by the adjusted r^2 (r^2_{adj}) and *P*-values. This revealed no relationship between tree age and RWI, thereby supporting the detrending technique.

Multicollinearity of regressors was tested using variance inflation factors (VIF). Studentized Residuals were calculated to check for the presence of outliers and to assess the normality of the response variables. In addition, Cook's D values were calculated to test for influential observations. Subsequently, *Acer* RWI and *Pinus* RWI were normalized using a $10^* \log_{10}$ transformation. In addition, the proportions of *Quercus* earlywood and latewood were normalized using the arcsine square root transformation. An influential observation was noted in the *Acer* RWI data; this point was checked and determined to be a valid observation. Statistical analyses performed with, and without, the influential observation revealed no change in the results. Thus, the observation in question was retained.

Multiple regression was used to determine which variables had the greatest effect on ring width index (RWI) for *Quercus* and *Acer*. I hypothesized that winter moth defoliation in the current year, the previous year, and the combination of the two years would negatively influence host tree radial growth. My goal was to estimate the strength of these potential relationships. Thus, model selection for *Quercus* and *Acer* RWI was performed using the corrected Akaike Information Criterion (AIC*c*) value (Burnham and Anderson 2002). As such, results will be presented and discussed in Information-Theoretic terms (i.e. AICc simple differences [ΔAIC*c*], Akaike weights [*w*], strength of support for models) as opposed to Frequentist statistical terms (i.e. *P*-values, statistical significance) (Anderson et al. 2001). The model with the lowest AIC*c* value was considered the "best" model in the set of models run for each response variable. However, models with ΔAIC*c* values less than or equal to two were considered competing models and were retained for discussion (Burnham and Anderson 2002).

The variables *site* and *year* were considered nominal random variables and were entered into candidate models as covariates to account for random variation due to site characteristics (*site*) and climate (*year*). *Percent current year winter moth defoliation* was treated as a fixed effect and was defined as the percentage of leaf surface lost by winter moth defoliation during a given growing season. For example, the percent winter moth defoliation in the year 2008 would correspond with the radial growth increment of 2008. *Percent previous year winter moth defoliation* was also treated as a fixed effect and was defined as the percentage of leaf surface lost by winter moth defoliation of a given tree during the previous year growing season. For example, the previous year defoliation for the 2008 radial growth increment would be defined as the 2007 winter moth defoliation percentage. The effect of the interaction between *percent current year winter moth defoliation* and *percent previous year winter moth defoliation* was also included in the model; this interaction was treated as a fixed effect. Defoliation data were available beginning in 2004. Thus, previous year defoliation levels were only available from 2005 and onwards. The application of AIC*c* for model selection requires that identical datasets be used in all models compared. As such, the year 2004 was excluded from the model analyses. Estimates of defoliation were pooled by species for analysis, which resulted in the use of 37 RWI values for *Quercus* and 29 RWI values for *Acer*. For *Pinus* (60 RWI values), we matched the best model for *Quercus* RWI.

Multiple regression was also used to determine the role of *percent current year winter moth defoliation*, *percent previous year winter moth defoliation*, the interaction of current year and previous year winter moth defoliation, *site*, and *year* in explaining *Quercus* earlywood (EW) and latewood (LW) RWI. As before, the model with the lowest AIC*c* value was used. In addition, the proportions of earlywood and latewood were separately regressed on total *Quercus* RWI to determine the strength of their relationships with total annual *Quercus* ring width index.

Results

The *Quercus* (*n* = 8) used in defoliation analyses had a mean diameter of 32.4 (SE ± 2.3) cm and a mean age of 33 (SE ± 5.3) years. *Acer* (*n* = 6) had a mean diameter of 32.1 (SE ± 4.8) cm and an average age of 45 (SE ± 5.7) years. *Pinus* (*n* = 12) had a mean diameter of 34.0 (SE ± 3.3) cm and a mean age of 50 (SE ± 4.9) years. Observed levels of defoliation ranged from 4% to 95% for *Quercus* (Figure 1) and from 0% to 52% for *Acer*.

A total of 16 models were evaluated for each response variable (*Quercus* RWI, *Quercus* EW RWI, *Quercus* LW RWI and *Acer* RWI). These models included the global model (*percent current year winter moth defoliation*, *percent previous year winter moth defoliation*, the interaction of current year and previous year winter moth defoliation, *site*, and *year*) and each nested iteration.

For *Quercus* RWI, one model was retained (Table 2). Based on this model (ΔAIC*c* = 0.0; $r^2_{adj} = 0.24$), variation in *Quercus* RWI was most strongly explained by *percent current year winter moth defoliation* (parameter estimate = -0.006; SE ± 0.0017), wherein winter moth defoliation caused up to a 68% reduction in *Quercus* RWI (Fig. 2).

Analysis of the *Quercus* earlywood and latewood growth indices revealed the complexity behind the total *Quercus* RWI reduction. Based on the best model (ΔAIC*c* = 0.0; $r^2_{adj} = 0.77$; Table 2), *Quercus* earlywood RWI was negatively related to *percent previous year winter moth defoliation* (parameter estimate = -0.001; SE ± 0.0005) and the random effect of *site* (variance component = 0.01; SE ± 0.006). This relationship resulted in up to a 79% reduction in *Quercus* earlywood RWI. By contrast, *Quercus* latewood RWI was negatively related to *percent current year winter moth defoliation* (parameter estimate = -0.006; SE ± 0.001), based on the one retained model (ΔAIC*c* = 0.00; $r^2_{adj} = 0.35$; Table 2). This relationship resulted in up to a 93% reduction in *Quercus* latewood RWI (Fig. 3). Simple regression analysis found that the proportion of *Quercus* earlywood in a given year decreased (and, thus, the proportion of latewood increased) with total *Quercus* RWI ($r^2_{adj} = 0.29$; Fig. 4). This relationship indicates that increased total *Quercus* RWI drives a reduction in the proportion of earlywood and an increase in latewood growth and lends further support for the *Quercus* RWI model wherein *percent current year winter moth defoliation* was the strongest predictor of *Quercus* RWI, as *percent current year winter moth defoliation* was shown (above) to reduce *Quercus* LW RWI.

For *Acer* RWI, the best model (ΔAIC*c* = 0.00; $r^2_{adj} = 0.73$; Table 2) contained *percent current year winter moth defoliation* (parameter estimate = -0.002; SE ± 0.002) and *site* (variance component = 0.04; SE ± 0.03). In addition to the best model, there were six competing models (ΔAIC*c* = 0.09 to 3.9) that attempted to explain *Acer* RWI. Based on the r^2_{adj} values of these competing models (Table 2), the majority of the variation in *Acer* RWI was explained by *site* rather than winter moth defoliation.

There was no relationship ($r^2_{adj} = 0.02$; Table 2) between *Pinus* RWI and winter moth defoliation when matched with the best model for *Quercus* RWI [*percent current year winter moth defoliation* (parameter estimate 0.002; SE ± 0.001) as the sole explanatory variable].

Discussion

Winter moth is well-established in southern New England (Elkinton et al. 2010) and has been responsible for extensive tree defoliation throughout eastern Massachusetts. The forests of eastern North America have a long history of invasion by exotic species. European gypsy moth, hemlock woolly adelgid (*Adelges tsugae* Annand), Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky), Dutch elm disease (*Ophiostoma novo-ulmi* Brasier and *Ophiostoma ulmi* (Buisman) Melin and Nannf.), chestnut blight (*Cryphonectria parasitica* (Murrill) M.E. Barr), and beech bark disease complex have all dramatically altered, or threaten to alter, native forest ecosystems of this region (Campbell and Sloan 1977; Jenkins et al. 1999; Orwig et al. 2008; Gandhi and Herms 2010; Dodds and Orwig 2011). Our results suggest that invasion by winter moth may act as an additional stressor in these forests.

Winter moth defoliation reduced the annual radial growth of infested *Quercus* trees in eastern Massachusetts by up to 68% in the year of defoliation. That this reduction is due to winter moth defoliation and not some stochastic change in the physical environment is suggested by the fact that winter moth defoliation failed to explain much variation in *Pinus* radial growth. Moreover, the positive parameter estimate for *percent current year winter moth defoliation* (parameter estimate = 0.002, Table 2) in the best model for *Pinus* RWI suggests that winter moth defoliation to neighboring host trees may have a slight release effect on *Pinus* radial growth. Thus, the radial growth reduction shown by *Quercus* cannot likely be explained by extraordinary environmental factors that happen to correlate with winter moth defoliation levels.

The large amount of variation in *Acer* RWI that was explained by *site* may have been caused by great variation in *Acer* ring widths among trees. The series intercorrelation for the *Acer* tree cores (0.033) was well below the critical correlation level (0.3281) required for statistical significance in COFECHA. Efforts were made to ensure the measurement accuracy of these cores. Consequently, the low series intercorrelation is likely a result of natural variation in *Acer* growth across our sites. Unfortunately, the low series intercorrelation value precluded any discussion of the effects of winter moth defoliation on *Acer* radial growth.

The effect of winter moth defoliation on *Quercus* radial growth was likely caused by a reduction in photosynthate production and/or allocation to radial growth. The earlywood and latewood growth reductions are consistent with the biology of winter moth and *Quercus*. As ring-porous species, the earlywood growth of *Quercus* is proportionally driven by resources produced and stored during previous growing seasons (Palacio et al. 2011) and is initiated prior to spring bud burst (leaf expansion) (Wareing 1951; Zasada and Zahner 1969). Conversely, latewood growth of ring-porous species is mainly a function of photosynthate allocation in the year concurrent with growth (Varley and Gradwell 1960; Palacio et al. 2011). Winter moth larval feeding occurs in the expanding buds in the early spring and is, thus, concurrent with earlywood production. As such, winter moth defoliation in a given year does not have an effect on the earlywood growth for that year. However, as winter moth defoliates *Quercus* while the leaves are expanding, and since latewood growth is proportionally dependent upon actively produced photosynthate from within the current year, the photosynthetic capabilities of the defoliated tree may be reduced and/or photosynthate may be allocated to processes (e.g. defense, re-leafing) other than latewood growth. This relationship between defoliation in the current year and latewood growth has been demonstrated with other defoliators (Krause and Morin 1995; Muzika and Liebhold 1999; Speer et al. 2001; Vejpustková and Holuša 2006; Fajvan et al. 2008). Although defoliation can incite compensatory production of photosynthate in the remaining or regrowth leaf tissue of trees (Heichel and Turner 1983; McGraw et al. 1990; Hoogesteger and Karlsson 1992) increased levels of defoliation likely reduce the net CO_2 assimilation within defoliated *A. rubrum* and *Q. rubra* (Heichel and Turner 1983). Moreover, as repeated defoliation can reduce root carbon reserves in mature trees (Landhäusser and Lieffers 2012), the benefit of compensatory photosynthesis is likely diminished after multiple years of defoliation.

My results are consistent with previous studies that have evaluated the effects of winter moth defoliation in Nova Scotia and Europe. Embree (1967) showed a reduction in radial growth and basal area of *Q. rubra* trees defoliated by winter moth in Nova Scotia. As part of their classic studies at Wytham Wood, England, Varley and Gradwell (1960) found a negative relationship between the percent latewood growth of *Q. robur* L. and caterpillar densities of winter moth and the green oak leaf roller (*Tortrix viridana* L.). Further, Tikkanen and Roininen (2001) found a radial growth reduction in *Prunus padus* L., *Sorbus aucuparia* L., and *Populus tremula* L. trees defoliated by winter moth in eastern Fennoscandia. Given these similarities, our results suggest that winter moth defoliation in New England may lead to tree decline and mortality, as repeated defoliation by winter moth caused crown dieback and tree mortality in *Q. rubra* stands in Nova Scotia (Cuming 1961; Embree 1967).

The effect of winter moth defoliation on the radial growth of *Quercus* was similar to those documented for other outbreak species and further implies this insect species will have a negative effect on the growth and survivorship of *Quercus* trees in mixed forests of Massachusetts. Studies have found a negative relationship between defoliation by the European gypsy moth and standardized total radial increment of *Q. rubra* trees (Muzika and Liebhold 1999; Naidoo and Lechowicz 2001). Moreover, consistent with our results, Muzika and Liebhold (1999) and Fajvan et al. (2008) also noted a reduction in latewood growth of *Q. rubra* concomitant with gypsy moth defoliation. Further, earlywood production in *Quercus* species was reduced in the season following gypsy moth defoliation (Fajvan et al. 2008). The implications of our findings are considerable, as gypsy moth is often referred to as one of the most devastating threats facing eastern U.S. forests (Muzika and Liebhold 1999; Fajvan et al. 2008) and these two species have potentially overlapping spatial distributions.

It is critical to note that winter moth is an additional stressor to tree health in an ecosystem that has been largely influenced by outbreaks of polyphagous defoliators, namely the European gypsy moth, which was introduced to the region in the late 1860s, and the native forest tent caterpillar. In eastern Massachusetts, where high density gypsy moth populations are primarily regulated by a nucleopolyhedrovirus (LdMNPV) (Elkinton and Liebhold 1990) and the fungal pathogen *Entomophaga maimaiga* Humber, Shimazu *et* Soper (Malakar et al. 1999), winter moth has become the dominant defoliator. The phenologies of these insects are such that a tree in a given season may be subject to a sequence of defoliation that is initiated by winter moth, followed by forest tent caterpillar, and then by gypsy moth. The combined effects of these insects on tree growth and mortality are currently unknown, but could have serious consequences for tree health in northeastern forests as multiple defoliation events on deciduous trees in a given year may result in tree mortality (Kozlowski and Pallardy 1997). In years of high densities of winter moth and other defoliators, *Quercus* trees could ostensibly receive at least two major waves of defoliation in a given season. The first, by winter moth, could result in a re-flush of new leaves that are subject to forest tent caterpillar and/or gypsy moth defoliation. While defoliation may induce a chemical response in leaves that could reduce gypsy moth fitness (Wallner and Walton 1979), consumption of these leaves may reduce the pathogenicity of LdMNPV on gypsy moth larvae (Hunter and Schultz 1993). Although this multitrophic interaction has been contested, mainly due to timing of host secondary chemical induction and virus consumption by gypsy moth larvae (D'Amico et al. 1998), no studies have evaluated the effects of early-season defoliation by winter moth on gypsy moth fitness. It is possible that winter moth defoliation could induce host secondary chemical production early enough in a growing season to influence the interactions between gypsy moth larvae and nucleopolyhedrovirus. This potential multitrophic interaction could have dramatic effects on defoliator population dynamics.

In addition to radial growth reduction, insect defoliation can lead to widespread tree decline and mortality. In the northeastern United States, relationships between tree mortality and defoliation have been well-documented (e.g. Campbell and Sloan 1977; Mattson et al. 1991; Davidson et al. 1999; Eisenbies et al. 2007; Fajvan et al. 2008). Insect defoliation may initiate a chronosequence of decline and mortality that involves secondary wood borers and root decay fungi, notably *Armillaria* species (Staley 1965; Wargo 1996). While endemic defoliating insects are an important natural component of forest systems (Mattson and Addy 1975), prolonged forest decline initiated by exotic/invasive herbivores may have detrimental cascading effects (Gandhi and Herms 2010).

The results presented here indicate that winter moth is a significant threat to the forests of southern New England and *Quercus* forests throughout North America. As winter moth populations are well-established throughout eastern MA, and assuming the results presented herein can be extrapolated to other sites, the *Quercus* resource that dominates much of eastern MA will likely decline in the presence of winter moth defoliation. Given the growth decline associated with winter moth defoliation, current efforts to establish biological control agents (Elkinton et al. 2010) for this species are well-warranted.

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Table 1. Location, species, diameter at breast height (DBH; 1.4 m), age, and years of winter moth defoliation estimates of individual trees at seven study sites in eastern Massachusetts, USA.

Site	Tree #	Species	DBH (cm)	Age	Years w/ Defoliation Estimates
Hanson, MA (A)	*Quercus* 1	*Quercus velutina*	25.6	15	2004-2010
	Acer 1	*Acer rubrum*	53.1	71	2004-2010
Hanson, MA (B)	*Quercus* 2	*Quercus rubra*	37.6	58	2004-2010
Hingham, MA (A)	*Quercus* 3	*Quercus rubra*	35.1	28	2004-2010
	Acer 2	*Acer rubrum*	24.8	38	2004-2010
Hingham, MA (B)	*Quercus* 4	*Quercus rubra*	29.1	44	2004-2010
	Acer 3	*Acer rubrum*	34.2	43	2004-2010
Wellesley, MA	*Quercus* 5	*Quercus velutina*	22.6	50	2008-2010
	Acer 4	*Acer saccharum*	19.5	45	2009-2010
Wenham, MA	*Quercus* 6	*Quercus velutina*	30.8	21	2006-2010
	Acer 5	*Acer rubrum*	34.4	34	2006-2010
West Bridgewater, MA	*Quercus* 7	*Quercus rubra*	37.6	27	2004-2010
	Quercus 8	*Quercus rubra*	40.7	22	2004-2010
	Acer 6	*Acer rubrum*	26.7	45	2004-2010

Table 2. Results of multiple regression with *Quercus*, *Acer*, and *Pinus* response variables from the years 2005 – 2010 with defoliation estimates on individual trees throughout eastern Massachusetts. Parameter estimates are shown for fixed effects, variance components are provided for random effects. RWI = ring width index; EW = earlywood; LW = latewood; SE = standard error; ΔAICc = corrected Akaike Information Criterion simple differences; PE = parameter estimate; VC = variance component.

Model	Model Effects	Δ AICc	r^2 adj	PE / VC	SE	Log Likelihood	Akaike Weight	Evidence Ratio
***Quercus* RWI**								
	% current year	0.00	0.24	-0.006	0.002	1.00	0.72	1.00
***Quercus* EW RWI**								
	% previous year	0.00	0.77	-0.001	0.000	1.00	0.68	1.00
	Tree ID (random)			0.010	0.006			
***Quercus* LW RWI**								
	% current year	0.00	0.35	-0.006	0.001	1.00	0.70	1.00
***Acer* RWI**								
	% previous year	1.41	-0.02	-0.002	0.003	0.49	0.13	2.02
	% previous year	1.02	0.72	0.000	0.002	0.60	0.16	1.67
	Tree ID (random)			0.042	0.030			
	% current year	0.09	0.02	-0.004	0.003	0.96	0.25	1.05
	% current year	0.00	0.73	-0.002	0.002	1.00	0.26	1.00
	Tree ID (random)			0.041	0.029			
***Pinus* RWI**								
	% current year	1.85	0.01	0.002	0.001	0.40	0.17	2.52
	% previous year			-0.001	0.001			
	% current year	1.19	0.05	0.003	0.001	0.55	0.24	1.81
	% previous year			0.000	0.001			
	% current * % previous			0.000	0.000			
	% current year	0.00	0.02	0.002	0.001	1.00	0.43	1.00

Figure 1. Defoliation estimates on eight *Quercus* trees in eastern Massachusetts from 2004-2010. Source: Brenda Whited and Joseph Elkinton, University of Massachusetts - Amherst.

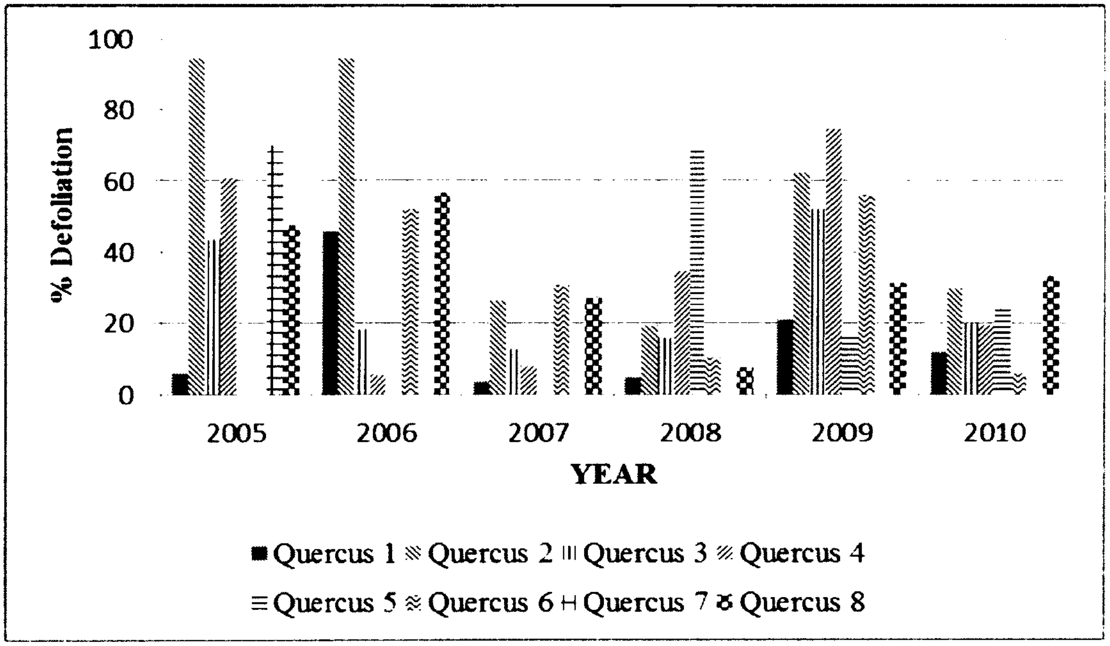


Figure 2. *Quercus* RWI by *percent current year winter moth defoliation*. Defoliation estimates ($n = 37$) among eight trees throughout eastern Massachusetts from 2005-2010. *Quercus* RWI = 1.202 – 0.006 * *% current year winter moth defoliation*.

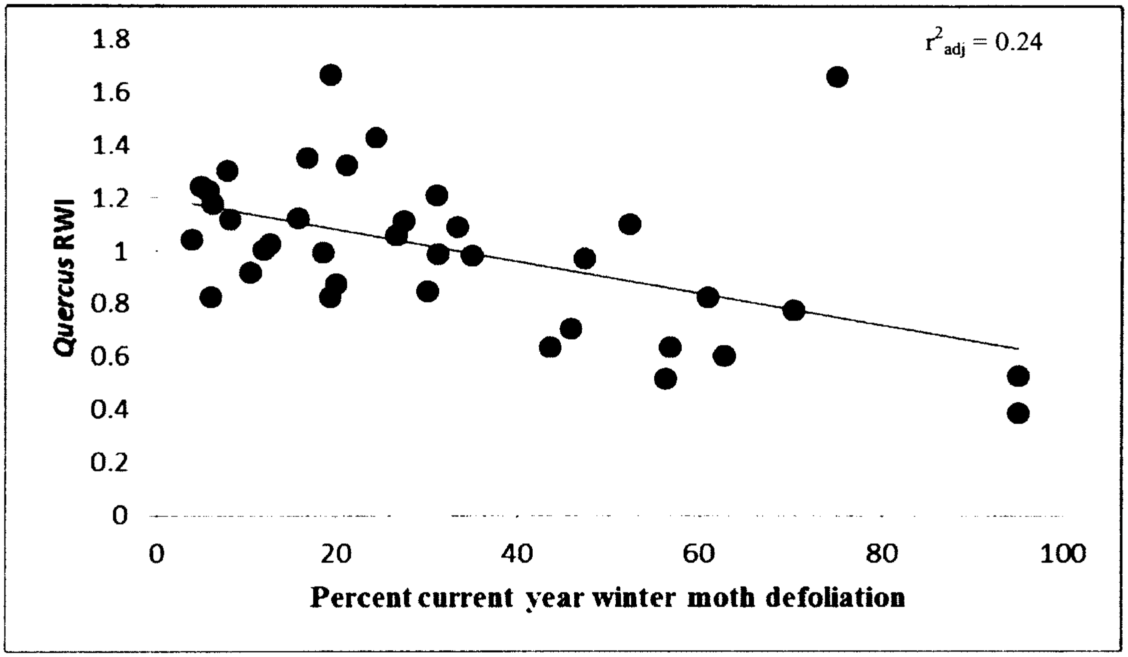


Figure 3. *Quercus* latewood RWI by *percent current year winter moth defoliation*. Defoliation estimates ($n = 37$) among eight trees throughout eastern Massachusetts from 2005-2010. *Quercus* LW RWI = 0.866 – 0.006 * *% current year winter moth defoliation*.

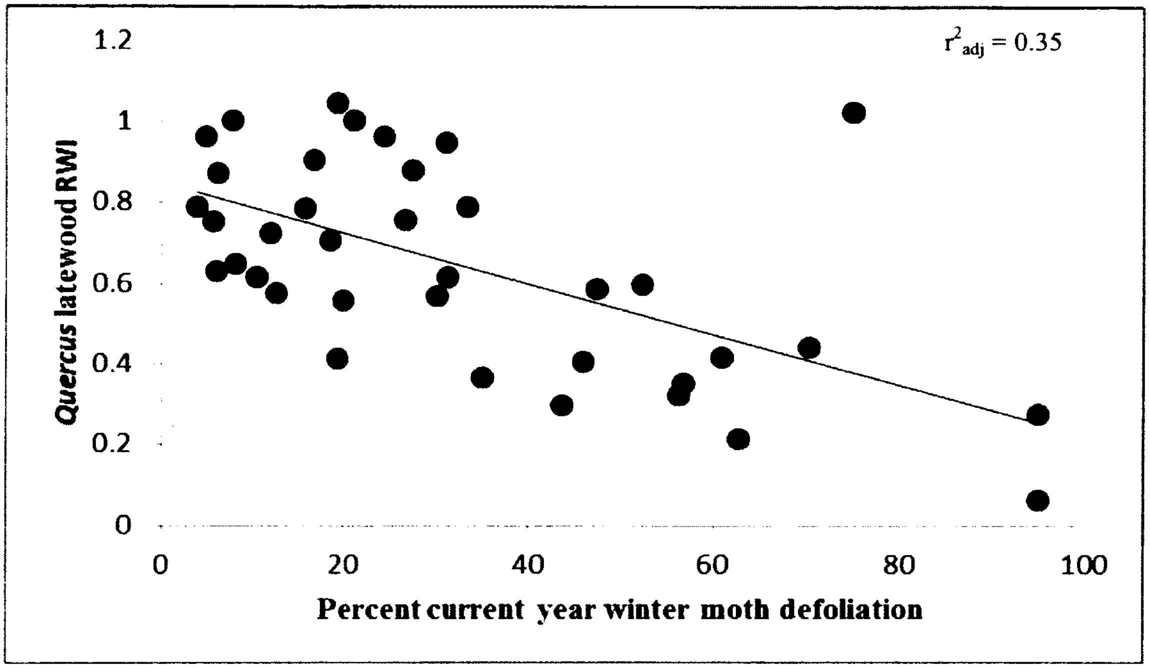
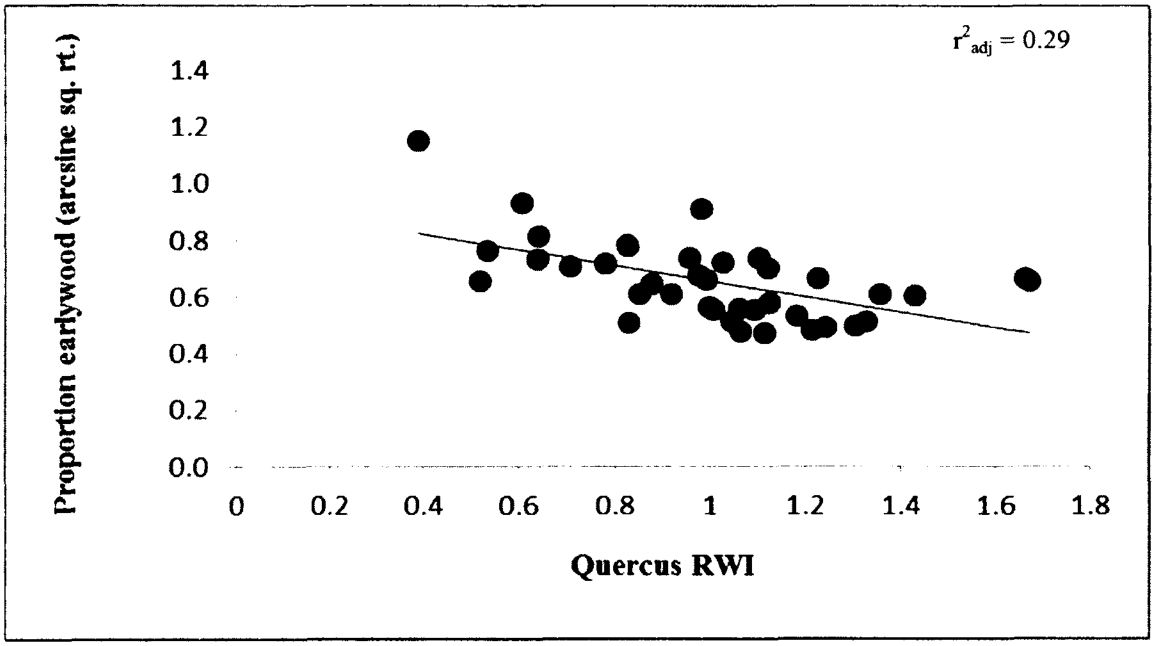


Figure 4. Proportion of *Quercus* earlywood by *Quercus* RWI on annual ring widths (*n* = 45) among eight trees throughout eastern Massachusetts from 2005-2010. Proportion earlywood (arcsine sq. rt.) = 0.930 – 0.271 * *Quercus* RWI.



CHAPTER III

THE EFFECTS OF NOVEL WINTER MOTH DEFOLIATION IN FOREST STANDS IN EASTERN MASSACHUSETTS, USA

Abstract

Widespread and prolonged defoliation by the European winter moth, *Operophtera brumata* L., has been observed in forests of eastern Massachusetts for more than a decade and populations of winter moth continue to invade new areas of New England. To date, the forest stand level impacts of winter moth invasion in New England have not been documented. This study characterized the forests of eastern Massachusetts invaded by winter moth and related the duration of winter moth defoliation estimated using dendrochronology to observed levels of tree mortality and understory woody plant density. Winter moth has successfully invaded mixed *Quercus* and mixed *Quercus* - *Pinus strobus* forests in eastern Massachusetts. Mortality of *Quercus* in these forests was related to site quality and the number of winter moth defoliation events. In addition, winter moth defoliation events lead to a subsequent increase in understory woody plant density.

Introduction

Winter Moth in Massachusetts

Winter moth, *Operophtera brumata* L. (Lepidoptera: Geometridae), has been responsible for widespread defoliation of trees in eastern Massachusetts for over a decade and tree mortality has been attributed anecdotally to winter moth defoliation events (Childs et al. 2003). Native to Europe, winter moth is believed to have been present in the region since the early to mid-1990s, when heavy and prolonged defoliation began in eastern Massachusetts. However, winter moth was not officially confirmed as the causal agent of this prolonged defoliation until 2003 (Elkinton et al. 2010). Since this confirmation, winter moth has been detected throughout much of eastern Massachusetts and portions of Rhode Island, Connecticut, eastern Long Island (NY), New Hampshire, and Maine (Elkinton et al. 2010). The distribution of winter moth in New England is expanding (Elkinton et al. 2010) and defoliation damage has recently reached historic levels in Massachusetts (89,000 ac defoliated in 2011; USFS, MA DCR 2012). Elevated levels of defoliation have been recently reported for the first time in coastal Maine (Maine Forest Service 2012).

Winter moth has a history of invasion in North America, with accidental introductions to Nova Scotia in the 1930s (Cuming 1961) and the Pacific Northwest in the 1950s (Gillespie 1978; Roland 1988). These introductions resulted in prolonged outbreaks that were eventually controlled by the release of the biological control agent, *Cyzenis albicans* (Elkinton et al. 2010). Winter moth has been an important defoliator of *Quercus* forests in England (Varley and Gradwell 1960; Feeny 1970) and Nova Scotia (Embree 1967) and has recently invaded mixed hardwood forests of eastern

Fennoscandia (Tikkanen and Roininen 2001). Invaded forests in New England have not as yet been characterized as to tree species composition and structure.

Winter moth is an early-season defoliator that feeds in the expanding buds and leaves of its hardwood host (Cuming 1961; Feeny 1970; Varley et al. 1973). The life history of winter moth in New England is similar to what has been described in its native habitat in Europe and its prior introduction in Nova Scotia. Briefly, winter moth is a univoltine species that overwinters as an egg; larval eclosion typically occurs in April and larvae feed for approximately six weeks. Pupation occurs in the soil beginning in early-June. Adults emerge from the soil in late-fall to early-winter, when, upon mating, the flightless female lays eggs in bark crevices and branches of selected host trees (Cuming 1961; Varley et al. 1973). Although winter moth is a polyphagous feeder, host preference and the level of defoliation associated with winter moth larval feeding is largely determined by the degree of synchrony between budburst and larval eclosion (Feeny 1970; Tikkanen and Lyytikäinen-Saarenmaa 2002; Tikkanen and Julkunen-Tiitto 2003). In Nova Scotia, *Quercus rubra* L. has been cited as a principal forest host (Embree 1991) and I have observed this trend in Massachusetts as well.

The effects of winter moth defoliation have been studied in its native and exotic ranges. Tikkanen and Roininen (2001) found a radial growth reduction in host trees defoliated by winter moth in eastern Fennoscandia. In Nova Scotia, winter moth defoliation caused a reduction in radial growth (Embree 1967) and an increase in mortality of *Q. rubra* trees (Cuming 1961; Embree 1967). In eastern Massachusetts, winter moth defoliation caused a reduction in radial growth of individual *Q. rubra* and *Q. velutina* Lam. trees (chapter 1). Radial growth (Monserud 1976; Wyckoff and Clark

2000) and defoliation (Gottschalk et al. 1998) can be used as predictors of tree mortality, indicating that winter moth defoliation may increase tree mortality in forest stands. To date, no studies have documented the impact of winter moth defoliation on forest stand level mortality in New England.

The forests of eastern North America have been host to several exotic, invasive pests and pathogens that have contributed to tree mortality and altered stand composition and structure (Gandhi and Herms 2010). Current insect invasions in New England include European gypsy moth, *Lymantria dispar* L., Asian longhorned beetle, *Anoplophora glabripennis* Motschulsky, hemlock woolly adelgid, *Adelges tsugae* Annand, and emerald ash borer, *Agrilus planipennis* Fairmaire, among others (Dodds and Orwig 2011). Winter moth is a recent addition to this suite of exotic pests and little is known about its impacts to forests in New England. The specific objectives of this study were to: 1) characterize tree species composition and stand structure of forests invaded by winter moth in eastern Massachusetts and, 2) relate tree radial growth chronologies, stand-level tree mortality, and understory plant density to winter moth defoliation and site quality.

Methods

Study Region

Eastern Massachusetts is part of the Northeastern Coastal Zone ecoregion (Hall et al. 2002) and comprises the southern New England Coastal Plain, Bristol Lowlands, and Boston Basin ecological subregions (Hall et al. 2002; McDonald et al. 2006). One of the most developed portions of New England (Foster et al. 2010), eastern Massachusetts is a mosaic of urban areas, undeveloped private lands, and state, municipal, and private forests. These post-agricultural forests are dominated by *Quercus* spp., *Acer* spp., and *Pinus* spp. (Hall et al. 2002). The species composition and climate of these forests offer ideal habitat for winter moth (Elkinton et al. 2010).

Study Sites

At the time I began my research, the forests of Massachusetts represented the oldest and best documented case of winter moth infestation in the eastern United States. In order to describe infested forest stands across this region, in 2010 I used historic aerial detection survey (ADS) maps (years 2004-2010), provided by US Forest Service Forest Health Protection in Durham, New Hampshire, to locate areas known to have been defoliated in recent years. I also conferred with personnel of the Massachusetts Department of Conservation and Recreation (MA-DCR) and University of Massachusetts-Amherst to locate areas with winter moth defoliation. Once defoliated sites were identified, I selected 13 sites that met the following criteria: 1) were located on state or municipal forests, 2) were on upland soils, 3) had a major hardwood component, 4) were discreet forest stands with clear boundaries, and 5) collectively assured representation of all geographic areas within the region of defoliation.

Vegetation Sampling

Forest stand surveys were conducted systematically within each site. Fixed-radius (12 m) circular plots were established to sample forest stand composition and structure. Tree species and diameter at breast height (dbh, 1.4 m) were recorded for each tree $\geq$7.5 cm dbh. In addition, each tree was tallied as either "live" or "dead". In order to roughly age mortality at each site, standing dead trees and 'windthrows' were evaluated and classified using the five-class decay models presented by Thomas (1979), and Pyle and Brown (1998). Nested 1 m circular plots, located in the four cardinal directions at six meters from the plot center, were established to sample tree and shrub saplings (< 7.5 cm dbh) and seedlings (<1.4 m tall). These tree and shrub estimates were combined for one total measure of understory woody plant density.

Total basal area, basal area by species per hectare, and total stem density by species per hectare were calculated. In addition, the percentages of live and dead canopy trees were calculated. The combined percentage of *Q. rubra* and *Q. velutina* basal area in dead stems was calculated for each site as a potential metric of winter moth defoliation impact, as my observations suggest that these two species seem to suffer disproportionate damage. My study was mainly concerned with defoliation impacts to trees in the dominant/co-dominant canopy stratum. In order to capture this, I used percentage of basal area in dead stems as a metric of tree mortality instead of percentage of total trees in dead stems as the former is more heavily weighted towards larger diameter trees typical of mature overstory strata. Thus, mortality estimates were not exaggerated by the density-dependent mortality associated with highly stocked areas of smaller diameter trees or, as is more applicable to *Quercus* dynamics on our study sites, the mortality associated with the overtopping of trees in subordinate canopy classes within the same cohort.

Determination of Winter Moth Presence

Winter moth trapping studies were implemented in late fall/early winter 2010/2011 to confirm the presence of winter moth at the study sites. Two sticky band traps (Bug Barrier Tree Band; Envirometrics Systems, Inc. Victor, NY) were placed around the bole at approximately 1.0 and 1.3 m above the ground on one to three overstory (dominant or codominant) trees within each site to trap adult females as they emerged from the soil organic layer and migrated up tree boles for oviposition. The occurrence in the late-fall of these flightless females in the sticky band traps confirms the presence of winter moth within the stand during the previous growing season. Due to similarities in life history, these traps are also effective at trapping native members of the spring defoliator guild including fall cankerworm, *Alsophila pomentaria* Harris (Lepidoptera: Geometridae) and Bruce spanworm, *Operophtera bruceata* Hulst (Lepidoptera: Geometridae) and the presence of these insects was noted as well.

Stand Classification

Cluster analysis (relative Euclidean distance and Ward's minimum variance method; PC-Ord 5.0 software by McCune and Mefford 1999) was used to classify each of the 13 forest stands by tree species composition and size-class distribution. Specifically, the attributes were species abundances in each size class (e.g. density of *Q. rubra* in the 7.5-15 cm class; *A. rubrum* L. in the 15.1-25.0 cm class, etc.). Thus, stands were clustered based on the similarity of species abundances within size classes. Analysis of variance (JMP® Pro 10.0.0 software; SAS Institute Inc.) was used to test for differences among attributes of the forest types defined by the above cluster analysis procedure. Specifically, I tested for differences in: 1) the percentage of *Quercus* basal area in dead stems calculated from vegetation surveys; 2) percentage of total trees in dead stems; 3) stand relative density; 4) site index; and 5) winter moth activity (as defined below). Percentage of *Quercus* basal area in dead stems and percentage of total trees in dead stems were arcsine square root transformed to meet the assumption of normality.

Dendrochronology

Tree core analysis was used to relate radial growth chronologies to winter moth defoliation and to estimate the frequency of winter moth activity in each site. At each of the study sites, one radial increment core was extracted from each of 30 (if available) overstory (dominant or codominant crown classes) host trees (*Q. rubra*/*Q. velutina*), and 30 overstory non-host trees (*P. strobus* L.), when available. Trees were selected for core extraction systematically throughout the stand such that the core samples provided an accurate stand-level representation of tree radial growth. Cores were labeled in the field and returned to the lab for preparation and analysis. In total, 787 (*Q. rubra* = 227; *Q. velutina* = 167; *P. strobus* = 311) trees were cored from the 13 study sites. *Quercus rubra* and *Q. velutina* belong to the *Erythrobalanus* subgenus and readily hybridize (Burns and Honkala 1990). Consequently, these two species were combined for radial growth analyses and are herein referred to as *Quercus* when applied to tree core and mortality results. Although *Q. alba* L. was present at some of the study sites, this species did not occur in sufficient numbers across all sites to include in radial growth analyses.

Increment cores were stored in paper straws and allowed to dry. Cores were then glued to wooden mounts and sanded with progressively finer sandpaper, concluding with 600-grit. Cores were aged using a dissecting microscope. A Velmex measurement system (Velmex, East Bloomfield, New York), in combination with Measure J2X v. 4.1.2 software (VoorTech Consulting) was used to measure annual growth ring widths to the nearest 0.001 mm. Once measured, cores were visually cross-dated based on event years (i.e., years having low growth due to known drought, insect defoliation, etc.; Yamaguchi 1991; Tardif and Conciatori 2006) using scatterplots created in MS Excel® (Microsoft

Inc.). The program COFECHA (Holmes 1983) was used to verify and improve cross-dating and to test measurement error.

In order to remove age-related growth trends, the raw ring width data for each cored tree were detrended and converted to a dimensionless ring-width index (RWI) following procedures outlined by Bunn (2008). Using the dplR computer package (Bunn 2008) within the R statistical program (R Development Core Team 2009), a modified negative exponential curve was fit to the raw ring width data for each core; subsequently, these data were detrended within dplR by dividing the annual raw ring widths by the predicted values estimated by the fitted modified negative exponential curve. *Quercus* and *P. strobus* radial growth chronologies were constructed for each site using the average of all the RWI values for each species per site. Region-wide *Quercus* and *P. strobus* chronologies were constructed by pooling all *Quercus* and *P. strobus* RWI chronologies from all sites.

In addition to the above tree core analyses, dendrochronology was also used to age *Quercus* mortality at one of the 13 study sites. For this, I selected the site with the highest percentage of *Quercus* basal area in dead stems and felled 10 snags in order to extract a radial disk at 1.3 m above the ground. These radial disks were then dried and sanded with progressively finer sandpaper, again concluding with 600-grit. Three radii per disk, at least 60° from each other, were selected for measurement of annual radial growth ring widths using a Velmex measurement system and Measure J2X software. These three radii were not averaged, but served as replicates to assist in cross-dating.

Once measured, the three radii per tree were visually "cross-dated" based on within-tree growth patterns using scatterplots in Microsoft Excel®. Next, I attempted to assign calendar years to the radial growth measurements of the radii by cross-dating them with event years determined by the live tree core analysis at the study site in order to assign a year of mortality for the tree from which the disks were extracted. Correlation analysis (JMP 10.0) was used to investigate the relationship between snag class and years since mortality. To be conservative with these estimates, four of the ten disks were excluded from analysis due to ambiguity in cross-dating.

Defining Winter Moth Activity

Three criteria were used to identify winter moth activity at both the region-wide (all 13 sites) and individual site levels (Figure 1). First, repeated measures analysis was used to test for divergence between *Quercus* and *P. strobus* RWI chronologies across all 13 sites (region-wide) and within each individual site from the years 1980 to 2010, as indicated by the Greenhouse-Geisser Epsilon univariate test of the interaction between time (year) and species (JMP® Pro 10.0.0 software; SAS Institute Inc.). For the region-wide chronologies, I pooled all of the *Quercus* and *P. strobus* RWI chronologies for each of the 13 sites. For the individual site analyses, I pooled and tested the individual tree chronologies for each species by site. The year 1980 was chosen as the starting point of analysis due to the widespread gypsy moth defoliation event that occurred in 1981 in which both *Quercus* and *P. strobus* were heavily defoliated. By incorporating this event into my radial growth analyses of winter moth activity, I was able to start the analyses from a point at which both species were affected by the same limiting factor.

As the second criterion of determining winter moth activity, one-sided *t*-tests were used to identify individual years of divergence in which *Quercus* RWI was significantly *lower* than *P. strobus* RWI; these tests were performed a posteriori on *Quercus* and *P.*

strobus RWI chronologies that differed significantly, as determined by the above repeated measures analysis. The significance level (α) of these *t*-tests was calculated using the sequentially rejective, Bonferroni-adjustment (Holm 1979; Rice 1989). The sequential Bonferroni adjustment, in comparison with the classic Bonferroni adjustment, may provide more statistical power in detecting multiple alternative hypotheses, while also reducing the Type I error rate (Rice 1989). As the winter moth invasion is believed to have initiated in the early- to mid-1990s, the domain of the *t*-tests was from the years 1995-2010, inclusive. The year 1995 was chosen as the beginning of individual year analyses as this year incorporates much of the early winter moth invasion, but also limits the influence of gypsy moth defoliation that occurred in the region in the early 1990s. As such, the adjusted alpha for each set of divergences was calculated, beginning with the lowest *P*-value and working successively towards the highest *P*-value, as: α/n; $\alpha/(n-1)$; $\alpha/(n-2)$;...$\alpha/1$, where alpha (α) = 0.05 and n = the number of individual *t*-tests ($n = 16$ for the years 1995-2010).

Finally, the third criterion of winter moth activity required that the *Quercus* RWI value fall below a critical threshold of 1.094 in the individual years in which *Quercus* RWI was significantly lower than *P. strobus* RWI. This threshold was determined using the regression equation for current year winter moth defoliation and *Quercus* RWI provided in chapter 1, as follows. The defoliation level at which the upper 95% confidence interval of *Quercus* RWI was equal to the y-intercept value of the regression was calculated using JMP® Pro 10.0.0 software (Figure 2). This value (17.0%) represents the threshold above which *Quercus* RWI was negatively affected by winter moth defoliation; below this value *Quercus* RWI was not significantly different from the y-intercept value of 1.202 (the expected RWI value of *Quercus* not influenced by winter moth defoliation). This value was calculated as approximately 17.0%; thus, a threshold defoliation percentage for identifying winter moth activity was set at 18%, which equals a RWI threshold value of 1.094. Thus, criterion three was satisfied when individual year *Quercus* RWI values fell below 1.094.

Tikkanen and Roininen (2001) used a similar suite of methods to identify recent winter moth defoliation events in the tree ring record of *Prunus padus* L. trees in Russia using a combination of repeated measures analysis and subsequent *t*-tests. In addition, the authors also identified individual year outbreaks in forests throughout eastern Fennoscandia by applying a threshold in which an individual year was considered an outbreak when the mean annual increment of that year fell below a minimal growth index measured from years of known winter moth outbreaks.

Individual years that met these three criteria (Figure 1) were defined as years of elevated winter moth defoliation. Subsequently, winter moth activity (per site and across all 13 sites) was quantified by the number of elevated defoliation events within the 1995-2010 period and these were entered as a covariate predictor into multiple regression models explained below.

Percent of Quercus *Basal Area in Dead Stems*

I hypothesized that the percentage of *Quercus* basal area in dead stems estimated from our vegetation surveys was positively related to number of elevated winter moth defoliation events (*Number of WM Defoliation Events*) and the covariates of *Stand Relative Density* (RD, a surrogate for competition) and *Quercus Site Index* (SI, a metric of site quality). Stand relative density estimates were calculated for each site using the method developed and outlined by Ducey and Knapp (2010) for mixed species forests of the northeastern US. Specifically, relative density (RD) was calculated per hectare by the summation of individual, live tree relative density values as calculated by:

$$RD = \Sigma\,(0.00015 + 0.00218SG_i)\,(DBH_i/25)^{1.6}$$

where SG = the specific gravity of individual tree species, as provided in Ducey and Knapp (2010).

Quercus site index (SI) for each stand was calculated by plotting total height estimates of dominant and/or co-dominant crown class *Quercus* trees from the vegetation surveys versus *Quercus* age, as estimated from tree core analyses, on the Upland Oaks Site Index Curves by Olson (1959; in Carmean 1989).

Multiple regression was used to determine which explanatory variables (*Number of WM Defoliation Events*; *Stand Relative Density; Quercus Site Index*) had the greatest effect on *Percent of Quercus Basal Area in Dead Stems*. Variance inflation factors (VIF) were used to test for multicollinearity of regressors and Studentized residuals were calculated and plotted to test for normality of variables and the presence of outliers. Subsequently, *Percent of Quercus Basal Area in Dead Stems* (in proportional form) was arcsine square root transformed. Statistical analyses were performed using JMP® Pro 10.0.0 software (SAS Institute Inc.).

My goal was to evaluate the strength of the potential relationships between the above variables. Thus, model selection for *Percent of Quercus Basal Area in Dead Stems* (arcsine square root) was performed using the corrected Akaike Information Criterion (AIC*c*) value (Burnham and Anderson 2002). As such, results will be presented and discussed in Information-Theoretic terms (i.e. AIC*c* simple differences [ΔAIC*c*], Akaike weights [*w*], strength of support for models) as opposed to Frequentist statistical terms (i.e. *P*-values, statistical significance) (Anderson et al. 2001). The model with the lowest AIC*c* value was considered the "best" model, however, models with ΔAIC*c* values less than or equal to four (relative likelihood ≥ 0.135) were considered candidate models. Evidence ratios were calculated for each model within the set of candidate models and were used to evaluate and identify the model(s) that best explained *Percent of Quercus Basal Area in Dead Stems* (Burnham and Anderson 2002).

Understory Density

Multiple regression was also used to test the influence of *Stand Relative Density* and *Number of WM Defoliation Events* on the density of understory tree and shrub seedlings and saplings, as estimated from the vegetation surveys. Tree and shrub seedling and sapling densities were pooled together for one overall understory density variable which is herein referred to as *Understory Density*.

Drought

To test if drought events influenced radial growth during the 1980 to 2010 time period, *Quercus* and *P. strobus* RWI were regressed (individually) on 1) the May Palmer Drought Severity Index (PDSI), 2) June PDSI, 3) July PDSI, 4) the June-July two month average PDSI, and 5) the 12-month average Palmer Drought Severity Index (PDSI) values for Massachusetts from (NOAA National Oceanic and Atmospheric Administration, National Climatic Data Center, http://www.ncdc.noaa.gov/, accessed 3 17 2013).

Aerial Detection Survey Data

Aerial detection survey (ADS) data provided by US Forest Service Forest Health Protection in Durham, New Hampshire were used as a supporting metric of winter moth defoliation history at each study site. Using ArcMap® 10.0 (ESRI, Inc.) geographic information systems (GIS) software, a one-mile (1.61 km) buffer was created around each study site and ADS data for winter moth defoliation and for all other defoliators were clipped within this buffer. Massachusetts ADS data available as a GIS shapefile date back to 1997 and winter moth defoliation aerial surveys began in 2004. I tested the relationship between the numbers of years of defoliation events at each site from ADS with *Number of WM Defoliation Events* (see above) using correlation analysis (JMP® Pro 10.0.0). ADS data were used solely as a presence/absence indicator of defoliation to support my identification of radial growth trends, not as a measure of defoliation intensity.

Results

Study Sites

Thirteen stands covering much of the latitudinal range of eastern Massachusetts were identified and surveyed (Table 1; Figure 3). Study sites were dominated by *Q. rubra*, *Q. velutina*, *P. strobus*, and *Acer rubrum* L. in various mixtures and size classes (Appendix A). Sites varied in total live and dead stem densities and basal area, as well as percentage of overstory trees characterized as live or dead (Appendix B and C). Total stem density of live and dead *Quercus* varied between sites and *Quercus* quadratic mean diameter ranged from 23.5 (± 0.8) to 39.6 (± 1.8) cm (Table 1). Understory woody plant density ranged from 11,306 to 261,313 stems per hectare (Table 1). The topography of most sites was flat to gently rolling.

Across all 13 sites the age of *Quercus* in the overstory ranged from 59 to 106 years and *P. strobus* ranged from 53 to 107 years (Table 2). *Quercus* site index (SI) and stand relative density (RD) values differed among sites, as did the percentage of *Quercus* basal area in dead stems. *Quercus* site index values ranged from 46 to 77; stand relative density values ranged from 0.60 to 0.88 (60-88%) (Table 2). The percentage of *Quercus* basal area in dead stems ranged from 0% to 30% among the 13 study sites (Table 2). Of this mortality, seven sites had greater than 60% of the snags in more recent snag classes 1-3 (Figure 4).

Presence/absence trapping studies were conducted at nine of the study sites and winter moth was present at each of these sites in varying abundances (Table 3). Bruce spanworm was not trapped at any site and a limited number of fall cankerworm individuals were present on traps at five sites (Table 3). Winter moth presence was confirmed at the additional four sites by interviews with natural resource managers and previous/tangential trapping studies (G. Boettner UMass Amherst, personal communication). Trapping results were not used for further analysis of winter moth density at each site.

Cluster analysis of the 13 stands based on tree species abundances in size-classes produced five distinct groups (1-5) at the level of 70% information remaining (Figure 5). Group 1 (Amesbury Town Forest and Centennial Park) was dominated by *Q. rubra* and *Q. velutina* in the large diameter size classes (Fig. 6). The diameter distributions of group 1 were defined by a large proportion of *A. rubrum* and, to a lesser extent, "other" species (species that, individually, comprised a small proportion of the overall species composition) in the small diameter size classes and a distribution of *Q. rubra* and *Q.*

velutina that approximated normal (Fig. 6). At Amesbury Town Forest, "other" species included *Fagus grandifolia* Ehrh., *Castanea dentata* (Marsh.) Borkh., *Betula lenta* L., and *Carya glabra* (Mill.) Sweet. At Centennial Park, "other" species included *C. dentata*, *B. lenta*, *Juniperus virginiana* L., *A. saccharum* Marsh., and *Fraxinus americana* L.. The overall size class distributions of these two sites appeared slightly right-skewed, with a higher proportion of stems in the first five size classes. A notable difference in species composition between the two sites was the presence of *Q. alba* in most size classes at Centennial Park.

Group 2 included a single site (Turkey Hill) dominated by *Q. velutina* in the largest size classes. With high abundance of *A. rubrum* in all but the largest size class, Turkey Hill was unique in terms of overstory species composition (Fig. 7). The diameter distribution of Turkey Hill appeared right-skewed and bi-modal, with peaks in the 7.5 to 15.0 cm and 22.6 to 30.0 cm size classes. In addition to *A. rubrum* and *Q. velutina*, *P. strobus* and "other" species, including *F. grandifolia*, *Prunus serotina* Ehrh., *B. populifolia* Marsh., *P. pensylvanica* L. f., and *J. virginiana* were also present across the lowest four diameter classes. *Q. rubra* and *Q. alba* were also minor components in many of the size classes.

The size class distributions of Group 3 (Borderland State Park, Iron Rail, and Bradley Palmer State Park) were highly right-skewed, with *Quercus* (Borderland and Iron Rail) or *P. strobus* (Bradley Palmer) comprising the larger diameter classes. Group 3 was dominated by "other" species, including *F. grandifolia*, *C. dentata*, *Nyssa sylvatica* Marsh., *Cornus florida* L., *Ostrya virginiana* (Mill.) K. Koch, *Sassafras albidum* (Nutt.) Nees, *A. saccharum*, *B. alleghaniensis* Britton, *P. serotina*, *Tsuga canadensis* L., *C.*

glabra, *C. ovata* (Mill.) K. Koch, and *J. virginiana* in the 7.5 to 15 cm size class and had high species richness in the three smallest size classes (Fig. 8).

Group 4 (Great Brook Farm State Park (GBF), Willowdale State Forest (WSF), and Lockwood Town Forest (LTF)) was dominated by *Q. velutina* and *P. strobus* (GBF), *Q. rubra*, *Q. velutina*, and *P. strobus* (WSF), or *Q. rubra* (LTF) in the large diameter size classes. This group was defined by the abundance of *P. strobus* in the 7.5 to 15.0 cm size class and by an overall rotated-sigmoid size class distribution (Fig. 9).

Quercus and *P. strobus* dominated the large diameter size classes of Group 5 (Blue Hills State Reservation, Profile Rock State Park, Wildcat Conservation Area, and Wompatuck State Park) and this group is defined by the presence of *Acer rubrum*, *P. strobus*, and "other" species in the two smallest diameter classes. Across all sites, "other" species include *F. grandifolia*, *B. lenta*, *Populus grandidentata* Michx., *T. canadensis*, *C. glabra*, *C. ovata*, *P. resinosa* Ait., *S. albidum*, *B. alleghaniensis*, *C. dentata*, *N. sylvatica*, *B. populifolia*, *B. papyrifera* Marsh., and *Ilex opaca* Ait.. The diameter distributions for these sites appeared right-skewed (Fig. 10). Blue Hills was dominated by *P. strobus* in the larger diameter size classes. *Quercus rubra* and *Q. velutina* appeared normally distributed at Wildcat and Wompatuck. The Wompatuck distribution is characterized by an abundance of stems in the 7.5 to 15.0 cm, 15.1 to 22.5 cm, and 22.6 to 30.0 cm diameter classes.

Dendrochronology

Across all 13 sites, repeated measures analysis of *Quercus* and *P. strobus* annual RWI values from 1980-2010 revealed a significant interaction between time and species (univariate Greenhouse-Geiser Epsilon $P < 0.0001$; Figure 11). Two periods of divergence (1985-1990 and 2003-2010) may have influenced the significance of the interaction between time and *Quercus* RWI and *P. strobus* RWI. Although the 1985-1990 divergence was outside the focus of the present study, and thus did not receive further analysis, a possible contributing factor for this divergence may include gypsy moth defoliation during the early 1980s. Post hoc *t*-tests of *Quercus* and *P. strobus* RWI from 1995-2010 revealed a significant divergence in *Quercus* radial growth compared to *P. strobus* from 2000-2001 ($P < 0.0001$ and $P = 0.0005$, respectively), 2003 ($P = 0.0449$), and 2005-2010 ($P = 0.0130$; $P < 0.0001$; and $P < 0.0001$; $P < 0.0001$; $P < 0.0001$, $P < 0.0001$, respectively). Of these years, the *Quercus* RWI values fell below the 18% defoliation threshold of 1.094 in 2006-2010, indicating five years of region-wide growth divergence between *Quercus* and *P. strobus* RWI.

At the individual site level, repeated measures analysis showed a significant interaction between time and species (*Quercus* vs. *P. strobus*) from 1980 to 2010 at each of the 13 sites. Post hoc tests from 1995-2010 revealed that nine sites contained winter moth defoliation events as defined by individual years in which the *Quercus* RWI value was significantly lower than the *P. strobus* RWI value *and* fell below the defoliation threshold of 1.094, with the earliest event occurring in 1996 (Table 2). Eight of the study sites showed multiple winter moth defoliation events; one (Bradley Palmer State Park) showed a prolonged radial growth reduction from 2007-2010 and three (Blue Hills State Reservation, Borderland State Park, and Willowdale State Forest) showed a reduction from 2008-2010 (Table 2). Thus, *Number of WM Defoliation Events* at the 13 study sites ranged from 0 to 4 years (Table 2).

Dendrochronological analysis of snag tree disks (*n* = 6) at the site of maximum *Quercus* mortality (Wompatuck State Park) indicated that this mortality occurred from 1987 through 2008 (Table 4), but five of the six trees died after 1995. Years since mortality was highly correlated (r = 0.9163) with snag class (Table 4). Of the four disks that were unable to be cross-dated, one was in snag class 2, one in snag class 3, and two were in snag class 4.

Analysis of variance indicated that there were no significant differences among the groups of sites defined by cluster analysis in *Percent of Quercus Basal Area in Dead Stems*; *Percent of Total Trees in Dead Stems*; *Stand Relative Density*; *Quercus Site Index*; or *Number of WM Defoliation Events* (Table 5).

Drought

Drought was not a significant predictor of *Quercus* RWI from 1980-2010 when tested using the May, June, July, June and July two month average, and July to June 12 month average PDSI values (Table 6). By contrast, *P. strobus* RWI was positively related to July PDSI ($P = 0.0119$) and the June and July two month average PDSI ($P = 0.0403$; Table 6).

Aerial Detection Survey Data

There was no correlation (r = -0.0994) between the numbers of years of defoliation events at each site from ADS data and the variable *Number of WM Defoliation Events.*

Percent of Quercus *Basal Area in Dead Stems*

Twelve models evaluated the relationship between the dependent variable *Percent of Quercus Basal Area in Dead Stems* and the explanatory variables *Number of*

WM Defoliation Events, *Quercus Site Index*, and *Stand Relative Density*. These models included the global model (*Percent of Quercus Basal Area in Dead Stems*, *Number of WM Defoliation Events*, *Quercus Site Index*, and *Stand Relative Density*, and the interactions between each variable) and each nested iteration. Five candidate models (ΔAIC*c* $\leq$ 4.00) were identified and, from these, variation in *Percent of Quercus Basal Area in Dead Stems* (arcsine square root) was explained by two competing models (Table 7). Based on the "best" model (ΔAIC*c* = 0.0; $r^2_{adj} = 0.20$), variation in *Percent of Quercus Basal Area in Dead Stems* was most strongly related to *Quercus Site Index* (parameter estimate = -0.009; SE ± 0.004); *percent of Quercus Basal Area in Dead Stems* declined as *Quercus Site Index* increased (negative parameter estimate, Fig. 12). Conversely, a highly competitive model (ΔAIC*c* = 1.04; $r^2_{adj} = 0.13$) indicated that variation in *Percent of Quercus Basal Area in Dead Stems* was positively related to *Number of WM Defoliation Events* (parameter estimate = 0.050; SE ± 0.030; Fig. 13). A third, albeit less competitive model (ΔAIC*c* = 2.78; $r^2_{adj} = 0.22$), explained *Percent of Quercus Basal Area in Dead Stems* as a function of both *Quercus Site Index* (parameter estimate = -0.007; SE ± 0.005), and *Number of WM Defoliation Events* (parameter estimate = 0.034; SE ± 0.030).

Understory Density

Four models evaluated the relationship between *Understory Density*, *Stand Relative Density* and *Number of WM Defoliation Events* (Table 8). In the best model (ΔAIC*c* = 0.00; $r^2_{adj} = 0.31$) variation in *Understory Density* was positively related (Figure 14) to *Number of WM Defoliation Events* (parameter estimate = 27,121.03; SE ±

10,759.48); none of the other three models competed strongly (ΔAIC*c* $\leq$ 4.00) with this "best" model (Table 8).

Discussion

Mixed - *Quercus* and *P. strobus* – *Quercus* forest communities are abundant throughout Massachusetts (Swain and Kearsley 2001) and these forest types dominated my study sites. Winter moth was present in the forests I sampled and dead *Quercus* basal area at these sites was positively associated with the number of winter moth defoliation events, although *Quercus* site index was an equally effective predictor. *Quercus* species are important components of forests in the eastern United States (Abrams 1996) and mixed - *Quercus* and *P. strobus* – *Quercus* forest communities are abundant in other areas infested with winter moth including New Hampshire (Sperduto and Nichols 2004), Maine (Maine Natural Areas Program), Connecticut (Hochholzer 2010) and Rhode Island (Enser et al. 2011). Although my study was limited to upland forest sites, the polyphagous winter moth is likely present and active in a variety of additional habitats in eastern Massachusetts.

Winter moth may be responsible for a reduction of *Quercus* radial growth in some of the 13 studied forest stands. Annual radial growth (RWI) of *Quercus*, a winter moth host, and *P. strobus*, a non-host species, showed similar patterns between 1980 and 2010, but *Quercus* RWI was lower during two periods: 1985-1990 and 2003-2010. Figure 11 incorporates the widespread gypsy moth outbreak of 1981and it is evident that both *Quercus* and *P. strobus* radial growth was influenced negatively by this event. *Quercus* and *P. strobus* both appeared to recover in the years following this outbreak; however, in 1985 to 1990 *P. strobus* RWI exceeded that of *Quercus*. Although the radial growth trend from 1985 to 1990 is somewhat consistent between the two species groups, some factor or combination of factors reduced *Quercus* radial growth in relation to *P. strobus*.

In the period 1995 to 2010, radial growth of *Quercus* was significantly lower than *P. strobus* in 2000 and 2001, 2003, and from 2005-2010 (Figure 11). The radial growth divergence between these species groups in the years 2000 and 2001 is more reflective of an increase in *P. strobus* radial growth than of a decrease in *Quercus* radial growth. However, the trend that initiated in 2003 and continued from 2005-2010 is indicative of a stagnation of *Quercus* radial growth and a concomitant increase in *P. strobus* radial growth. These patterns, and the reduction of *Quercus* RWI below the 18% winter moth defoliation threshold from 2006-2010, suggest that some factor specific to *Quercus* was active during this time period. Our drought results may help explain this phenomenon. Except for the year 2005, in which July (PDSI = -0.57) and June and July two month average (PDSI = -0.61) PDSI values were slightly below normal (PDSI = 0), all the years in the 2003-2010 time period experienced a normal or excess of precipitation. For comparative purposes, a PDSI value of -2 suggests moderate drought conditions (Palmer 1965). The normal to above-normal PDSI values that occurred in Massachusetts from 2003-2010 (except 2005) and the positive relationship between *P. strobus* RWI and PDSI suggest that soil moisture conditions were sufficient for tree growth during this time period.

While the lack of relationship between *Quercus* RWI and PDSI could merely indicate physiological differences between *Quercus* and *P. strobus*, it could also indicate a *Quercus*-specific limiting factor. Speer et al. (2009), working in the southern Appalachian mountains of the United States, found a significant positive correlation between June and July PDSI and the radial growth of several *Quercus* species, including *Q. rubra* and *Q. velutina*. In addition, in southwestern Quebec, Canada, Tardif and Conciatori (2006) found a positive relationship between *Q. rubra* and *Q. alba* and June and July precipitation. That *Quercus* RWI was not related to PDSI in the present study implies that moisture was not a limiting factor for *Quercus* growth during the 2003 to 2010 time period and suggests that some other limiting factor weakened the relationship between *Quercus* radial growth and PDSI. Moreover, the positive growth trend of *P. strobus* suggests that this species was experiencing favorable growing conditions during the 2003 to 2010 period. When considering the positive relationship between winter moth defoliation (as defined by dendrochronological analysis) and the percentage of *Quercus* basal area in dead stems, these patterns suggest that *P. strobus* RWI was positively affected by preferential winter moth defoliation on *Quercus* through reduced competition for canopy space (dead *Quercus*) and possibly reduced competition for soil water and nutrients.

While many factors likely influence the growth and vigor of *Quercus* at our study sites, several pieces of evidence point to winter moth as a causal agent of relatively low radial growth at some sites since 1995. First, winter moth has been a dominant defoliator in eastern Massachusetts during the past decade (JS Elkinton, personal communication) and winter moth presence was confirmed at each of our study sites. Second, the significant radial growth divergence between *Quercus* and *P. strobus* RWI during this time period suggests the presence of a stressor that is specific to *Quercus* at these sites. Third, radial growth analyses of individual trees throughout this region (including at some of the study sites of the present study) found that winter moth defoliation was a strong predictor of radial growth of *Quercus* trees defoliated by winter moth, when tested concurrently with site and year as random covariates (Chapter 1); however other potentially influential factors (e.g., other defoliators, pathogens, physical stressors) were not tested.

My results suggest that winter moth may have also induced tree mortality. I used percentage of *Quercus* basal area in dead stems as a measure of mortality, and as this variable is just a snapshot in time, it is not necessarily representative of *rates* of mortality. Thus, caution must be exercised when interpreting the impact of winter moth defoliation on tree mortality. However, the snag data provide insight into the utility of 'percentage of *Quercus* basal area in dead stems. Snag class distributions showed that greater than 60% of the *Quercus* standing dead trees at more than half of our sites were in snag classes 1 to 3. Dendrochronological analysis of snag trees at one site (Wompatuck State Park) revealed that snags in classes 2 and 3 died within the last 2 to 14 years (as dated from 2010). This suggests that much of the mortality at our study sites occurred between 1995 and 2010, the assumed period of winter moth activity in the study region. However, there is great error variation in aging standing and fallen dead trees (Daniels et al. 1997) and snag longevity can be influenced by geographic region and site conditions (Yamasaki and Leak 2006). As such, there may be limitations in assigning age to snag classes across all 13 study sites with a sample of six trees at one site; this warrants caution with the assumption that percent *Quercus* basal area in dead trees is reflective of recent stand mortality.

The percentage of *Quercus* basal area in dead stems at the 13 study sites was best predicted by *Quercus* site index and the number of winter moth defoliation events. The lack of a strong relationship between stand relative density and the percentage of *Quercus* basal area in dead trees indicates that the observed mortality at our sites was not driven by density-dependent mortality associated with stand competition. Rather, it implies that some other, density-independent factor was driving this mortality. Although I cannot be certain that *Quercus* mortality was strictly attributable to winter moth (and not some other defoliators, pathogens, or physical disturbances), the abundance of winter moth in eastern Massachusetts over the last decade, the known relationship between percent winter moth defoliation and radial growth (chapter 1), and the dominance of dead *Quercus* trees in snag classes 1 to 3 (and thus the assumption of tree mortality occurring within the 1995-2010 period) collectively implicate winter moth as an important contributor to *Quercus* mortality in these forests.

Quercus mortality at the 13 study sites was influenced by site quality and winter moth defoliation. The lack of a clear 'best' model explaining percent *Quercus* basal area in dead stems indicates the interrelationship between the variables *Quercus* site index and the number of winter moth defoliation events. At some sites the combination of low *Quercus* site index and multiple, consecutive winter moth defoliation events were associated with high levels of *Quercus* mortality, relative to other sites. For example, Blue Hills State Reservation and Borderland State Park each had relatively low *Quercus* site index values (45 and 50, respectively) and experienced three consecutive winter moth defoliation events, and these were associated with relatively high levels of *Quercus* mortality (18% and 12%, respectively). Conversely, at Amesbury Town Forest and Great Brook Farm State Park, the combination of relatively high *Quercus* site index values (77 and 71, respectively) and only two, disjunct winter moth defoliation events were associated with only 6% and 2% *Quercus* basal area mortality, respectively. In these cases, the high site productivity for *Quercus* at these sites may have compensated for any loss of vigor associated with nonconsecutive defoliation events.

At other sites, one of the variables (*Quercus* site index; number of winter moth defoliation events) may have been more influential than the other in explaining *Quercus* basal area mortality. This is evident in data from two neighboring sites, Willowdale State Forest and Bradley Palmer State Park. Although Willowdale State Forest experienced three consecutive years of winter moth defoliation from 2008 to 2010, the relatively high *Quercus* site index value of this site (68) may have compensated for winter moth defoliation and contributed to the relatively low observed *Quercus* basal area mortality (4%). By contrast, Bradley Palmer State Park experienced four years of consecutive winter moth defoliation, from 2007-2010, and although comparable in *Quercus* site index (66) to Willowdale State Forest, this site had the second highest percentage of *Quercus* basal area in dead stems (28%) among all 13 study sites. It is unclear what causes the large difference in mortality at sites with such similar characteristics, but this may reflect the additional year of stress attributable to winter moth defoliation.

Of course, other factors may have influenced this dramatic difference in *Quercus* basal area mortality between these two sites. The high percentage of *Quercus* basal area mortality at Bradley Palmer State Park may be a function of differences in overall species compositions between sites. Specifically, at Bradley Palmer the *Quercus* may have been further stressed due to competition by the dominance of *P. strobus* in the large diameter size classes (Figure 8c). Alternately, although I do not have data on re-leafing subsequent to defoliation, perhaps this phenomenon may explain these differing mortality figures between the two sites. Regrowth of leaves following defoliation has been observed in *Quercus* and this response may partially mitigate the impacts of defoliation (Heichel and Turner 1983). Perhaps conditions at Willowdale were more conducive to refoliation than at Bradley Palmer. Or, perhaps dead trees simply fall over more quickly at Willowdale and I did not capture this mortality in our plot sampling. Although coarse woody debris within our plots was limited, cursory observations throughout the stand revealed a fairly high occurrence of down dead trees.

Data from Wompatuck State Park highlight the importance of taking a temporal view of mortality when assessing the impact of defoliation and suggest that the effects of winter moth defoliation on forest stand dynamics may be complex. Wompatuck State Park had the highest percentage of *Quercus* basal area in dead stems (30%), the second lowest *Quercus* site index (46), and only two, nonconsecutive years of winter moth defoliation (2000 and 2008). However, elevated levels of winter moth defoliation have been noted at Wompatuck State Park throughout the winter moth infestation in Massachusetts (G. Boettner, UMass-Amherst and K. Gooch, MA-DCR, personal communication) and this site is located in one of the earliest regions (southeastern Massachusetts) heavily defoliated by winter moth (Childs et al. 2003). In addition, this site had the longest duration of winter moth activity from the ADS data (data not shown). *Quercus* mortality at this site occurred from 1987 to 2008 (Table 3). The lack of prolonged divergence between *Quercus* and *P. strobus* RWI suggest that, over time, the effects of being released from competition (i.e. from neighboring trees dying) have been greater than the effects of defoliation on extant trees. In gypsy moth invasions, a greater percentage of tree mortality may occur during the initial defoliation event than in subsequent defoliation events (Gottschalk 1993). Perhaps, at Wompatuck State Park, as an incipient wave of winter moth defoliation occurred, some trees died while others periodically experienced reduced radial growth (and perhaps reduced crown expansion). Subsequently, canopy gaps created by dead trees (likely induced by winter moth defoliation) may have reduced competition of extant trees which, over time, compensated for radial growth reduction attributable to winter moth defoliation.

Although there may be variation among sites, across all 13 study sites *Quercus* mortality increased with increasing number of winter moth defoliation events. Moreover, site quality influenced *Quercus* mortality, with mortality increasing on poor quality *Quercus* sites. On more productive *Quercus* sites, high *Quercus* site index may have compensated for winter moth defoliation and reduced mortality.

My result that winter moth defoliation may contribute to *Quercus* mortality is consistent with reports of novel winter moth defoliation in Nova Scotia, as Cuming (1961) and Embree (1967) observed deterioration and mortality of *Q. rubra* following repeated winter moth defoliation. In addition, my inference about winter moth defoliation, site quality, and tree mortality are similar to the effects reported for other defoliators, including European gypsy moth, *Lymantria dispar* L. In a review of the gypsy moth literature, Davidson et al. (1999) note that tree mortality is related to duration, intensity and frequency of defoliation and site quality. Campbell and Sloan (1977) concluded that two consecutive events of heavy gypsy moth defoliation increased tree mortality levels to a greater extent than one defoliation event. Fosbroke and Hicks (1989) also reported greater tree mortality with increasing years of gypsy moth defoliation and noted substantial increase in tree mortality rate following a second defoliation. Moreover, Fosbroke and Hicks (1989) found that the percentage of tree mortality at sites defoliated by gypsy moth was greatest (26% mortality) on poor quality sites (SI < 60).

Winter moth defoliation may alter the trajectory of forest stand dynamics, as defoliation can accelerate stand dynamics through the creation of canopy gaps via tree mortality (Campbell and Sloan 1977; Reinikainen et al. 2012). This phenomenon is shown by my understory density results. The density of understory tree and shrub, seedling and saplings increased with the number of winter moth defoliation events. This increase in understory woody plant establishment and/or growth was likely caused by 1) increased understory light conditions from canopy gaps caused by tree mortality and, 2) increased diffuse understory light conditions provided by partially defoliated tree crowns. Canopy gaps are important in shaping forest community structure (e.g., McClure and Lee 1993). Canopy disturbance and gap formation following insect defoliation can facilitate understory plant establishment and/or growth. For example, defoliation outbreaks by forest tent caterpillar, *Malacosoma disstria* Hübner, and spruce budworm, *Choristoneura fumiferana* Clemens, have contributed to the establishment of multiple cohorts of tree species in mixed-*Populus tremuloides* Michx. forests (Reinikainen et al. 2012). Likewise, gypsy moth defoliation has facilitated understory growth (Campbell and Sloan 1977; Fajvan and Wood 1996; Jedlicka et al. 2004).

That understory density increased with the number of winter moth defoliation events in my study suggests that winter moth creates canopy gaps that contribute to species, age, and structural diversity within these forests. For example, at Wompatuck State Park, which had the highest level of dead *Quercus* basal area, the diameter distribution (Figure 10d) and understory density reveal high abundances in the 7.5 to 30 cm diameter classes and in woody stems less than 7.5 cm, relative to most other sites. The abundances in these size classes may reflect multiple canopy disturbance events that included an initial event that released some of the smaller diameter trees (though greater than 7.5 cm) and allowed them to persist and grow into larger diameter size classes. This may be supported by the occurrence of *A. rubrum* in the 7.5 – 15.0, 15.1 – 22.5, and 22.6 – 30.0 cm diameter classes, as this species can establish as advance regeneration and compete successfully in gaps (McClure et al. 2000). In addition, the high density of woody vegetation in the understory suggests a more recent disturbance that facilitated the establishment of this smaller diameter cohort.

It is likely that winter moth defoliation is not the sole contributor to mortality noted at our sites. Rather, winter moth likely initiates a sequence of decline that involves a suite of factors. The relationship between insect defoliation and subsequent attack by secondary agents, notably the wood boring two-lined chestnut borer, *Agrilus bilineatus* Weber, and *Armillaria* species root fungi, is well established (Staley 1965; Wargo 1996). This decline complex (*sensu* Houston 1992) progresses as an inciting factor (e.g. insect defoliation; drought) stresses a forest stand and facilitates invasion and subsequent mortality by either *A. bilineatus* or *Armillaria* spp., or both (Wargo 1977). Mortality attributable to this decline complex can occur up to three years subsequent to prolonged defoliation (2-3 years of consecutive defoliation events) (Wargo 1996). Given the importance of *Armillaria* fungi in mixed-*Quercus* forests in western and central Massachusetts (Brazee and Wick 2009; Brazee et al. 2012), this has important consequences for our study area, as four of my study sites have experienced successive years of radial growth reduction (Table 2). The dynamics of winter moth defoliation suggest that the three to four year window of radial growth decline at these sites is likely attributable winter moth activity, as chapter 1 reports that winter moth defoliation can have a multiple year influence on radial growth. Specifically, winter moth defoliation caused a concomitant reduction in the radial growth of *Quercus* latewood and a reduction in *Quercus* earlywood in the following growth season. Thus, one can conclude that two years of heavy winter moth defoliation can negatively affect *Quercus* radial growth for at least three years of radial growth.

While endemic defoliating insects are an important natural component of forest systems (Mattson and Addy 1975), prolonged forest decline initiated by exotic/invasive herbivores may have detrimental cascading effects (Gandhi and Herms 2010). Simberloff and Von Holle (1999) suggested an "invasional meltdown" in which canopy gaps created by the invasion of exotic forest insects can facilitate the success of exotic invasive plants in the understory (Gandhi and Herms 2010). Evidence for this phenomenon has been reported with invasions by gypsy moth (McEwan et al. 2009), hemlock woolly adelgid (*Adelges tsugae*) (Orwig and Foster 1998), and, following eradication efforts, emerald ash borer (*Agrilus planipennis*) (Hausman et al. 2009). Although I did not specifically test for this phenomenon, our result that understory density increases with winter moth defoliation suggests that winter moth defoliation could contribute to invasional meltdown in eastern Massachusetts forests. *Frangula alnus* (glossy buckthorn) is an exotic, invasive shrub that is well established in eastern North America (Frappier et al. 2004) and was present in the understory of eight of our 13 study sites, often in high densities (data not shown). High densities of *F. alnus* can inhibit native tree regeneration (Frappier et al. 2004) and canopy gaps can facilitate the success of *F. alnus* in the understory (Burnham and Lee 2010). Canopy gap size may influence the success of *F. alnus*, with performance increasing with increasing gap size (Burnham and Lee 2010), to a certain degree (Lee and Thompson 2012).

Conclusion

I have presented information on a novel invasion of winter moth into forests of eastern Massachusetts. While the correlative nature of this study precludes specific assumptions, some general patterns on the invasion ecology of winter moth in this region emerge. First, winter moth has invaded mixed - *Quercus* and *P. strobus* - *Quercus* forests of varying age and structure. Second, winter moth defoliation caused a region-wide (eastern Massachusetts) reduction in *Quercus* radial growth, comparable to non-host *Pinus strobus*. Third, winter moth defoliation events may increase *Quercus* mortality in infested forests and influence understory plant density. Fourth, complex interactions among competition, site quality, and duration of winter moth activity may, ultimately, determine the severity of effects associated with winter moth defoliation.

Quercus species are important components of forests in the eastern United States (Abrams 1996) and winter moth defoliation contributed to *Quercus* mortality in forests throughout eastern Massachusetts. Winter moth has successfully invaded forests throughout New England (Elkinton et al. 2010) and continues to move into new areas. The findings of this study have broad application across eastern North America, as the species composition and climate of the deciduous forests of this region offer ideal habitat for winter moth (MacPhee 1967; Elkinton et al. 2010). Detection and control efforts for this insect are warranted.

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Table 1. Name, location, *Quercus* density and quadratic mean diameter (DBH), and understory woody plant density of 13 winter moth study sites, eastern Massachusetts. TF = town forest; SR = state reservation; SP = state park; TP = town park; CA = conservation area; SF = state forest.

Site	Location	*Quercus* Density (stems/ha)	*Quercus* Mean DBH (cm)	Understory Density (stems/ha)
Amesbury TF	42° 51'N; -70° 58'W	315.2	32.3 ± 1.3	35,230
Blue Hills SR	42° 13'N; -71° 07'W	245.3	25.9 ± 1.1	261,313
Borderland SP	42° 04'N; -71° 10'W	344.4	23.5 ± 0.8	136,943
Bradley Palmer SP	42° 39'N; -70° 54'W	114.9	33.7 ± 2.8	95,226
Centennial Park	42° 18'N; -71° 16'W	237.4	35.9 ± 1.3	42,794
Great Brook Farm SP	42° 33'N; -71° 21'W	177	37.0 ± 1.5	51,524
Iron Rail TP	42° 36'N; -70° 51'W	271	32.7 ± 2.2	48,168
Lockwood TF	42° 38'N; -70° 59'W	141.4	36.5 ± 1.8	60,830
Profile Rock SP	41° 48'N; -71° 03'W	140	39.5 ± 2.9	112,795
Turkey Hill CA	42° 41'N; -70° 52'W	78.72	39.6 ± 1.8	59,600
Wildcat CA	42° 41'N; -71° 01'W	309.4	27.8 ± 0.7	11,306
Willowdale SF	42° 40'N; -70° 54'W	201.5	37.2 ± 2.1	155,749
Wompatuck SP	42° 13'N; -70° 52'W	248.4	29.3 ± 0.8	92,554

Table 2. *Quercus* site index values, stand relative density, *Quercus* and *P. strobus* mean age, percentage of *Quercus* basal area in dead trees, and number of winter moth defoliation events, as determined by dendrochronology at 13 study sites, eastern Massachusetts. SI = site index; RD = relative density.

Site	***Quercus*** **SI**	**Stand RD**	***Quercus*** **Age**	***P. strobus*** **Age**	**%** ***Quercus*** **In Dead Trees**	**Years and # of WM Def. Events**
Amesbury TF	77	0.83	76	86	6%	1999; 2001 (2)
Blue Hills SR	45	0.76	85	84	18%	2008-2010 (3)
Borderland SP	50	0.69	106	68	12%	2006; 2008-2010 (4)
Bradley Palmer SP	66	0.84	89	107	28%	2007-2010 (4)
Centennial Park	65	0.86	89	65	4%	0
Great Brook Farm SP	71	0.74	95	81	2%	1996; 2005 (2)
Iron Rail TP	72	0.71	59	53	5%	0
Lockwood TF	62	0.60	89	78	0%	2001; 2010 (2)
Profile Rock SP	60	0.81	94	64	3%	2005 (1)
Turkey Hill CA	65	0.71	67	84	4%	0
Wildcat CA	66	0.60	72	85	7%	0
Willowdale SF	68	0.88	90	89	4%	2008-2010 (3)
Wompatuck SP	46	0.61	97	89	30%	2000; 2008 (2)

Table 3. Site, tree species, diameter, location of trap on tree, date range of trapping and results of sticky band trapping surveys at nine sites in eastern Massachusetts. WM = winter moth; FC = fall cankerworm.

Site	Spp	DBH (cm)	Upper / Lower	Date	WM	FC
Amesbury TF	#1 RO	34.3	Lower	11/20 - 12/4	0	
			Upper	11/20 - 12/4	0	
	#2 RO	43.7	Lower	11/20 - 12/4	2	
			Upper	11/20 - 12/4	0	
Blue Hills SR	#1 RO	39.1	Lower	11/20 - 12/4	40	
			Upper	11/20 - 12/4	8	
	#2 RO	23.9	Lower	11/20 - 12/4	4	
			Upper	11/20 - 12/4	3	
Borderland SP	#1 SO	35.3	Lower	11/27 - 12/11	32	3
			Upper	11/27 - 12/11	9	
	#2 RO	26.7	Lower	11/27 - 12/11	3	
			Upper	11/27 - 12/11	5	
Great Brook Farm SP	#1 RO	39.9	Lower	11/20 - 12/4	0	
			Upper	11/20 - 12/4	0	
	#2 BO	21.3	Lower	11/20 - 12/4	1	
			Upper	11/20 - 12/4	0	
	#3 SO	33	Lower	11/20 - 12/4	0	
			Upper	11/20 - 12/4	0	
Lockwood TF	#1 RO	25.4	Lower	11/20 - 12/4	72	1
			Upper	11/20 - 12/4	17	
	#2 RO	37.6	Lower	11/20 - 12/4	94	
			Upper	11/20 - 12/4	60	
Profile Rock SP	#1 RO	25.4	Lower	11/27 - 12/11	2	1
			Upper	11/27 - 12/11	0	
	#2 RO	27.9	Lower	11/27 - 12/11	3	1
			Upper	11/27 - 12/11	0	
Turkey Hill CA	#1 RO	30.1	only 1 trap	11/28 - 12/4	74	1
	#2 RM	13.7	only 1 trap	11/28 - 12/4	41	
Wildcat CA	#1 BO	21.3	Lower	11/20 - 12/4	0	
			Upper	11/20 - 12/4	1	
	#2 RO	34.3	Lower	11/20 - 12/4	4	
			Upper	11/20 - 12/4	0	
Willowdale SF	#1 RO	37.1	Lower	11/28 - 12/4	143	
			Upper	11/28 - 12/4	74	

Table 4. Diameter at 1.4 m (DBH), snag class, year of mortality and years since mortality (calculated from 2010) of six snag trees at Wompatuck State Park, Massachusetts.

Tree	DBH (cm)	Snag Class	Year of Mortality	Years Since Mortality
1	30.5	2	2008	2
2	27.3	2	2006	4
3	35.8	2	1999	11
4	25.6	3	1997	13
5	32.5	3	1996	14
6	24	4	1987	23

Table 5. Variable, *P*- value, F – ratio, and model and error degrees of freedom (DF) for analysis of variance between sites grouped by cluster analysis.

Variable	***P* - value**	**F - ratio**	**DF model**	**DF error**
% of Quercus BA in Dead Stems	0.2491	1.6684	4	8
% of Total Trees in Dead Stems	0.3202	1.3887	4	8
Stand Relative Density	0.6022	0.7193	4	8
Quercus Site Index	0.3206	1.3874	4	8
Number of WM Defoliation Events	0.5218	0.8699	4	8

Table 6. Results of linear regression between the region-wide (13 site) *Quercus* and *P. strobus* RWI dendrochronologies (dependent variable) and the May, June, July, two-month June and July average and 12-month July to June average Palmer Drought Severity Index (PDSI) in Massachusetts from 1980 to 2010. * indicates statistical significance ($P < 0.05$).

Species	**May PDSI**	**June PDSI**	**July PDSI**	**June-July 2 month avg.**	**July-June 12 month avg.**
Quercus	$P = 0.1354$	$P = 0.1378$	$P = 0.1404$	$P = 0.1226$	$P = 0.7135$
	$r^2_{adj} = 0.0433$	$r^2_{adj} = 0.0424$	$r^2_{adj} = 0.0415$	$r^2_{adj} = 0.0485$	$r^2_{adj} = -0.0087$
P. strobus	$P = 0.3091$	$P = 0.1565$	$P = 0.0119$*	$P = 0.0403$*	$P = 0.3444$
	$r^2_{adj} = 0.0024$	$r^2_{adj} = 0.0359$	$r^2_{adj} = 0.1714$	$r^2_{adj} = 0.1074$	$r^2_{adj} = -0.0026$

Table 7. Results of multiple regression on *Percent of Quercus Basal Area in Dead Trees* at 13 sites in eastern Massachusetts. ΔAIC*c* = corrected Akaike Information Criterion differences; SE = standard error.

Model Parameters	**Δ AIC*c***	**r^2_{adj}**	**Parameter Estimate**	**SE**	**Log Likelihood**	**Akaike Weight**	**Evidence Ratio**
Stand RD	4.03	-0.09	0.030	0.497	0.13	0.06	7.51
Site Index	3.48	0.18	-0.010	0.005	0.18	0.08	5.69
Stand RD			0.381	0.463			
Site Index	2.78	0.22	-0.007	0.005	0.25	0.12	4.02
# WM defoliation events			0.034	0.030			
# WM defoliation events	1.04	0.13	0.050	0.030	0.59	0.28	1.68
Site Index	0.00	0.20	-0.009	0.004	1.00	0.46	1.00

Table 8. Results of multiple regression on *Understory Density* at 13 sites in eastern Massachusetts. ΔAICc = corrected Akaike Information Criterion differences; SE = standard error.

Model Parameters	Δ AICc	r^2_{adj}	Parameter Estimate	SE	Log Likelihood	Akaike Weight	Evidence Ratio
Stand RD	9.42	0.19	77,065.34	178,423.80	0.01	0.01	110.89
# WM defoliation events			26,524.87	11,992.21			
*Stand RD * # WM defoliation events*			-50,165.78	135,010.40			
Stand RD	5.17	-0.03	159,237.48	196,194.80	0.08	0.06	13.27
Stand RD	4.04	0.26	80,855.00	170,282.20	0.13	0.11	7.55
# WM defoliation events			26,031.14	11,393.15			
# WM defoliation events	0.00	0.31	27,121.03	10,759.48	1.00	0.82	1.00

Figure 1. Winter moth defoliation event criteria decision tree.

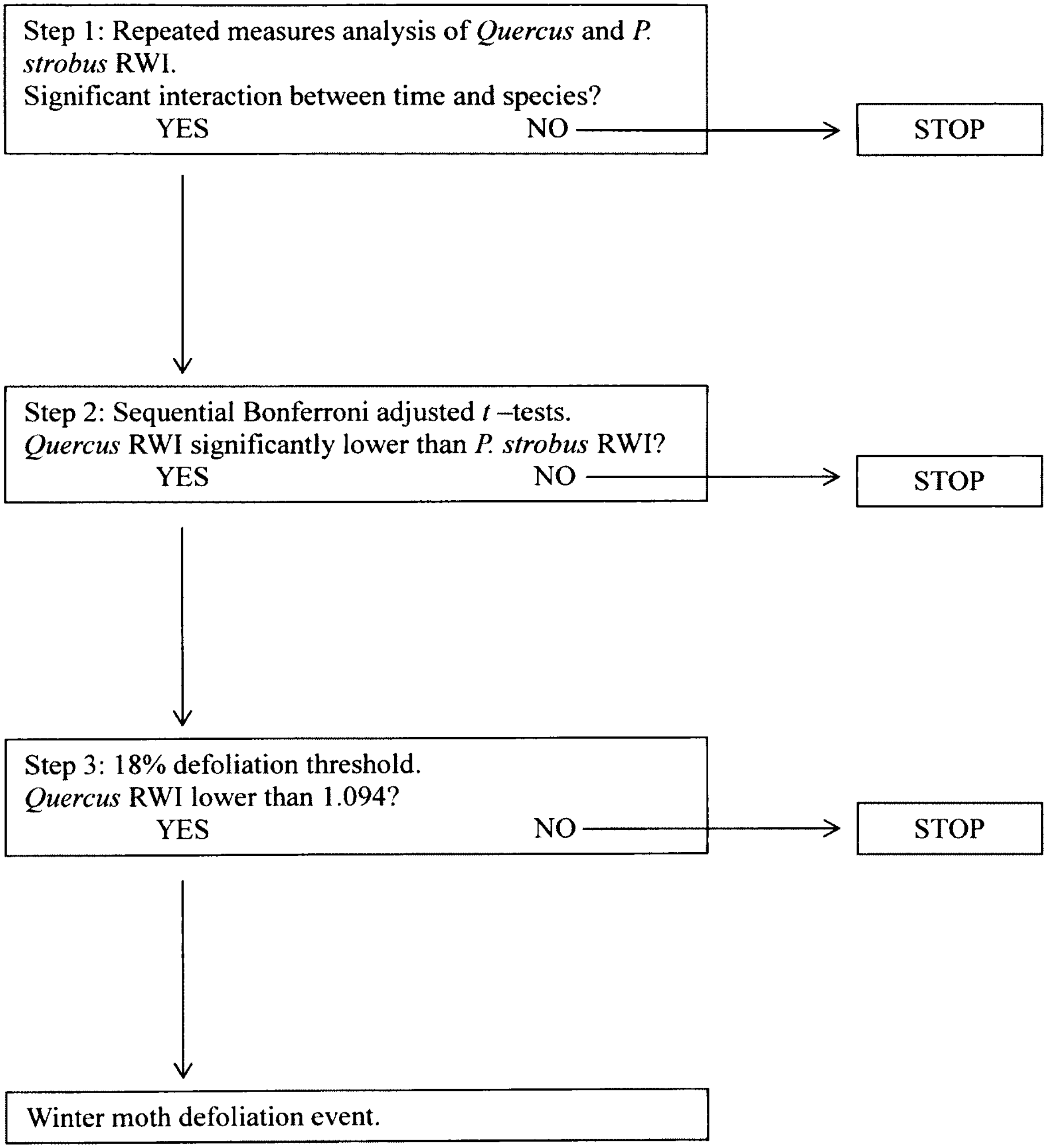


Figure 2. Leverage plot of *Quercus* RWI by defoliation (chapter 1) with 95% upper and lower confidence bands (red dashed line) and approximate location (blue solid lines) of point at which the upper 95% confidence limit equals the y-intercept RWI value of 1.202. Created in: JMP® Pro 10.0.0 software; SAS Institute Inc.

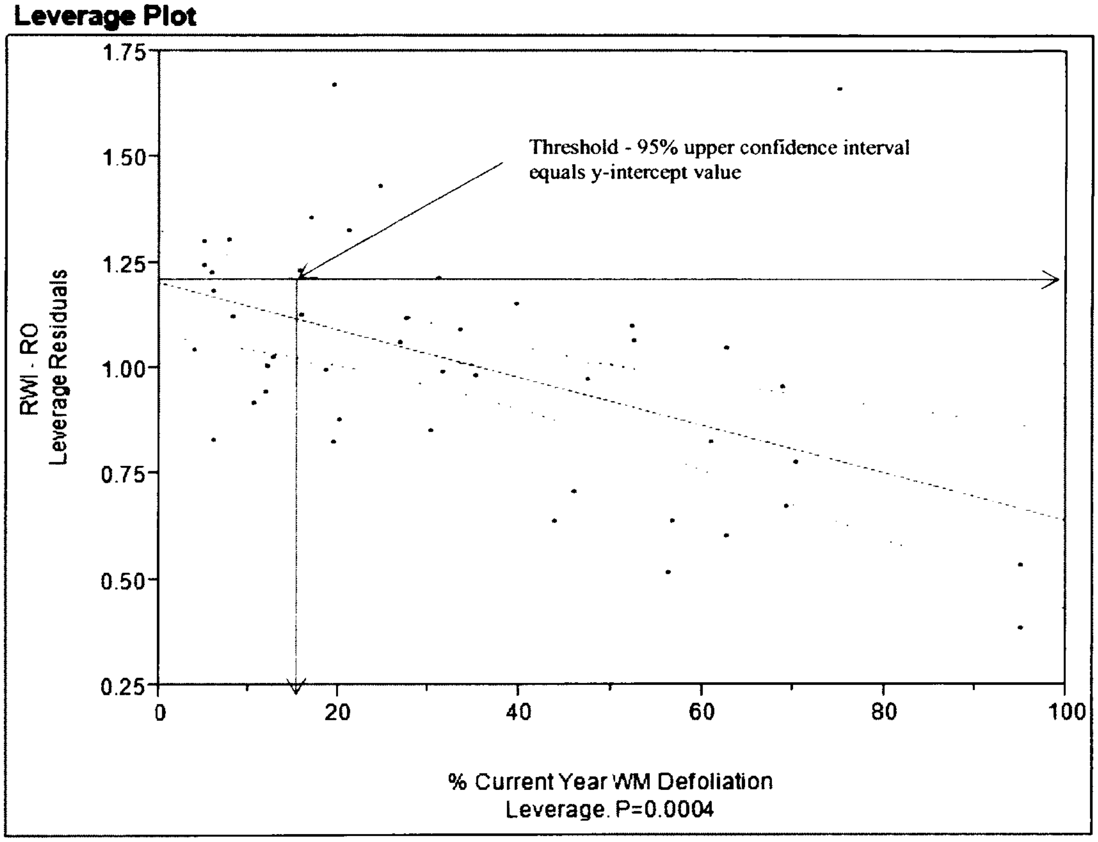


Figure 3. Winter moth study site locations; 13 sites, eastern Massachusetts. Citation: "Winter moth study site locations, eastern Massachusetts" [map]. 1:750,000. MJ Simmons GIS Data [computer files]. University of New Hampshire, 2013. Using: ArcMap® GIS [GIS software]. Version 10.0. Redlands, CA: Environmental Systems Research Institute, Inc., 2010. Basemap: USA State Plane Zones NAD 27 NAD 83, ArcGIS online; accessed from ArcMap® 10.0.

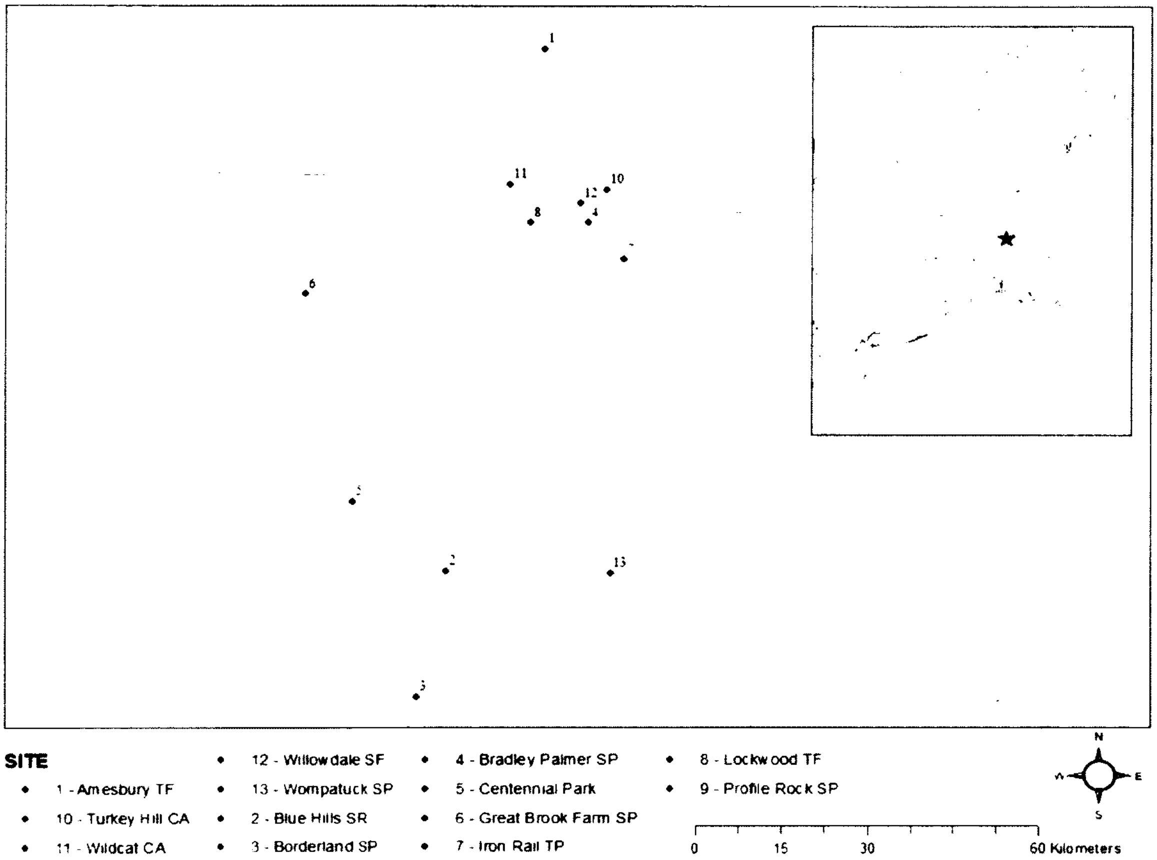


Figure 4. Percentages of dead trees in grouped by snag classes 1-3 (black bars) and snag classes 4 and 5 (gray bars) at all 13 sites in eastern Massachusetts.

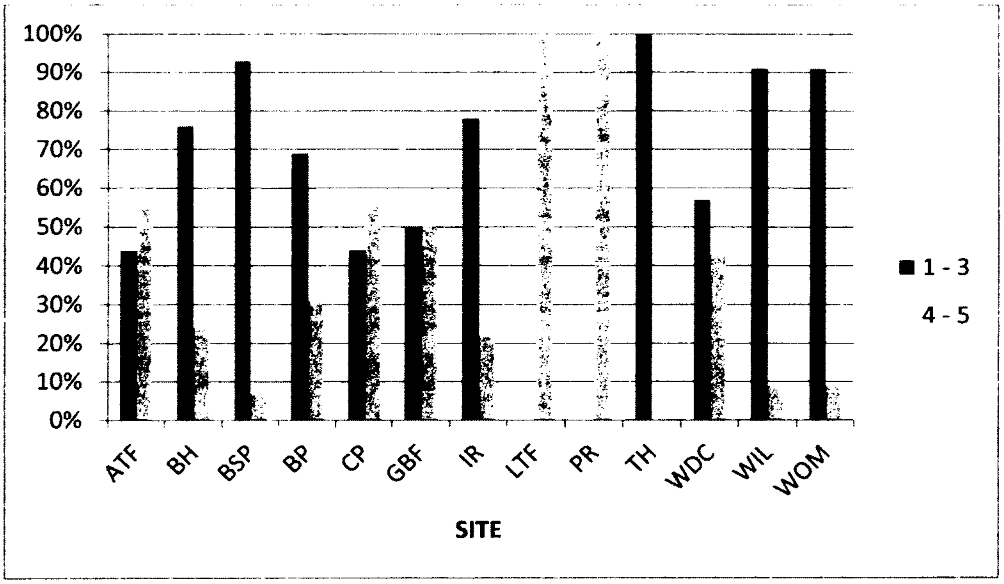


Figure 5. Cluster analysis dendrogram.

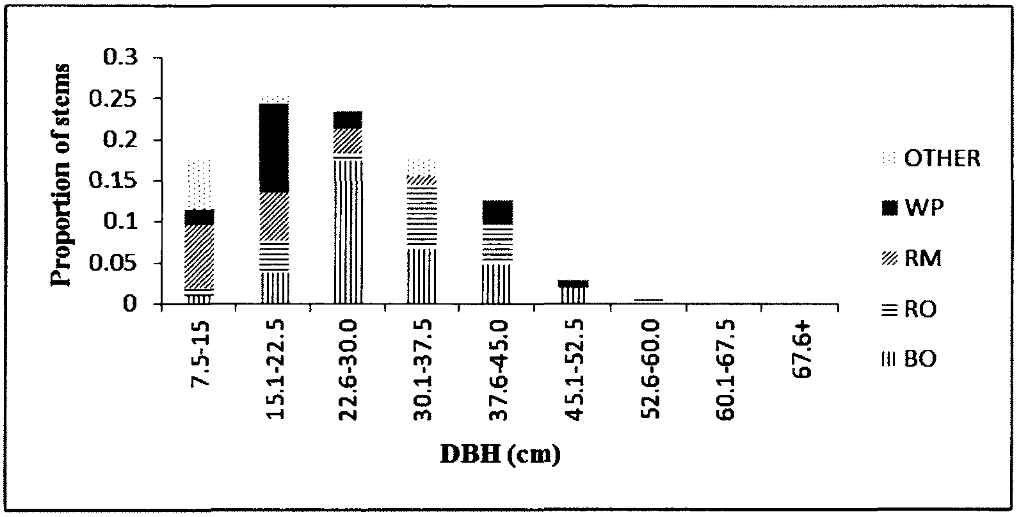
```
RED and WARDS = 0.00 chaining
Percent chaining =   0.00

                         Distance (Objective Function)
         0.056           1.414           2.773           4.132           5.491
          |-------+-------+-------+-------+-------+-------+-------+-------+
                         Information remaining (%)
     100.000          75.000          50.000          25.000           0.000
          |-------+-------+-------+-------+-------+-------+-------+-------+
ATF       ------|
                |----------------|
CP        ------|                |-------------------|
                                 |                   |
TH        -----------------------|                   |
                                                     |-------------------|
BSP       --|                                        |                   |
            |-|                                      |                   |
IR        --| |--------------------------------------|                   |
              |                                                          |
BP        ----|                                                          |
                                                                         |
BH        -----------|                                                   |
                     |-----|                                             |
PR        -----------|     |                                             |
                           |------------|                                |
WDC       ---------|       |            |                                |
                   |-------|            |                                |
WSP       ---------|                    |--------------------------------|
                                        |
GBF       |                             |
          |                             |
WSF       |-----------------------------|
          |
LTF       |
```

70% cutoff for group identification.

Figure 6. Tree size (diameter at breast height) class distribution for Group 1 – a) Amesbury Town Forest; b) Centennial Park.

a) Amesbury Town Forest



b) Centennial Park

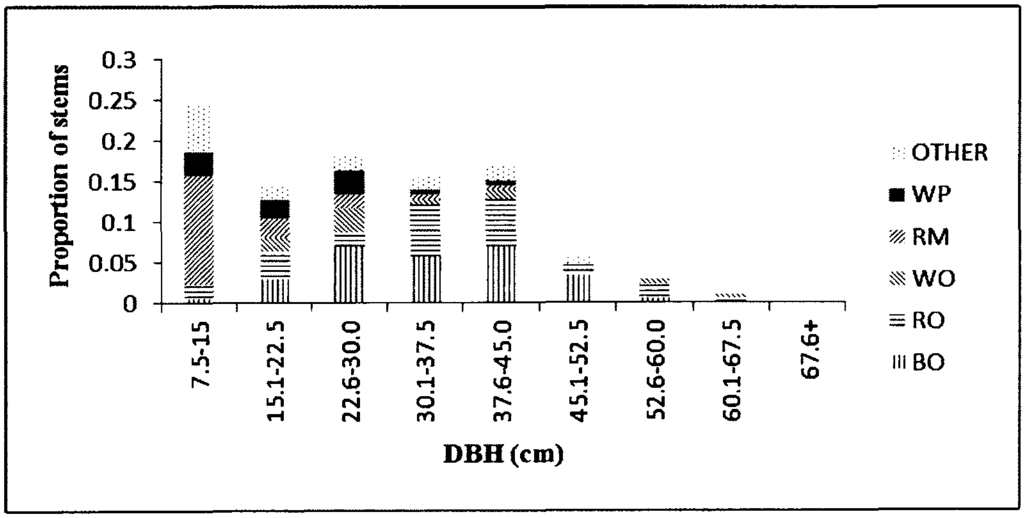


Figure 7. Tree size (diameter at breast height) class distribution for Group 2 – Turkey Hill Conservation Area.

Turkey Hill

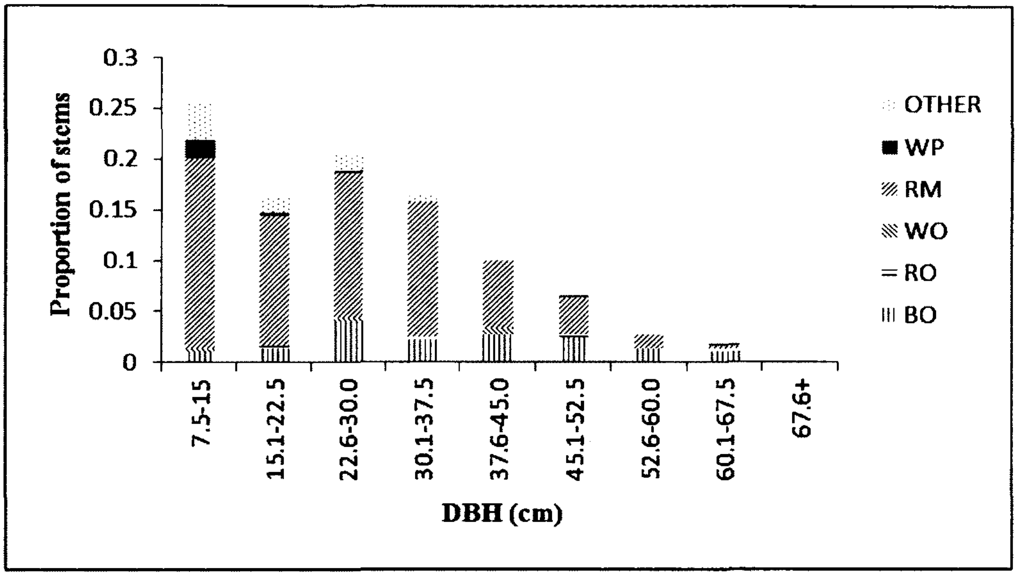
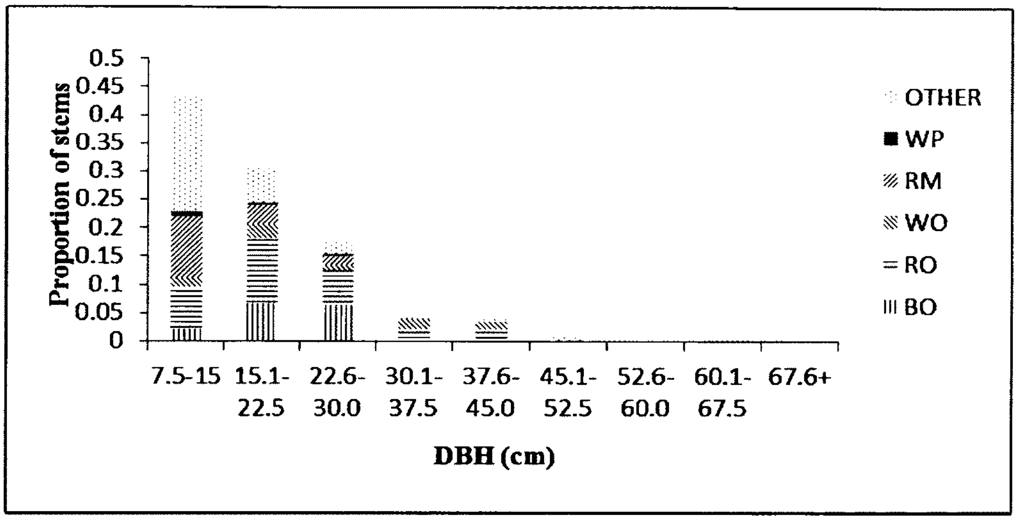
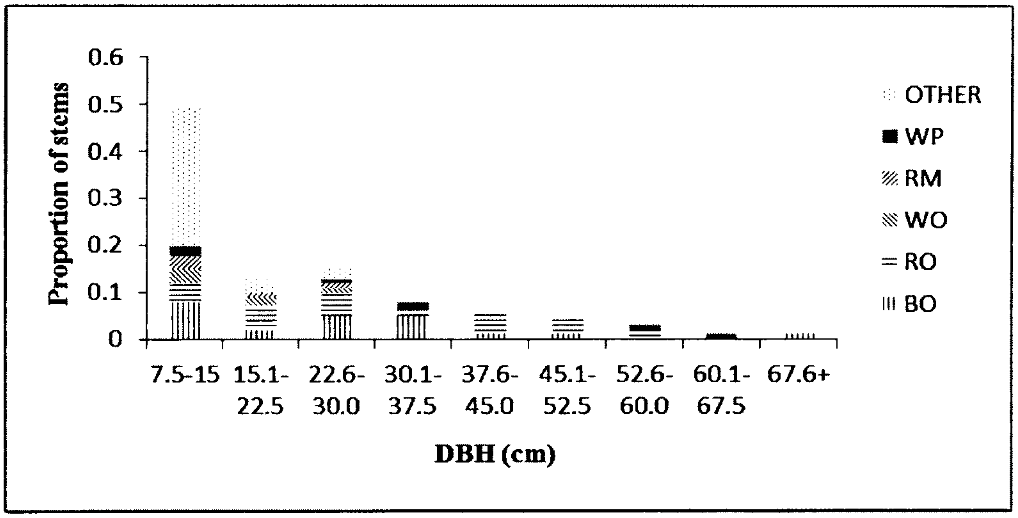


Figure 8. Tree size (diameter at breast height) class distribution for Group 3 – a) Borderland State Park; b) Iron Rail; c) Bradley Palmer State Park.

a) Borderland State Park



b) Iron Rail



c) Bradley Palmer

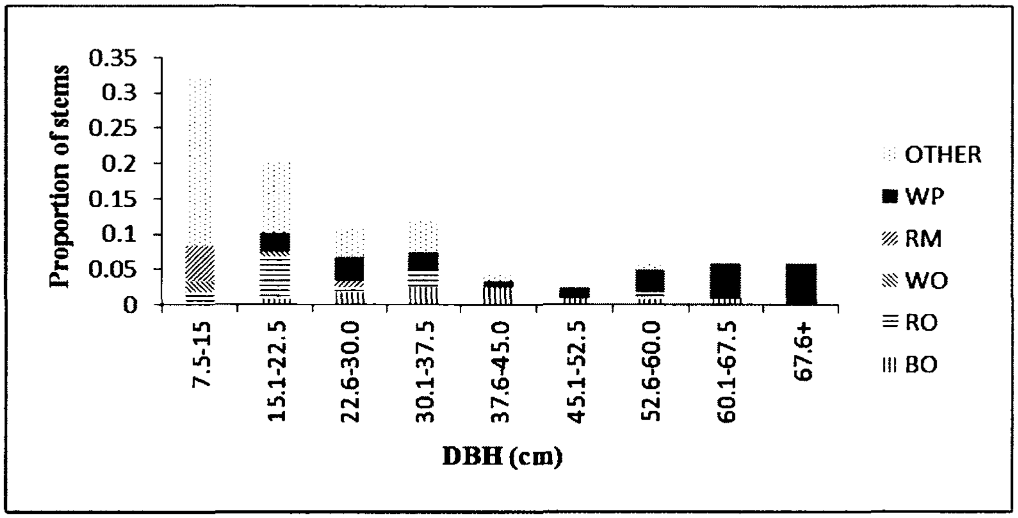
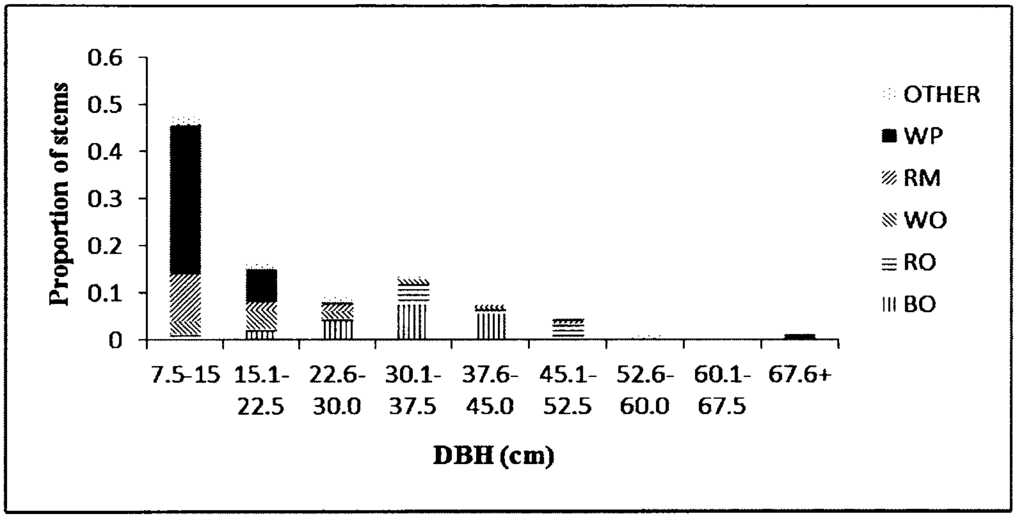
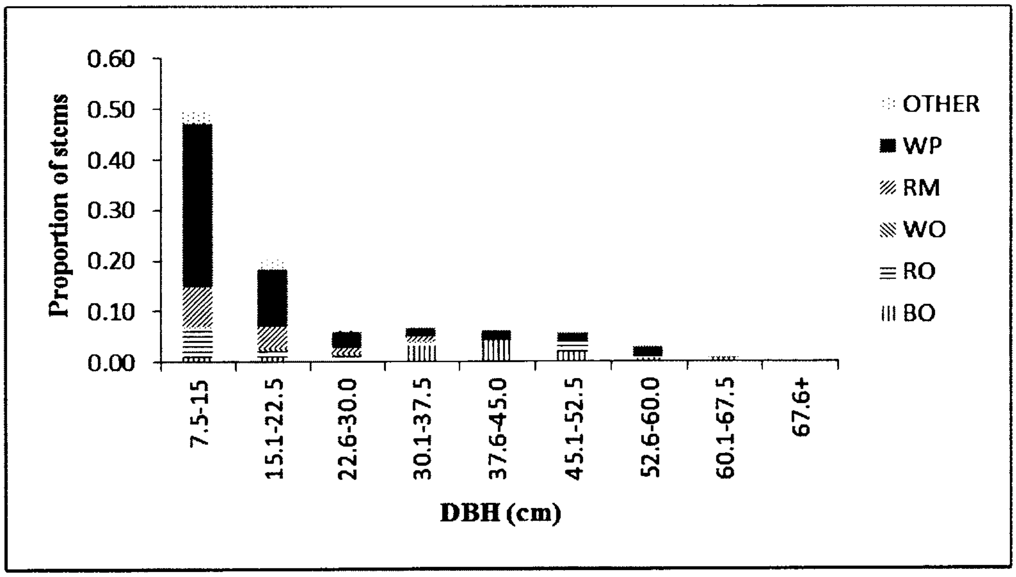


Figure 9. Tree size (diameter at breast height) class distribution for Group 4 – a) Great Brook Farm; b) Willowdale State Forest; c) Lockwood Town Forest.

a) Great Brook



b) Willowdale



c) Lockwood

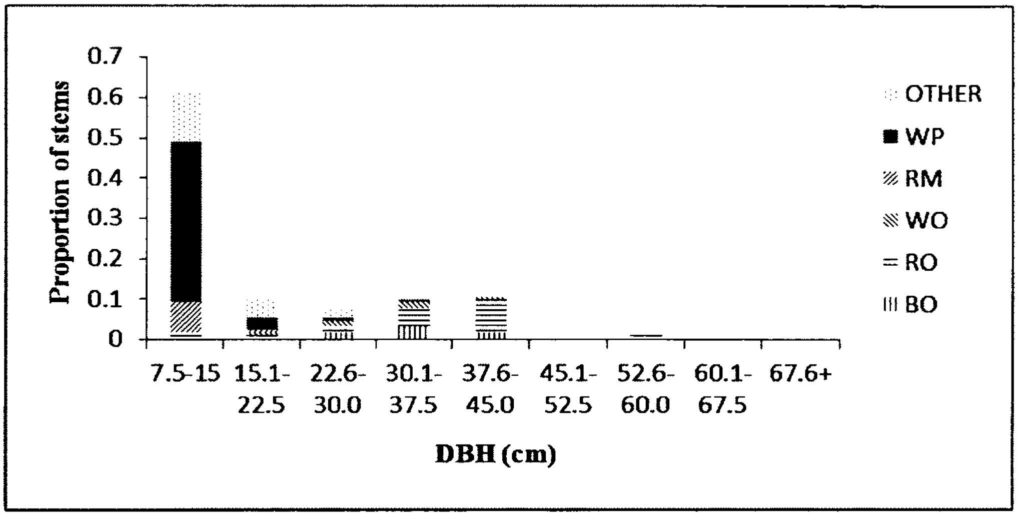
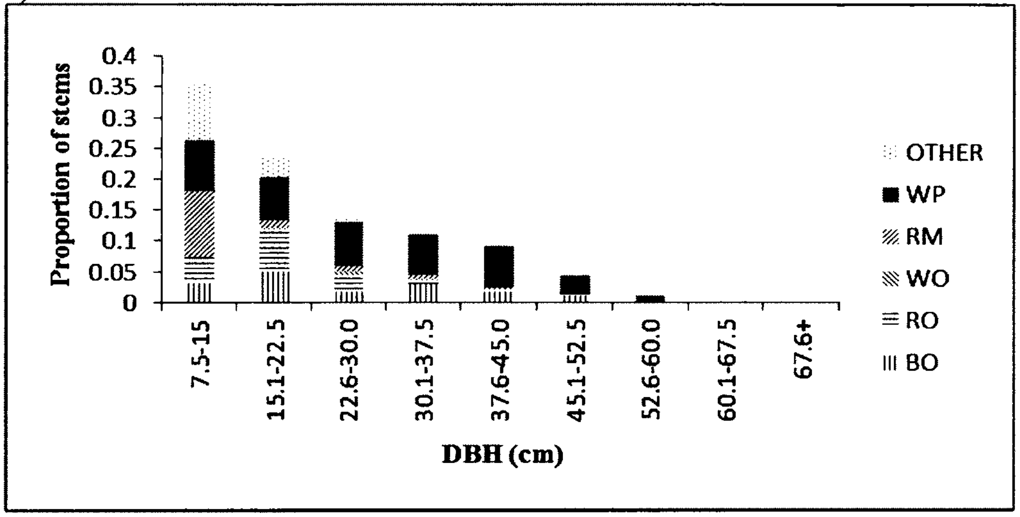
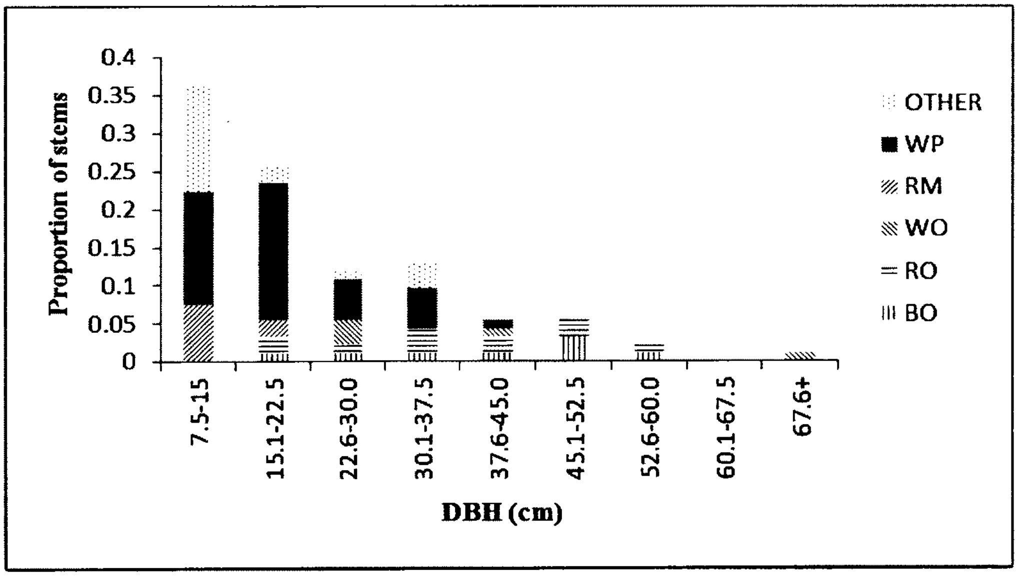

Proportion of stems
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
7.5-15
15.1-22.5
22.6-30.0
30.1-37.5
37.6-45.0
45.1-52.5
52.6-60.0
60.1-67.5
67.6+
DBH (cm)
OTHER
WP
RM
WO
RO
BO

Figure 10. Tree size (diameter at breast height) class distribution for Group 5 – a) Blue Hills State Reservation; b) Profile Rock State Park; c) Wildcat Conservation Area; d) Wompatuck State Park.

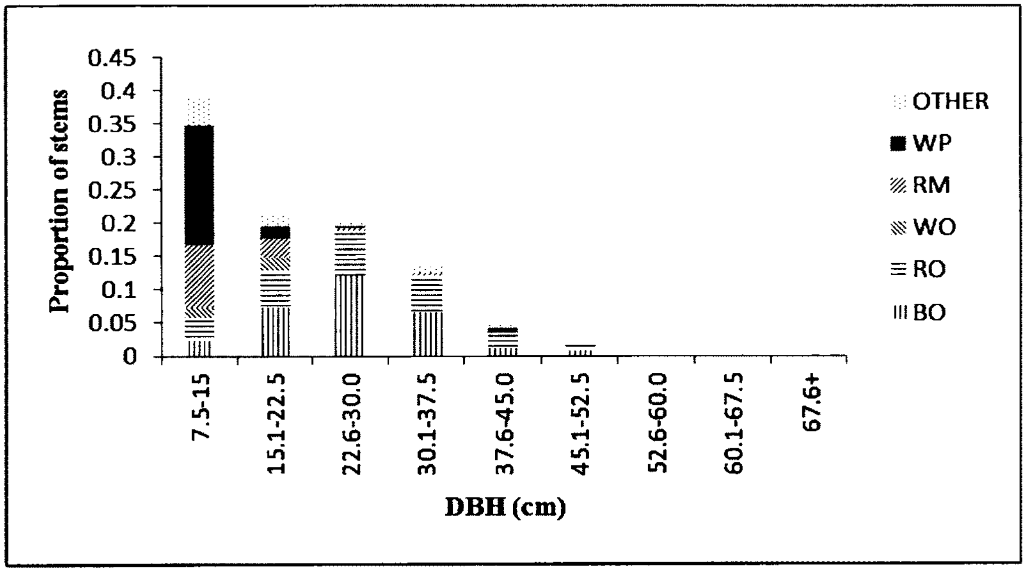
a) Blue Hills



b) Profile Rock



c) Wildcat



d) Wompatuck

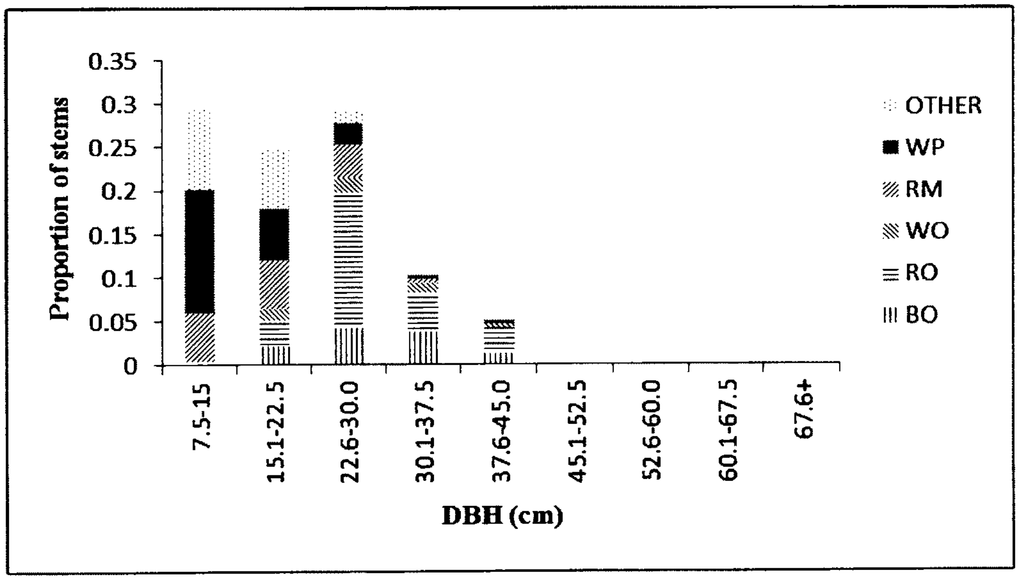


Figure 11. Region-wide *Quercus* and *P. strobus* ring width index (RWI) dendrochronologies pooled from 13 sites in eastern Massachusetts from 1980 – 2010. Distinct divergence trends exist from 1985 – 1990 and 2003 – 2010. * indicates years in which *Quercus* RWI is significantly lower than *P. strobus* RWI (using *t*-tests from 1995-2010.)

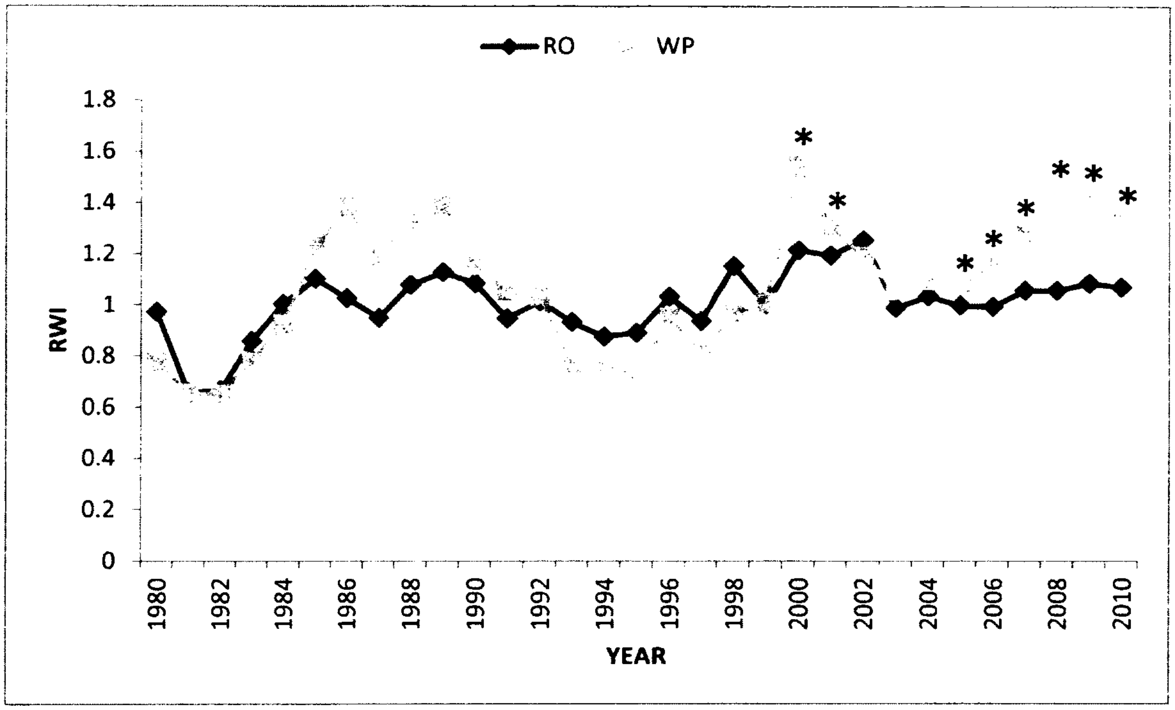


Figure 12. *% Quercus BA in Dead Stems* (arcsine square root) by *Site Index*. *% Quercus BA in Dead Stems* = 0.8086 + -0.0085 * *Site Index*.

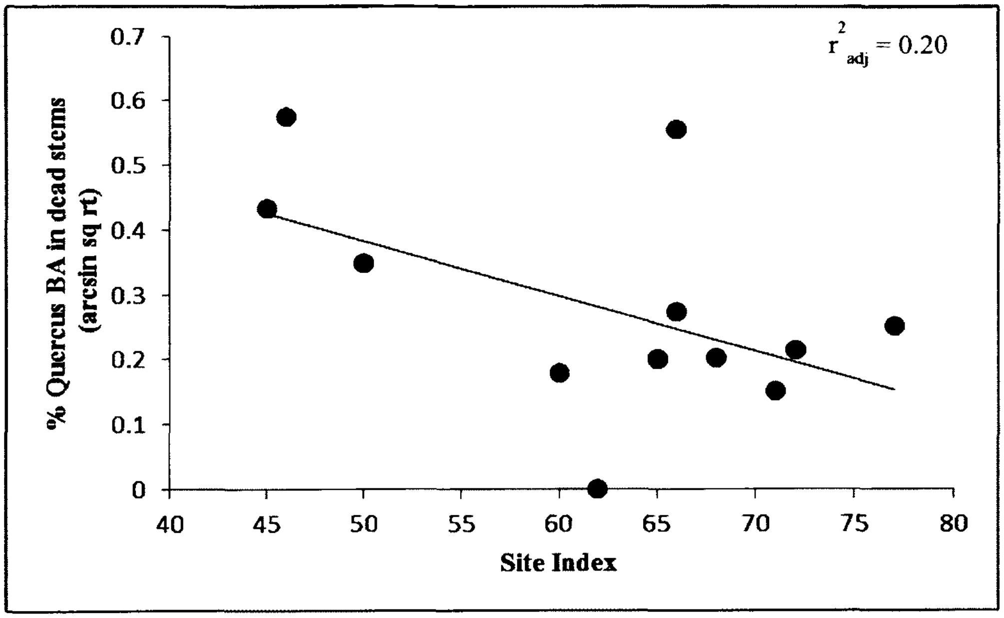


Figure 13. *% Quercus BA in Dead Stems* (arcsine square root) by *# of years of winter moth defoliation. % Quercus BA in Dead Stems* = 0.2231 + 0.0531 * *# of years of winter moth defoliation.*

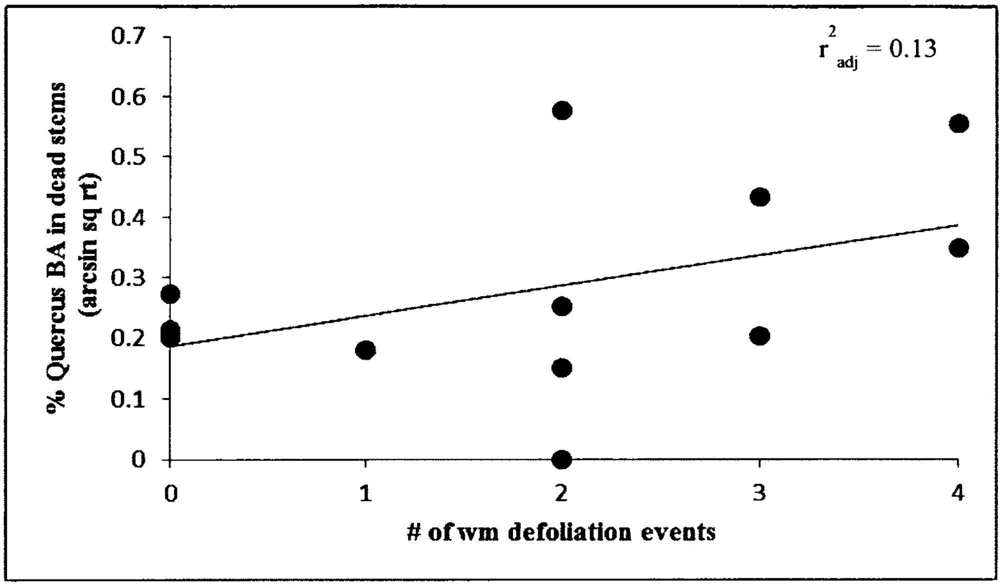
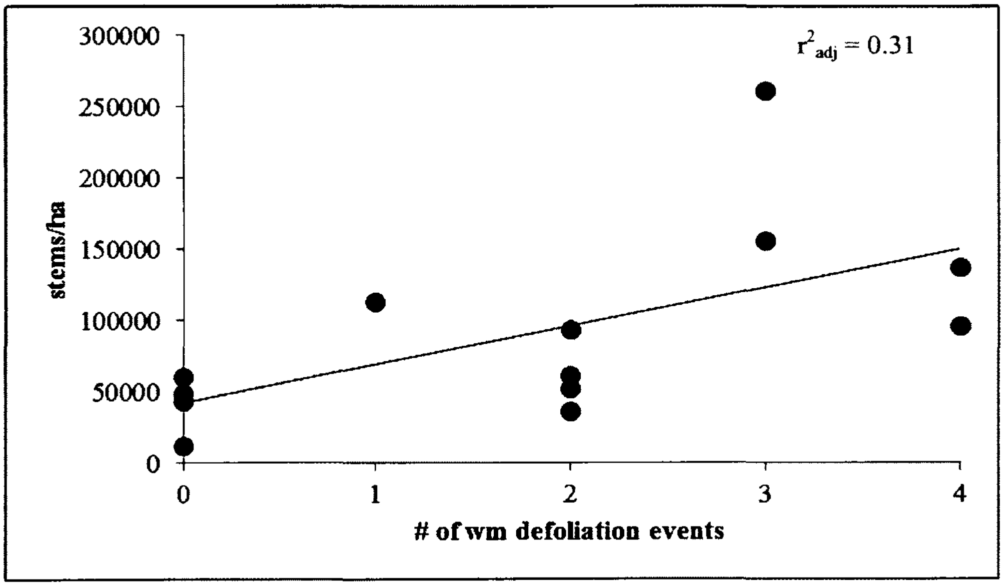


Figure 14. *Understory Density* by *Number of WM Defoliation Events*. *Understory Density* = 41,557 + 27,121 * *Number of WM Defoliation Events*.



APPENDICES

Appendix A.

Basal area (live and dead) and diameter at breast height (dbh – 1.4 m) estimates from 13 study sites throughout eastern MA. OTR = "other" species; see results for details.

	LIVE BASAL AREA m2/ha							DEAD BASAL AREA m2/ha							MEAN DBH					
Stand	**Total**	**RO**	**BO**	**WO**	**RM**	**WP**	**OTR**	**Total**	**RO**	**BO**	**WO**	**RM**	**WP**	**OTR**	**RO**	**BO**	**WO**	**RM**	**WP**	**OTR**
Amesbury TF	33.04	9.94	14.25	0.00	2.73	4.39	1.73	3.22	0.18	1.42	0.00	0.10	1.50	0.03	32.5	30.0	n/a	17.6	24.7	15.1
Blue Hills SR	36.46	3.16	7.51	0.90	1.57	22.17	1.15	3.41	0.61	1.68	0.00	0.04	0.88	0.21	19.4	26.7	31.0	12.8	28.3	12.4
Borderland SP	23.14	8.50	4.73	3.19	2.37	0.25	4.12	2.26	1.02	0.73	0.22	0.06	0.00	0.22	21.4	22.6	24.6	14.3	14.3	13.9
Bradley Palmer SP	47.76	2.18	5.23	0.30	0.43	32.63	6.99	4.29	1.31	1.55	0.00	0.03	0.85	0.55	24.3	38.4	16.7	12.6	52.2	19.5
Centennial Park	33.39	11.10	11.95	3.39	1.66	1.80	3.50	1.26	0.20	0.76	0.07	0.08	0.00	0.16	34.2	33.8	32.4	14.1	21.5	19.8
Great Brook Farm SP	29.87	6.81	11.78	2.28	2.23	5.16	1.61	0.88	0.18	0.25	0.13	0.08	0.23	0.00	35.5	35.0	21.2	16.0	13.2	21.9
Iron Rail TP	29.23	13.20	8.51	0.59	0.31	4.52	2.10	1.70	0.62	0.40	0.05	0.16	0.00	0.47	31.5	25.9	16.2	13.2	34.0	13.5
Lockwood TF	19.90	11.48	3.36	1.90	0.47	0.81	1.89	0.32	0.00	0.00	0.28	0.04	0.00	0.00	35.4	34.3	21.2	10.9	10.7	11.9
Profile Rock SP	34.24	8.61	8.03	4.45	0.87	9.02	3.26	2.74	0.55	0.00	0.78	0.00	1.19	0.23	36.2	39.5	38.7	12.5	18.9	15.9
Turkey Hill CA	30.09	0.70	8.60	0.37	19.20	0.72	0.50	1.67	0.00	0.39	0.01	0.92	0.06	0.29	39.0	36.6	28.9	25.5	20.9	16.4
Wildcat CA	23.70	8.10	9.26	0.20	1.12	1.77	3.25	1.72	0.53	0.83	0.17	0.09	0.07	0.03	26.7	26.0	15.2	13.3	12.1	19.6
Willowdale SF	39.91	8.16	13.48	0.75	2.44	14.28	0.81	3.22	0.36	0.55	0.07	0.26	1.94	0.04	26.5	38.4	24.9	15.6	17.7	14.5
Wompatuck SP	21.91	8.51	3.29	1.76	2.81	3.46	2.08	5.59	3.20	1.78	0.33	0.15	0.14	0.00	28.3	28.6	28.7	18.5	16.2	15.9
Mean	31.0	7.7	8.5	1.5	2.9	7.8	2.5	2.5	0.7	0.8	0.2	0.2	0.5	0.2	30.1	32.0	25.0	15.1	21.9	16.2
Standard Deviation	7.8	3.7	3.7	1.4	5.0	9.8	1.7	1.5	0.8	0.6	0.2	0.2	0.7	0.2	6.1	5.6	7.3	3.8	11.3	3.1
Standard Error	2.2	1.0	1.0	0.4	1.4	2.7	0.5	0.4	0.2	0.2	0.1	0.1	0.2	0.1	1.7	1.6	2.0	1.1	3.1	0.9

Appendix B.

Live and dead tree density estimates from 13 study sites throughout eastern MA.

	LIVE DENSITY (trees/ha)							DEAD DENSITY (trees/ha)						
SITE	Total	RO	BO	WO	RM	WP	OTR	Total	RO	BO	WO	RM	WP	OTR
Amesbury TF	459.0	21.7	36.1	0.0	19.3	13.3	9.6	110.6	10.0	35.0	0.0	10.0	40.0	5.0
Blue Hills SR	625.4	14.1	14.8	1.8	14.8	41.7	12.7	123.8	17.9	33.9	0.0	5.4	32.1	10.7
Borderland SP	625.7	26.3	14.1	7.6	18.7	2.0	31.3	142.2	40.0	24.4	8.9	4.4	0.0	22.2
Bradley Palmer SP	428.7	5.2	8.2	3.1	6.2	28.9	48.5	92.8	42.9	19.0	0.0	4.8	9.5	23.8
Centennial Park	422.3	24.2	26.1	7.8	19.6	9.8	12.4	46.9	11.8	41.2	5.9	11.8	0.0	29.4
Great Brook Farm SP	549.8	10.3	20.1	9.2	14.4	39.7	6.3	50.6	12.5	6.3	18.8	12.5	50.0	0.0
Iron Rail TP	436.9	26.6	22.8	5.1	5.1	8.9	31.6	121.7	22.7	22.7	4.5	4.5	0.0	45.5
Lockwood TF	579.0	18.3	6.1	3.8	7.6	45.0	19.1	8.8	0.0	0.0	50.0	50.0	0.0	0.0
Profile Rock SP	574.9	11.5	10.3	3.8	11.5	42.3	20.5	125.3	11.8	0.0	11.8	0.0	52.9	23.5
Turkey Hill CA	391.1	1.3	16.7	0.9	73.9	3.1	4.1	50.4	0.0	17.1	2.4	51.2	2.4	26.8
Wildcat CA	486.2	23.6	29.1	2.3	13.6	23.2	8.2	77.4	28.6	40.0	11.4	8.6	8.6	2.9
Willowdale SF	654.1	8.4	13.1	1.7	15.2	55.7	5.9	165.6	26.7	10.0	1.7	10.0	50.0	1.7
Wompatuck SP	527.2	21.5	7.9	4.7	17.8	26.7	21.5	115.9	52.4	28.6	4.8	4.8	9.5	0.0
Mean	520.0	16.4	17.3	4.0	18.3	26.2	17.8	94.8	21.3	21.4	9.2	13.7	19.6	14.7

Appendix C.

Estimates of percentage of live, stressed, or dead trees at 13 study sites throughout eastern MA.

	% LIVE					% STRESSED					% DEAD				
Stand	**RO**	**BO**	**WO**	**RM**	**WP**	**RO**	**BO**	**WO**	**RM**	**WP**	**RO**	**BO**	**WO**	**RM**	**WP**
Amesbury TF	60.0	24.3	0.0	44.4	57.9	30.0	56.8	0.0	44.4	0.0	10.0	18.9	0.0	11.1	42.1
Blue Hills SR	42.0	14.8	100.0	60.0	80.9	38.0	52.5	0.0	33.3	5.9	20.0	31.1	0.0	6.7	13.2
Borderland SP	45.7	25.6	57.9	76.9	100.0	28.6	46.2	21.1	17.9	0.0	25.7	28.2	21.1	5.1	0.0
Bradley Palmer SP	7.1	8.3	33.3	57.1	83.3	28.6	58.3	66.7	28.6	10.0	64.3	33.3	0.0	14.3	6.7
Centennial Park	46.2	10.6	61.5	50.0	100.0	48.7	74.5	30.8	43.8	0.0	5.1	14.9	7.7	6.3	0.0
Great Brook Farm SP	60.0	25.0	73.7	81.5	81.8	30.0	72.2	10.5	11.1	7.8	10.0	2.8	15.8	7.4	10.4
Iron Rail TP	26.9	17.4	60.0	60.0	100.0	53.8	60.9	20.0	20.0	0.0	19.2	21.7	20.0	20.0	0.0
Lockwood TF	95.8	100.0	83.3	81.8	98.3	4.2	0.0	0.0	9.1	1.7	0.0	0.0	16.7	9.1	0.0
Profile Rock SP	45.5	0.0	0.0	55.6	71.4	36.4	100.0	60.0	44.4	7.1	18.2	0.0	40.0	0.0	21.4
Turkey Hill CA	75.0	43.3	25.0	69.9	72.7	25.0	45.0	50.0	21.9	18.2	0.0	11.7	25.0	8.2	9.1
Wildcat CA	66.1	20.5	33.3	63.6	92.6	17.7	57.7	22.2	27.3	1.8	16.1	17.9	44.4	9.1	5.6
Willowdale SF	41.7	48.6	80.0	71.4	75.3	13.9	35.1	0.0	14.3	6.2	44.4	16.2	20.0	14.3	18.5
Wompatuck SP	34.9	29.6	72.7	83.3	92.7	30.2	25.9	9.1	11.1	0.0	34.9	44.4	18.2	5.6	7.3
Mean	49.8	28.3	52.4	65.8	85.2	29.6	52.7	22.3	25.2	4.5	20.6	18.6	17.6	9.0	10.3

CHAPTER IV

CONCLUSION

The objective of this thesis was to document the individual tree and forest stand level impacts of winter moth defoliation in eastern Massachusetts. Existing defoliation data from a winter moth life history and biology study at the University of Massachusetts-Amherst were utilized in conjunction with tree core analysis to estimate the effect of winter moth defoliation on individual host trees. The findings from this thesis indicate that winter moth defoliation contributed to radial growth decline of individual *Quercus rubra* and *Q. velutina* trees in Massachusetts from 2005-2010; no relationship was found between winter moth defoliation and the radial growth of individual *Acer rubrum* and *A. saccharum* trees. At the forest stand level, winter moth has successfully invaded mixed - *Quercus* and *Quercus – Pinus strobus* forests in eastern Massachusetts and winter moth defoliation contributed to *Quercus* mortality and, subsequently, an increase in understory woody plant density in these forests. Given these inferences, winter moth can be added to the long list of exotic, invasive herbivores affecting the forests of New England.