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Relationships among beech bark disease, climate, radial growth response and mortality of American beech in northern Maine, USA

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Summary

A majority of beech forests across Maine first experienced beech bark disease (BBD) from 1935 to 1960 when sap feeding by an introduced beech scale insect, *Cryptococcus fagisuga,* allowed lethal fungal infections primarily by *Neonectria ditissima* and/or *Neonectria faginata.* Beech stands along the Maine–Quebec border in northern Maine were excluded from this initial killing phase presumably due to cold winter temperatures that inhibited scale survival. However, a sharp increase in beech mortality after 2002 occurred in previously uninfected border stands and stands long affected by BBD. Beech mortality averaged 50% across northern Maine during 2003–2006. To identify plausible stresses that could explain the mortality, a dendropathological study was conducted from 2005 to 2006 in northern Maine that quantified temporal and spatial relationships between possible stressors with beech mortality and growth decline. Nineteen sets of high- and low-mortality plots were located randomly across four bioregions. Increment cores were taken from both beech trees (n = 565) and associated tree species (n = 450). A growth change index of increments was used to evaluate beech responses to biotic and climatic stresses. A prolonged period of relatively mild winters without temperatures lethal to scale insect (<−34°C) from 2000 to 2004 coupled with low August–October precipitation from 2000 to 2003 may have provided ideal conditions initiating a widespread scale epidemic. A major drought period from 1999 to 2002 coincided with growth decline and a significant increase in beech mortality across all regions included in this study. *Neonectria* was found infecting weakened trees across the region. Drought, beech scale and *Neonectria* are plausible explanations for the episode of high beech mortality in northern Maine. This is the first report of a major killing phase of beech within the BBD 'aftermath' forests.

1 Introduction

In 2003, Forest Inventory and Analysis data for western Aroostook County, Maine showed a 31% increase in American beech (*Fagus grandifolia* Ehrh.) mortality from 2002 (Kasson 2007). By 2006, widespread beech mortality, averaging 50% in most affected stands, also was observed in northern Somerset, Piscataquis and Penobscot Counties (Kasson 2007). Prior to this surge in mortality, statewide mortality of beech averaged 1.2% annually from 1999 to 2002 (McWilliams et al. 2005). The objective of this study was to identify which stresses are plausible explanations for the increased mortality. The stresses considered were beech bark disease (BBD), drought and site factors.

Beech bark disease has long affected Maine's beech forests. In North America, BBD occurs when beech stems previously infested with the exotic scale insect, *Cryptococcus fagisuga* (Lind.), are colonized by one or more fungi, primarily *Neonectria faginata* Castlebury et al. (formerly *Nectria coccinea* (Pers.:Fr.) Fr. var. *faginata* Lohman et al.) and *Neonectria ditissima* (Tul. & C.Tul.) Samuels & Rossman (formerly *Nectria galligena* Bres) (Castlebury et al. 2006). *Neonectria ditissima* is an endemic pathogen with a cosmopolitan distribution that also causes perennial target cankers on numerous hardwoods (Welsh 1934; Spaulding et al. 1936; Ferrandino et al. 2005), whereas *Neonectria faginata* is presently found only on beech in North America (Castlebury et al. 2006). Beech bark disease is a classic decline-dieback disease requiring the conjuncture of predisposing, inciting and contributing factors to facilitate disease (Manion 1991).

The temporal progression of BBD in the United States has been well documented (Shigo 1972). In Maine, the 'advancing front' began with the entrance of the scale into the state prior to 1932, after which *Neonectria* infections and beech mortality became widespread in Washington County (Ehrlich 1934). Concurrently, infections of *Neonectria* on scale-infested beech were discovered in Liberty, Maine (Waldo County), but were less severe as was mortality (Ehrlich 1934). The far north regions of the state experienced the advancing front of beech scale infestations by 1960 (Houston et al. 1979), although widespread mortality was not reported in these areas (Houston 1994a). In 1961, the Canadian Forest Service documented the appearance of beech scale within the last uninfested county in New Brunswick adjacent to northern Maine (Anonymous 2007). In Quebec, BBD was first reported in 1965 (Lachance 1983). By 1975, the distribution of *C. fagisuga* extended the entire length of Maine's western border with Quebec although *Neonectria* infections were limited to areas primarily further west and south of the study area (Lachance 1983). Apparently, temperatures lethal (<−34°C) to the unprotected beech scale (Barter 1953), along the Maine/Quebec border, were preventing the degree of scale feeding needed for *Neonectria* infections.

After the initial killing front, BBD developed into the 'aftermath' stage throughout a majority of Maine's beech forests (Houston 1975). These forests are characterized by thickets of young beech, mostly of vegetative origin, where sparse scale populations and scattered *Neonectria* infections persist indefinitely and cause the bark surface to be covered with limited cankers (Houston 1975).

Houston (1975) hypothesized that the causal agents associated with BBD were already widely distributed in Maine's aftermath forests, and additional outbreaks of mortality would occur pending the coincidental occurrence of enough stressors, such as an increase in scale populations. Otherwise, low scale infestations on beech trees in the aftermath forest cause minimal

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stress as indicated by the lack of a relationship between scale density and the increase in necrotic tissue associated with *Neonectria* infections (Cale et al. 2011).

In addition to stresses associated with BBD, a major drought occurred across northern Maine from 1999 to 2002 and may have affected beech survival (Lombard 2004). Also, stand factors, such as amount and density of beech, can impact the degree of BBD and drought stresses. Therefore, there was a need to evaluate the viability of multiple stresses that could explain the high beech mortality in Maine.

Our understanding of specific cause–effect relationships in tree decline diseases, including BBD, remains incomplete. Specific criteria used to separate causation (stress) from effect (disease) do not readily apply to decline diseases in trees. For example, criteria for ascertaining causal stresses imply that an observed effect is the result of only one specific causal agent (Johnson et al. 1992). Yet, by definition, decline diseases result from the combined effect of multiple agents with spatiotemporal variation in degree and duration (Manion 1991). In such cases, attempts to fulfil Koch's postulates are no longer appropriate. Instead, measures of spatiotemporal consistency, step-by-step linkages, responsiveness and biological plausibility between stresses and tree responses can be used in evaluating cause–effect relationships (Johnson et al. 1992). Dendrochronology is a valuable tool to test temporal consistencies through observations of a tree's reduced radial growth in response to stress that precedes tree dieback and mortality.

Dendrochronological methods have been frequently applied to identify climatic and biotic factors most closely associated with changes in radial growth patterns of trees (Payette et al. 1990; Foster et al. 1996; Stokes and Smiley 1996). Because a severe drought occurred at the time of the beech mortality outbreak (Lombard 2004), dendrochronology can be used to test whether growth decline could have been initiated by drought.

Temporal studies of insect outbreaks and fungal disease epidemics in trees such as BBD utilize dendrochronology to provide annual dating of disturbances. Dendroentomological studies have focused mainly on evaluating the incidence and frequency of defoliator outbreaks as well as the influence of these defoliators and other insect pests on growth loss (Davis et al. 2007; Muzika and Liebhold 1999; Muzika et al. 2004; Kanoti 2006).

Dendropathological investigations into diseased trees have focused primarily on single-species radial growth comparisons between healthy (i.e. resistant or presently non-symptomatic) and diseased trees (Gavin and Peart 1993; Gove and Houston 1996; Davis et al. 1997; Mallett and Volney 1999; McEwan et al. 2006; Waldboth and Oberhuber 2008) or between individual tree species infected by one of several pathogens concurrently (Cherubini et al. 2002). Other dendropathological studies have compared standardized radial growth chronologies of declining host and resistant non-host species in response to host-specific forest pathogens (Digregorio et al. 1999; McEwan et al. 2006; Black et al. 2010) or the combination of climatic factors and biotic causal agents (Han et al. 1991; Kasson 2007; Black et al. 2010). One benefit of these analyses is to better identify and remove shared growth fluctuations associated with climate alone (i.e. drought) that may confound the interpretations of the biotic agent's effect on growth (Han et al. 1991).

Dendrochronology can be used to document temporal relationships between tree increment growth and various stresses owing to climate, insect pests and fungal pathogens. This study will use the beech mortality in northern Maine as a case study on how to use dendrochronology to identify plausible causes of a dieback/mortality event ex post facto.

Three hypotheses were evaluated in this study. First, beech scale populations and subsequent invasion by *Neonectria* fungi increased prior to 2003, when a sharp increase in beech dieback and mortality occurred across northern Maine. This hypothesis was evaluated by examining temporal and spatial relationships of scale insect and fungal presence, occurrence of weather favouring scale population build-up, and a more severe decrease in beech increments but not in associated species. Our second hypothesis is that the onset of growth reductions and/or mortality in beech coincided with drought based on examination of spatiotemporal relationships of meteorological data and tree-ring patterns including both beech and associate tree species. Our third hypothesis is that mortality was exacerbated by individual stand factors as indicated by statistical relationships among elevation, disease presence and severity, beech basal area, and beech density.

2 Methods

2.1 Study area

The study area encompasses several biophysical regions totalling 2.1 million ha in northern Maine, USA, and includes the St. John Uplands (BR 1), the Boundary Plateau (BR 2.1 & 2.2) and the western edge of the Aroostook Hills (BR 3) (Fig. 1) (McMahon 1990). The North Maine Woods, a 1.4-million-ha multiuse forest, comprises the core of our study area (Fig. 1). Included within this region are western Aroostook County, northern Somerset County, northern Piscataquis County and northern Penobscot County (Fig. 1). Tree species composition across all stands sampled is typical of northern hardwood forests of this region (Society of American Foresters forest cover type 25), consisting primarily of American beech, sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton). These stands are found predominantly on upland sites and along ridges (Table S1).

2.2 Survey and sampling procedures

Sampling was stratified using pre-existing climatic zones demarcated by Briggs and Lemin (1992) and biophysical regions of Maine delineated by McMahon (1990). Biophysical regions were delineated on the basis of vegetative patterns, physiography, climate and soils, whereas climate zones were delineated using 37 climate-related variables (McMahon 1990; Briggs and Lemin 1992). Boundaries were altered (Kasson 2007) to ensure that sampling was similar across climatic zones and biophysical

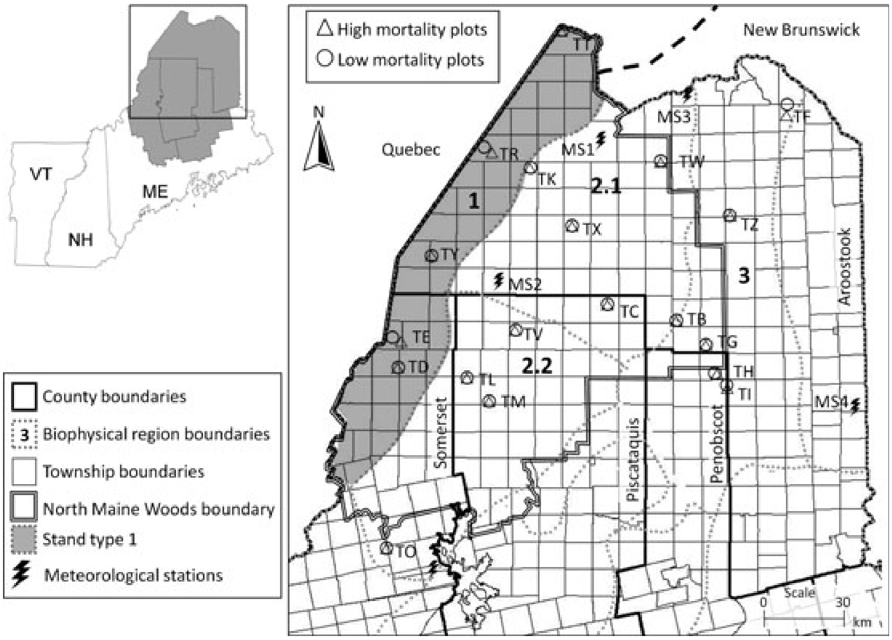

Fig. 1. General location of 19 paired beech mortality plots sampled from 2005–2006 and associated meteorological stations in northern Maine. Biophysical Regions (BR 1, 2.1, 2.2, and 3) were used to stratify plot sampling (adapted from McMahon 1990). Four N.O.A.A. meteorological stations MS1 (Allagash) MS2 (Clayton Lake), MS3 (Fort Kent), and MS4 (Houlton) were selected based on proximity to plots and length of record.

regions. Re-delineation resulted in four similar-sized biophysical regions (400–600 k ha/bioregion), referred to hereafter as BR 1, 2.1, 2.2 and 3 (Fig. 1).

A subset of 10 townships within each bioregion was selected at random. Favourable hardwood stand types were identified within the township using existing cover-type maps. A single point within the township was selected at random. Hardwood stands were examined starting with those closest to the random point and spiralling outward.

2.3 Plot design and layout

Plots were established between June 2005 and August 2006 (Fig. 1). Sampled stands contained both beech and a second species having dominant/co-dominant stems within the stand, where beech basal area (B.A.) was at minimum *ca.* 4 m^2/ha (combined living and dead beech trees) to ensure enough trees to core and provide a meaningful estimate of mortality. A total of 38 fixed radius plots were randomly located and paired across 19 townships: five plot pairs for BR 1, five plot pairs for BR 2.1, four plot pairs for BR 2.2 and five plot pairs for BR 3 (Fig. 1). Beech basal area ranged from 3.6 to 16.8 m^2/ha (Table S1). Total basal area averaged 21.2 m^2/ha across all plots and did not differ between high- and low-mortality plots (Table S1).

The first stand of beech (*ca.* 4 m^2/ha B.A. in beech) with greater than 20% of the stems ≥12.7 cm diameter at breast height (d.b.h., at 1.3 m) showing mortality was designated as the high-mortality plot (site class 1). The next nearest stand of beech with the stems having ≤ 50% the mortality of the high-mortality plot within that same township was designated as the low-mortality plot (site class 2). Townships that failed to meet both high and low site criteria were not sampled.

Eight-hundred-square metre plots (0.08 ha radius) were established in the approximate centre of each stand. Crown class, d.b.h., species and vitality measurements were collected for all trees ≥12.7 cm d.b.h. Procedures used to measure tree-level data were as described in the Northeast Research Station Forest Inventory and Analysis (FIA) field guide (U.S.D.A. 2003). To examine whether site factors influenced the amount of mortality, plot-level variables including basal area, elevation, BBD incidence and severity, species composition and stem density were recorded.

2.4 Disease and insect density indices

External defects attributed to BBD, disease severity and beech scale density were measured on the lowest 2 m of the bole for all on-plot beech trees ≥12.7 cm d.b.h. Off-plot trees were likewise evaluated and cored if the number of on-plot beech trees was less than 12. Defects associated with BBD were modified from previous indices of defect for beech trees (Twery and Patterson 1984; Burns and Houston 1987; Gavin and Peart 1993). Unlike previous indices where external defect categories were ranked by increasing damage to the vascular cambium, defect associated with BBD was ranked solely on external symptomology and was used as an relative indicator of disease duration within these stands where 0 = no defect, 1 = cracked bark/tarry spot (most recent colonization resulting in coalescing patches of cambial death), 2 = raised legions (recent fungal colonization without cambium death), 3 = pocket cankers (previous fungal infections and cambial death), 4 = sunken legions (multiple disease events resulting in coalescing cankers and callus) and 5 = deep fissures with callous tissue (prolonged periods of occupation by both scale and fungi). Mean defect categories were averaged for each plot and are referred to as the disease rating.

Disease severity was an estimation of the cumulative effects of BBD (%) on the entire beech bole. Because height measurements were not taken, cumulative effects could only be approximated by visually estimating percentage of bark area having BBD-related defects on the lowest 2 m of the bole. Disease severity was averaged for each plot.

Scale insect densities were also recorded for all cored trees and averaged for each plot using methods similar to that of Houston et al. (1979). A mean scale intensity (MSI) of 1–5 was used where 1 = no infestation, 2 = trace, 3 = light, 4 = moderate and 5 = heavy infestation. Trace densities represented 1–10 individual colonies on a single tree, and heavy densities resulted in extensive 'white washing', e.g. hundreds of individual colonies on an infested stem. In this study, MSI was evaluated only on the lowest 2 m of the stem, similar to that of Kanoti (2006) who quantified trunk phase of balsam woolly adelgid (*Adelges piceae* Ratz.) on the first 1.8 m of the balsam fir (*Abies balsamea* (L.) Mill.) tree boles. MSI provides a coarse snapshot of scale populations present at time of survey.

2.5 Presence of *Neonectria* fungi

Presence of *Neonectria* perithecia (sexual structures) was reported for all measured beech. Where perithecia were most abundant (i.e. occurring on >30% of beech trees), bark discs bearing recently formed, mature perithecia were removed from each tree with an arch punch (2.5 cm diam.) for morphological and/or molecular identification and used for a peripheral study (Kasson and Livingston 2009).

2.6 Climate data

Temperature data were obtained for four nearby weather stations from the National Oceanic and Atmospheric Administration (N.O.A.A.) National Climate Data Center (http://www.ncdc.noaa.gov/oa/climate/stationlocator.html) including Allagash (MS1), Clayton Lake (MS2), Fort Kent (MS3) and Houlton (MS4) (Fig. 1). Data collected included number of days from November to April during which minimum temperature was ≤ −34°C (lethal to scale insect, (Barter 1953)), −30 and −25°C (both sublethal but damaging to scale insect).

Plot-level precipitation estimates were obtained from the Oregon State University's parameter-elevation regressions on independent slopes model (PRISM) climate mapping system. Houston and Valentine (1988) reported that years of sharp decline in cankering were preceded by heavy October rains that potentially interfered with settling of the crawler stage of *C. fagisuga*. Because the vulnerable crawler stage generally occurs from August through October, precipitation during this period was summed by plot and then averaged for each year by bioregion.

Drought events were reported by Lombard (2004) who used annual 7-day low-flow measurements to assign recurrence intervals for historic Maine droughts, including the most recent 1999–2002 drought period. Flow measurements were based on each United States Geological Survey (USGS) stream flow gauging station used in that study.

2.7 Dendrochronology

2.7.1 Tree core sampling

Two cores per tree were taken from all dominant/co-dominant beech, living or dead, ≥12.7 cm d.b.h. In plots containing fewer than 12 beech trees, additional beech were sampled off-plot in stands immediately adjacent where slope, aspect and general site variables were similar bringing the total number to 12 trees. An associate dominant/co-dominant species also was selected and cored so that growth trends between host and non-host species could be compared to indicate when stress was affecting one species (e.g. scale on beech) but not the other. Additional trees of the associate species were cored off-plot if plots contained <12 co-dominant or dominant trees. Associate non-host species included red maple (*Acer rubrum* L.), sugar maple, yellow birch and red spruce (*Picea rubens* Sarg.).

Radial cores were extracted using 5.15-mm Haglof increment borers (Haglof Inc., Madison, MS, USA). Cores were collected at d.b.h. 180º apart and parallel to the contour line to minimize capturing tension or compression wood. Within rotten and highly defective trees, cores were taken from the least affected two sides regardless of contour location. At times, stump height was the only place on the bole where usable cores could be extracted. Increment cores were taken from non-cankered regions whenever possible. All cores were transferred to prelabelled wax-paper straws for drying and later processing.

2.7.2 Tree core processing

Procedures for drying, mounting, labelling and sanding were as described by Stokes and Smiley (1996) and Swetnam et al. (1985). Cores were air-dried inside straws for 3–7 days, glued into routed wooden blocks and taped to secure cores for 2–5 days for additional drying. Tape was removed, and intact cores were sanded with 100-, 220-, 320- and 800-grit paper. Cores that were not intact were discarded. Cores exhibiting desirable attributes that included complete pith, proper wood orientation, lack of branch wounds and decay, and presence of tight bark plug were selected for annual ring measurements.

2.8 Radial growth analysis for beech and associate species

2.8.1 Tree-ring measurements

Ring width measurements to the nearest 0.01 mm were taken using Windendro (Regent Instruments, Inc., Quebec City, QC, Canada). Pith estimators (concentric circle transparencies of varying magnifications) were used on cores showing curvature but lacking pith (Applequist 1958). Ages were not estimated for cores lacking curvature.

Marker years, years in which increment width is much narrower than adjacent increments, were tallied in list form for both beech and associated species. These years are presumably associated with species-specific events and climatic events that affected one or more species and aid in cross-dating tree cores (Yamaguchi 1991). Series were shifted by inserting locally absent ring values when justified (Yamaguchi 1991). A core segment of the most recent 50 years was cross-dated for all species and plots.

All ring width series were evaluated using the program COFECHA (Holmes 1983). Cores deemed problematic were re-examined using a Velmex sliding stage micrometer (Velmex Inc., Bloomfield, NY, USA). These cores were remeasured, the source of error was located, and values were corrected.

To compare host and non-host associate species growth chronologies, the following growth change index was utilized:

$$\mathrm{GC}_x = [(\mathrm{RW}_x - \mathrm{RW}_{x-1})/(\mathrm{RW}_{x-1} + \mathrm{RW}_x)],$$

where GC_x is growth change for a given year x, RW_x is the ring width for that particular year and RW_{x-1} is the ring width of the year preceding it. All values of the index fall between −1 and 1, with zero indicating no change in ring width from the previous year.

Repeated-measures analysis (SYSTAT 12.0, Chicago, IL, USA) was used to compare trends of the growth change index over time, between hosts, bioregions and site class using the following model:

$$\mathrm{GC}_{\mathrm{x}}\ (1990...2004) = \text{CONSTANT} + \text{site class}^{2} + \text{host}^{1} + \text{bior}^{1} + \text{host*bior}^{1} + \text{site class*bior}^{2} + \text{site class*host}^{2} + \text{host*site class*bior}^{2} + [\text{township(bior)}]^{1} + [\text{site class*township(bior)}]^{2}$$

GC_x (1990...2004) is the repeated-measures factor with individual years 1990–2004. Because only recent growth trends were of interest, years prior to 1990 were not included. Site class differentiates high- and low-mortality plots within a given township, and bior refers to biophysical region (a geographically specific region, Fig. 1). Host refers to beech or non-beech associated species, which is a grouping of up to four different species (red maple, sugar maple, yellow birch and red spruce). Superscript numbers associated with individual factors and interactions denote error terms used. Error terms are delineated with brackets. Years in which beech had significantly lower GC than the associated species indicates a stress is uniquely affecting beech.

Huynh–Feldt correction values were used to evaluate the assumption of compound symmetry for within-subject comparisons. As the Huynh–Feldt Epsilon value approaches a value of 1.00, the greater the support that the assumption of compound symmetry is met.

2.8.2 Stand factors and mortality

Analysis of variance was used to evaluate relationships between mortality and various stand factors. Individual tree-level factors included disease ratings, disease severity, beech scale intensity, d.b.h. and age of beech. Plot-level factors include the following beech measurements: density or stems/ha, percentage mortality, basal area/ha and elevation. All tree-level factors were averaged across each plot before analysis. The ANOVA model was as follows:

$$\mathrm{Y} = \text{CONSTANT} + \text{site class}^{2} + \text{bior}^{1} + \text{site class*bior}^{2} + [\text{township(bior)}]^{1} + [\text{site class*township(bior)}]^{2}$$

Superscript numbers associated with individual factors and interactions denote error terms used to calculate *F*-ratios and p-values for a given term. Error terms are marked with brackets. Bonferroni *post hoc* tests were used to test all pairwise comparisons.

ANOVA assumptions were tested for plot- and tree-level factors. The assumption of normality was evaluated using Lilliefors tests with an α-level of 0.10. A Levene's test was used to test the assumption of equal variances with an α-level of 0.10.

3 Results

3.1 Drought, climate data and factors affecting the scale insect

Lombard (2004) clearly shows that a severe drought occurred across all bioregions used in the study from 1999 to 2002 using multiple measures including annual 7-day low-flow measurements at several stream flow gauging stations.

When assessing the viability of beech scale as a stress factor, beech growth decline and mortality must be associated with climate data showing periods lacking lethal temperatures (<−34°C) below which scale insects, without protection, rapidly succumb (Barter 1953). Only three periods, hereafter referred to as windows W1 (2000–2004), W2 (1986–1990) and W3 (1980–1983), with ≥4 consecutive years of lethal-free temperatures were detected for all meteorological stations, since the arrival of *C. fagisuga* into the northern part of the state in *ca.* 1960 (Fig. 2). Windows of four years were chosen based on previous data that showed population levels of *C. fagisuga* in newly established sites can increase from trace to moderate infestation levels in four years time (Houston 1994b).Within the lethal-free periods, these stations also experienced decreases in the frequency of days <−30 and −25°C; episodes below these temperature also may result in significant scale mortality especially if they occur with regularity (Houston and Valentine 1988).

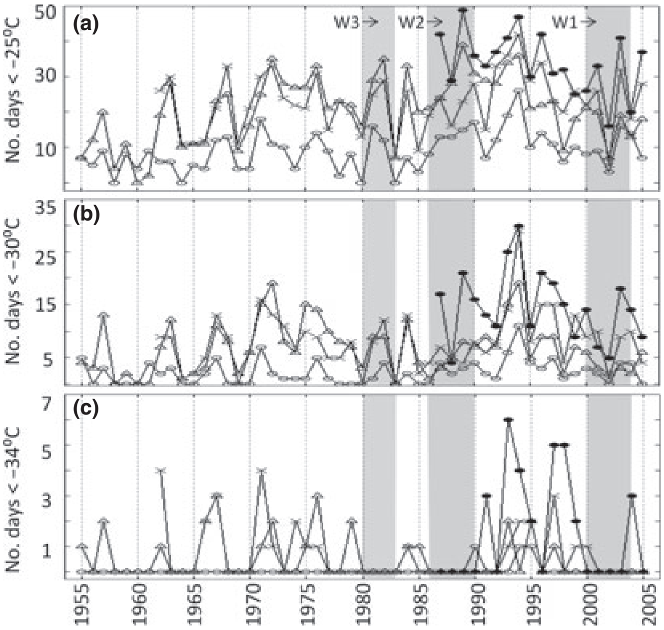

Fig. 2. Frequency of days below sub-lethal (a) −25°C, (b) −30°C, and lethal (c) −34°C temperature thresholds for beech scale (*Cryptococcus fagisuga*) from 1955–2005 by year and meteorological station. Stations include Allagash (●) with a record length of 19 years, Clayton Lake (x) with a record length of 44 years, Fort Kent (Δ) with a record length of 69 years, and Houlton (O) with a record length of 104 years. W1 (2000–2004), W2 (1986–1990), and W3 (1980–1983) correspond to periods of ≥4 consecutive years of lethal-free temperatures which is required for trace scale populations to reach moderate to high levels.

A second factor adversely affecting scale populations is heavy August–October precipitation that can wash unattached or unprotected crawlers in stem flow (Fig. 3.). Although below average August–October precipitation (<10 cm) overlapped all windows (W1–W3), the frequency and severity of these deficits were greater in W1 compared with those in W2 and W3. Additionally, W1 had all bioregions experiencing low precipitation means (<10 cm) from 2000 to 2002, a situation not apparent in W2 or W3. Also important were precipitation surpluses (rainfall ≥ 15 cm August–October) in 1999, 2003 and 2005 (Fig 3). High precipitation can limit scale build-up and possibly 'erase' any evidence of scale infestation that occurred in prior years, effectively 'resetting' the population in the following year.

3.2 Tree-ring chronologies

A total of 1015 cores were extracted, 84 (15%) of 565 cores from beech and 108 (24%) of the 450 cores from associate species were unreadable and eliminated from analyses. Total usable cores by bioregion for beech and non-beech, respectively, were as follows: BR 1 : 94 beech and 77 non-beech; BR 2.1 : 144 and 90; BR 2.2 : 88 and 63; and BR 3 : 155 and 112. Sampling depth averaged 64 trees with a range of 49–86 trees across all bioregions and site classes for beech and averaged 55 trees with a

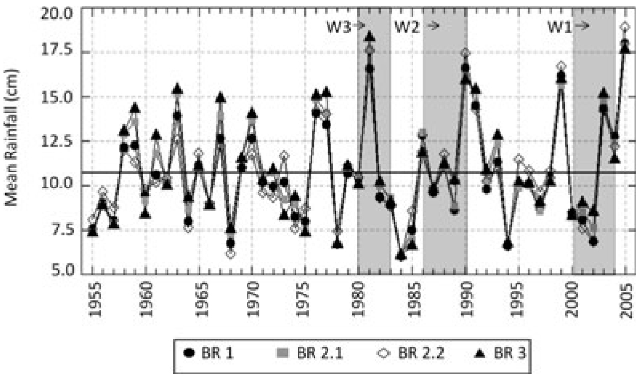

Fig. 3. Mean late-season (August–October) rainfall by bioregion. The solid horizontal line *ca.* 10-cm value denotes mean rainfall across all bioregions during the period from 1896–2005. Shaded regions, W1–W3, correspond to lethal-free temperate windows in Fig. 2.

range of 45–63 trees for associate species. Ring width data prior to 1956 were discarded as they preceded the arrival of *C. fagisuga* and BBD into northern Maine. Minimum sampling depth for beech was similar in both 1956 and 2004 (final year of growth used in study) with average minimum depths of 51 trees and ranges of 35–68 trees. Minimum sampling depths for associate tree species averaged 40 trees with a range of 23–54 trees.

Initially, >55% of interseries correlations for all cross-dated tree-ring series fell below the critical correlation coefficient of 0.3281 for the 99% confidence level, given a 50-year segment length (Grissino-Mayer 2001). If just a 30-year segment was used (1975–2004), 70% (53 of 76) had correlations above the critical value indicating statistical support for cross-dating (Table S1).

Because of low correlations, presence of universal marker years was used to cross-date the cores as well. Narrow rings were common in 1991, 1995 and 2003 (Table S2). The latter two years were associated with low August–October precipitation during the year prior to increment formation (Fig. 3). These marker years ensured accurate cross-dating in the most recent 15 years of growth, which included the years of interest for this study. Still, there were five series of beech and two series of associate species that did not have high interseries correlation or good marker years (Table S2). Cross-dating of these cores was primarily dependent on finding no better interseries correlation based on COFECHA analysis combined with re-examination of cores to confirm that no incorrect measurements were taken.

3.3 Radial growth changes in beech and associate species

A period when a stress uniquely affects beech is indicated by the repeated-measures analysis of GC between beech and associate species (Table S3). Significant interactions occurred between year, beech vs. associate species, site class and bioregion (Table S3). Therefore, comparison of means by each combination of main effects by year was needed. Analysis included only years 1990–2005 because this time span included the entire 2000–2005 period during which mortality increased to 50% across the most affected stands. In addition, lack of marker years < 1990 resulted in reduced confidence during this period, especially for plots with low correlation values for the outermost radial segments. Huynh–Feldt p-values were indistinguishable from unadjusted p-values, indicating the assumptions of compound symmetry are reasonable.

Univariate f-tests were used to investigate which of the repeated factor levels were associated with the overall significance. F-tests for each bioregion and site class revealed significantly lower GC on beech for 1 to 3 years from 1999 to 2004 in all bioregions, whether on high-mortality or on low-mortality plots (Fig. 4). These results indicate that beech was suffering from a species-specific stress and does overlap with conditions that favoured a build-up of scale populations (Fig. 2). Analysis detected significantly reduced beech growth only in one year prior to 1999 (1993) in BR 2.1L, 2.2L and 3L (Fig. 4). Review of Maine Forest Service reports during this window did not indicate any observations that could explain this decrease, nor does examination of weather records indicate a possible stress (data not shown).

Comparing raw ring width master chronologies (Fig. 5) against change index chronologies (Fig. 4) clarifies relative growth differences between species. For example, the master chronology of BR 3L showed that raw ring widths were less for beech chronologies after 1992, but they continued to parallel the variation of the associate species until 2004 (Fig. 5). Presumably, both species were responding similarly to climate factors during this time, including the drought of 1999–2002 (Lombard 2004).

Significant divergence in growth between beech and associate species beginning in 1999 coincides with outer ring formation in both dead trees and severely affected trees with locally absent rings (Fig. 6). For both groups, there was an increasing trend of cessation of cambial activity across all plots from 1999 to 2004, peaking in 2003 for dead stems and in 2004 for severely affected living beech, with a majority of both groups terminating growth after 2002. Prior to 1999, mortality averaged <5 trees/year. (Fig. 6). These observations support FIA data in that mortality surged after 2002 for all plots (Fig. 6). Additionally, observations showed that the most weakened trees that were still alive during the 2005 and 2006 field seasons had not put on new radial growth at d.b.h., for >5 years in some instances (Fig. 6).

3.4 Tree and stand factors

Tree- and stand-level factors were analysed for each bioregion and site class to determine whether certain stand factors were associated with higher mortality. Assumptions for analyses of variance were met ($p > 0.1$) for all factors tested. Analyses of variance produced significant interactions for mean disease rating ($p < 0.001$) and mean beech diameter ($p < 0.05$) between bioregion and site class.

Pairwise comparisons of mean disease rating for BBD were significantly lower ($p < 0.001$) in BR 1 (1.59) compared to all other bioregions (2.64) but not significantly different between site classes (i.e. high- and low-mortality sites), suggesting that disease damage present at the time of this study did not contribute to higher mortality (Fig. 7a).

Mean disease severity also was significantly lower ($p < 0.001$) in BR 1 (16%) compared to those of the other bioregions (49%) but was not significantly different for site class, suggesting that disease severity, similar to mean disease rating, did not contribute to higher mortality (Fig. 7b).

As expected, mortality was highly significant ($p < 0.001$) for site class with high-mortality plots containing more than 4 × greater mortality (50%) compared with low-mortality plots (12%) (Fig. 7c). However, despite significant differences in mean disease ratings and disease severity for BR 1 compared to all other bioregions, mortality was consistent across high-mortality plots for all bioregions (Fig. 7c). Mortality for all other species combined was below 4.2% (18 trees total), supporting hypothesis 1 that a host-specific agent was leading to increased mortality in beech.

Beech density did not differ significantly between site classes, but densities, on average, tended to be lower in low-mortality plots (Fig. 7d). Mean diameter was slightly higher for high-mortality plots (22.7 cm, $p < 0.05$) compared with that of

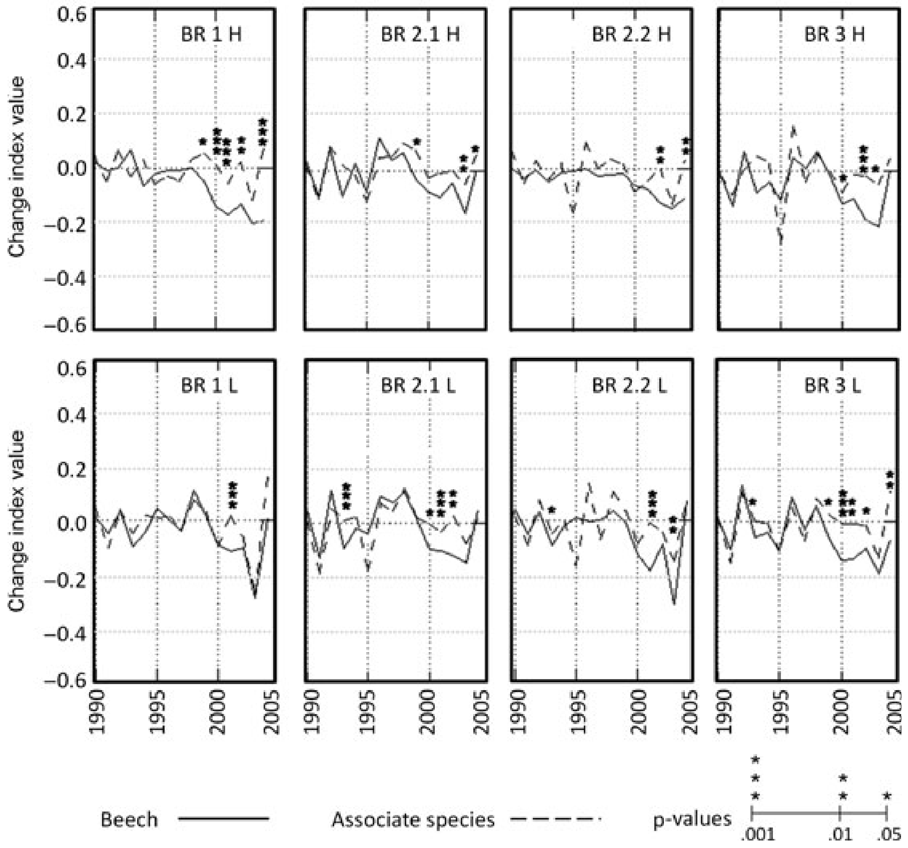

Fig. 4. Change index chronologies for beech and associate species by bioregion and site class from 1990–2004. Change index $(GC_x) = [(RW_x - RW_{x-1})/(RW_x\text{-}1 + RW_x)]$ where RW_x is the ring width for a particular year *x*, and RW_{x-1} is the ring width for the year preceding it. Asterisks denote where beech had significantly reduced growth change compared to associate spp. All values of the index fall between −1 and 1 with zero indicating no change in ring width from the previous year.

low-mortality plots (21.4 cm, $p < 0.05$) (Fig. 7e). Finally, an interaction ($p < 0.01$) between bioregion and site class was observed. Beech BA was not significantly different between bioregions, but low-mortality plots had significantly less beech BA than high-mortality plots ($p < 0.05$) regardless of bioregion, averaging 7.5 m^2/ha for low-mortality plots across all bioregions and 10.0 m^2/ha for high-mortality plots across all bioregions (Fig. 7f).

Elevation differed significantly ($p < 0.05$) between BR 2.2 (406 m) and BR 3 (274 m) but not for the other bioregions or for site class, indicating that mortality was widespread regardless of differences in elevation (Graph not shown). Elevation ranged from 232 to 468 m and generally decreased from south-west to north-east (Table S1).

Age was excluded from the analysis owing to difficulty in assigning accurate ages, especially in the earlier age segments of beech. Ages reported in Table S1 include only those cores lacking problematic segments.

Scale intensity did not differ significantly between bioregion or site class and averaged 1.83 (trace scale density) across all bioregions (Table S1). Observations on a limited number of beech across all plots sampled during the summers of 2005 and 2006 revealed beech scale was still present at moderate to high densities on 20 (≈4%) individual beech trees. Among these 20 trees, three were from BR 1, nine from BR 2.1, two from BR 2.2, and six from BR 3.

Presence of *Neonectria* fungi was confirmed by the occurrence of perithecia in 2005 and 2006 on 132 beech trees (23%) sampled, of which 59 beech (45%) were dead and 73 (55%) were alive at time of plot establishment. Of the 73 living beech with perithecia, 47 (64%) had radial growth, where cessation of cambial activity at d.b.h. preceded year of death. Severely affected beech and dead beech comprised a majority (80% or 106 total trees) of beech with perithecia at the time of sampling. Both *Neonectria faginata* and *Neonectria ditissima* were present, and their spatial distribution varied not only between plots and among adjacent trees within the same plot but also between different niches on individual trees (Kasson and Livingston 2009).

Seventy-six additional beech (13% of all beech sampled in this study) had heavy tarry spots at the time of plot establishment but lacked perithecia. These trees were distributed across 20 plots and across all four bioregions. Of these 76 beech trees, nine were dead and 67 were alive at the time of plot establishment. Of the nine dead trees, six individuals exhibited cessation of radial growth prior to 2005, whereas only four individuals of the remaining 67 live beech exhibited cessation of radial growth prior to 2005. Individual trees having >100 fluxes of tarry spot at time of observation were prevalent in BR 1 owing to a more recent establishment of beech bark disease in these stands.

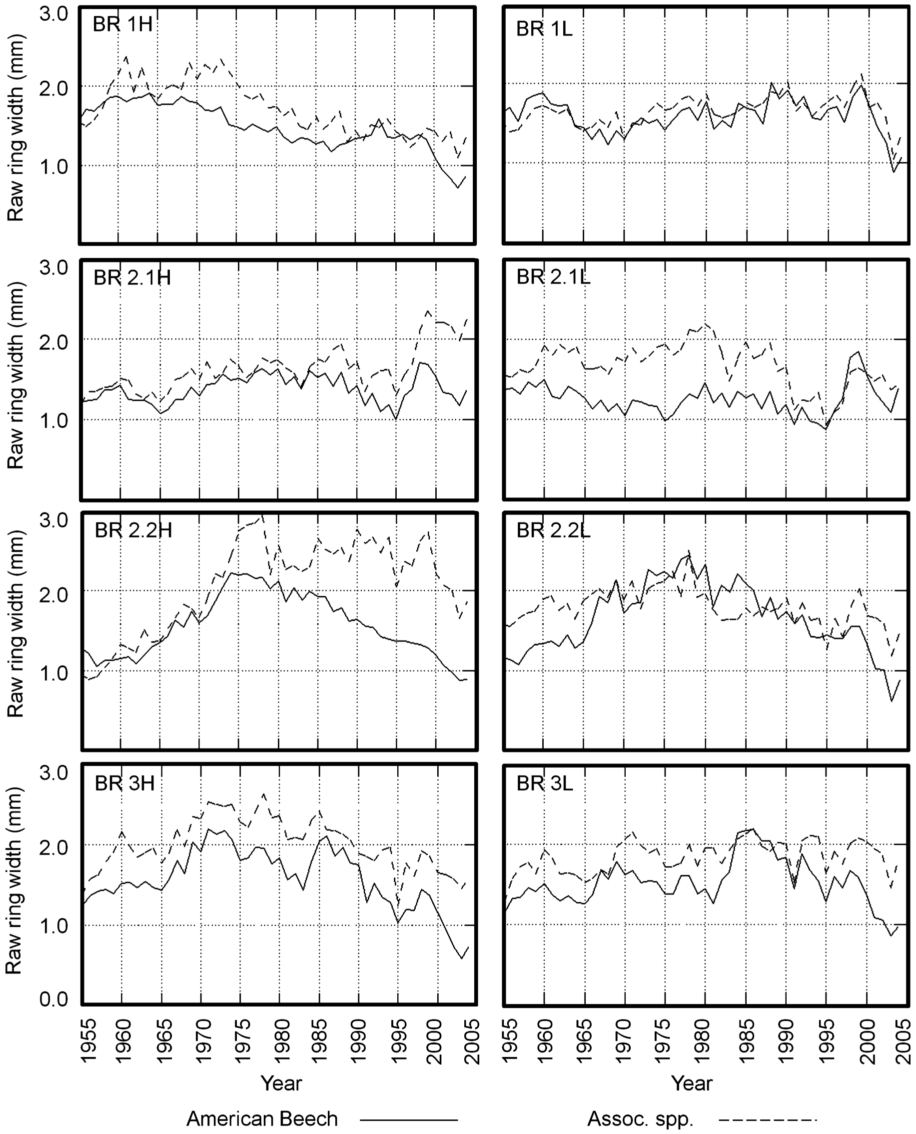

Fig. 5. Master chronologies for host and associate species by bioregion and site class from 1955–2005. Chronologies were truncated to include only the growth period after 1955 when *Cryptococcus fagisuga* first appeared in the northern part of Maine. H = high mortality plots and L = low mortality plots.

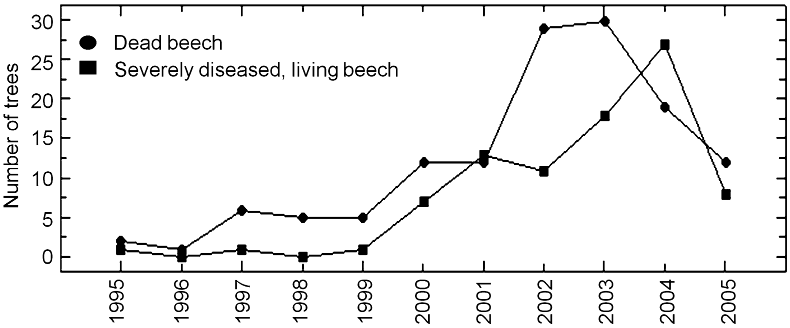

Fig. 6. Number of dead and severely stressed trees based on year of last outer ring formation across all bioregions in northern Maine. Severely stressed trees are described as those trees where cessation of cambial activity at d.b.h. precedes tree death. Of the 481 beech cores used in this study, 190 (40%) had year of outer ring formation prior to 2005, the first year of sampling.

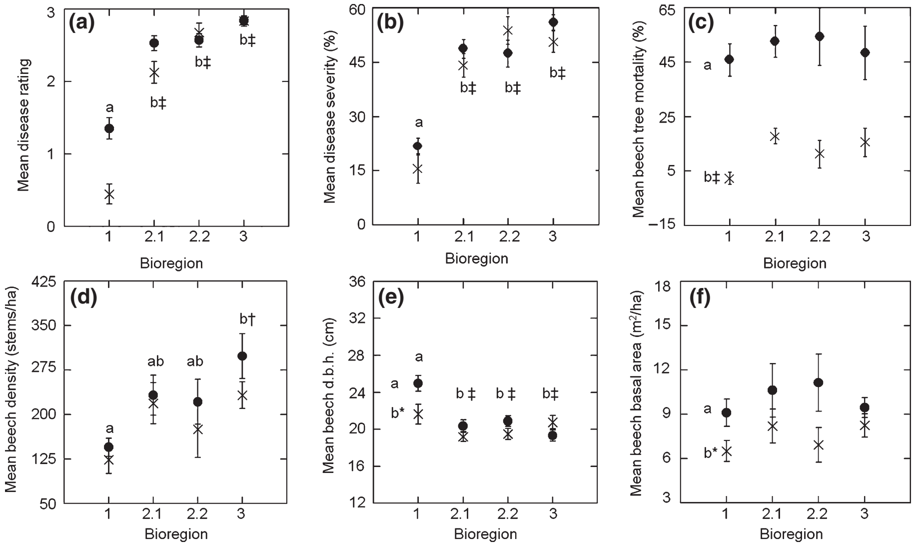

Fig. 7. Significant tree and plot level variables for bioregion and site class. (a) Mean beech bark disease ratings for external defect was ranked solely on external symptoms and was used as a relative indicator of disease duration within these stands. (b) Beech bark disease severity was an estimation of cumulative defects from BBD along the lowest 2 m of the tree. (c) Mean beech mortality was the percentage of dead beech for all trees >12.7 cm d.b.h. (d) Mean beech density was number of beech stems/ha estimated from total number of on-plot beech >12.7 cm d.b.h. (e) Mean beech d.b.h. was expressed in cm. (f) Mean beech basal area was expressed in m^2/ha. Site class was denoted by an x for low mortality plots or by a ● for high mortality plots. Means between site classes were not different for (a), (b), and (d); pooled means were used for comparisons among bioregions for these analyses. Bonferroni pairwise comparisons were used to test for significant differences between bioregions and site classes and are indicated by different letters. p values are denoted as *($p < 0.05$), †($p < 0.01$), or ‡($p < 0.001$). *N* values for tree level variables (a), (b), and (e) are 56 and 50 for high and low mortality plots respectively in BR 1, 95 and 92 for BR 2.1, 99 and 79 for BR 2.2, and 86 and 65 for BR 3. *N* values for plot level variables (c), (d), and (f) are 5, 5, 4, and 5 for BR 1, 2.1, 2.2, and 3, respectively. Range bars indicate one SE.

4 Discussion

4.1 Beech scale and *Neonectria* as plausible factors in beech mortality

Beech mortality occurred in two stand types. Stand type 1 (ST1) includes all plots within BR 1, and it represents the region along the Maine–Quebec border (Shaded region, Fig. 1) where beech were significantly larger, lacked cankers (Figs 7a and 8) and had GC values essentially identical to those of associated species except for 2001, confirming reduced stress compared to beech in all other bioregions (Figs 4 and 5). Stand type 2 (ST2) includes all plots in BR 2.1, 2.2 and 3, and it represents the region further east where BBD is well established and in the aftermath phase, i.e. limited cankers are present (Figs 7a and 8, Table S1).

If scale was not a plausible inciting factor for ST 1, weather conditions would have remained unfavourable for scale population build-up. Yet the results of this study show that conditions most favourable to the proliferation of the scale do overlap with the onset of the observed mortality in both ST1 and ST2 (Figs 2 and 3). Therefore, a beech scale outbreak is plausible throughout the study area beginning in 2000.

Despite favourable conditions for beech scale, reports of scale outbreaks in Maine are lacking. However, in 2002, reports of scale build-ups were observed on canker-free trees in adjacent regions of New Brunswick (Carter 2005) (E. Hurley, Personal communication, NRC-CFS, Fredrickton, NB, Canada). Such heavy infestations had not been observed in New Brunswick for several decades. Comparisons of beech radial growth increments with those of associate species indicated that a stress unique to beech, such as a scale outbreak, had become significant primarily in 2000 and later (Fig. 4). The decrease in growth is associated with beech mortality, which doubled from 2001 to 2002 (Fig. 6). Increased beech mortality for Madawaska County, New Brunswick, also was reported during late season 2002 (Carter 2005). Forty-five hundred ha of beech damage and mortality as high as 30% were mapped in New Brunswick, including areas bordering BR 1, BR 2.1 and BR 3 with mortality (Carter 2005). These values were similar to mortality levels reported in northern Maine in 2003 (Kasson 2007).

However, by fall 2003, scale populations fell to unexpectedly low levels and could not be further quantified in Canada (E. Hurley, Personal communication). In Maine, average scale intensity rating was heavy (MSI = 5) on only 4% of the beech in 2005 and 2006. The reports of low scale populations are consistent with high level of scale mortality that would be associated with high August–October precipitation in 2003 and 2005 (Fig. 3).

Reports of beech scale outbreak in neighbouring New Brunswick, the concurrent favourable weather conditions in Maine and the large decrease in beech increments indicate that beech scale is a plausible stress involved with beech mortality in northern Maine. This stress was severe enough to decrease increments across the region despite the tendency of the sampled beech to have low interseries correlations (Table S1), indicating that beech populations rarely respond simultaneously to environmental factors.

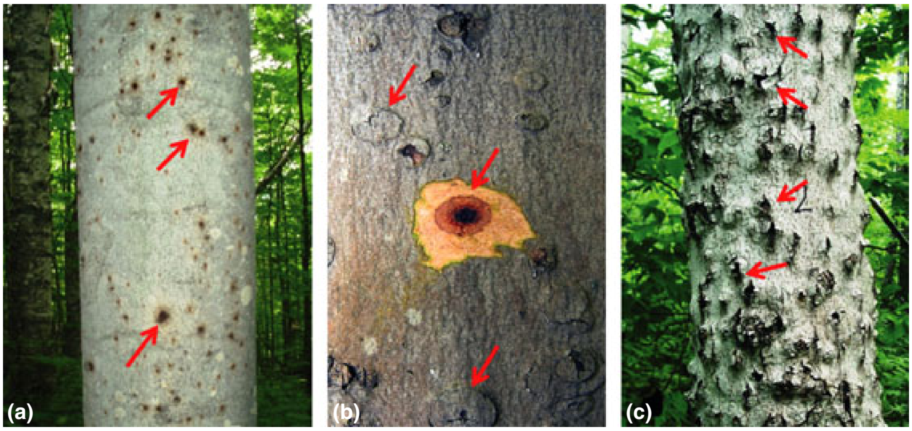

Fig. 8. Symptom progression associated with mean disease ratings for beech bark disease on American beech in northern Maine. Symptoms were ranked solely on external symptoms and was used as a relative indicator of disease duration within these stands and included (a) cracked bark + tarry spot (Mean disease rating, MDR = 1), (b) raised circular legions (MDR = 2), and (c) pocket cankers (MDR = 3). Arrows correspond to specific symptoms associated with each disease rating. Photo in panel (b) courtesy of Michael Mardosa UMaine Today.

Perithecia of *Neonectria* were found on 23% of the sampled beech, 80% of which were dead and dying. These results are consistent with a typical BBD outbreak in which fungal colonization happens after trees are severely stressed (Houston 1994b). Actual *Neonectria* incidence was likely much higher on diseased beech because perithecial production by *Neonectria* fungi continues for only about 24 months after tree death (Lohman and Watson 1943; Ferrandino et al. 2005), indicating that trees dying before 2004 or trees not yet dead would not show perithecia.

While W1 had the most favourable conditions for scale outbreak, there are two additional windows, W2 and W3, where conditions were not limiting to scale populations. The Maine Forest Service did observe an increase in scale incidence during 1986–1990 period (W2) (Anonymous 1988, 1990, 1991), during which lethal temperatures and August–October precipitation were low but not as favourable as during W1 (Fig. 2). Less-favourable conditions for scale development is consistent with beech increments not being lower than those increments of associated species in 1990 (Fig. 4).Therefore, scale incidence was not severe enough to incite a radial growth decline. These observations in combination with the earlier discussion strongly support the observations that winter temperatures >–34°C and August–October precipitation < 10 cm total will favour a beech scale outbreak in this region of Maine but not necessarily induce tree mortality.

Unique weather conditions beginning in 2000 are consistent with beech scale being a plausible stress associated with beech mortality. *Neonectria* infections observed on dead and dying beech also make this factor a plausible stress associated with mortality.

4.2 Drought and beech mortality

A severe drought began in 1999 (Lombard 2004) just prior to the reported beech scale outbreak in adjacent regions in Canada. Therefore, beech increments (Fig. 5) and mortality (Fig. 6) could have been affected by both stresses simultaneously. The drought, with severity that occurs less than once every 100 years, was primarily indicated by low-stream-flow measurements, a measure of sustained or cumulative period of low water status in a watershed compared with precipitation deficits which can rebound from month to month (Lombard 2004).

Short- and long-term drought have been implicated as major causes of accelerated root mortality in several species, which may negatively impact radial growth and survival of stressed trees (Santantonio 1982; Marshall 1986). Leuschner et al. (2001) reported that beech fine roots are among the plant organs most sensitive to drought although any appreciable influence is largely dependent upon the duration of drought. Mainiero and Kazda (2006) reported high-carbohydrate partitions to fine root investment patterns for *Fagus sylvatica* in central Europe during a 2003 drought, which would likely deplete tree reserves.

The ability of beech to reduce radial growth at d.b.h. for extended periods under extreme stress, as demonstrated by the absence of growth rings in severely affected trees (Fig. 6), is possibly due to small parenchyma-to-vessel pits (<10 μm). The small size of these pits inhibits the production of tyloses, thus allowing for continued water uptake in previous years' sapwood (Chattaway 1949). Cherubini et al. (2002) also reported that year of cessation of radial growth at d.b.h. preceded year of death in European beech affected by drought.

Drought stress beginning in 1999 is a plausible factor in the mortality of beech in northern Maine.

4.3 Site factors and beech mortality

Higher mortality occurred in plots with higher beech basal area. A beech basal area increase of 2.4 m^2/ha was associated with an increase in mortality from less than 20% to more than 45% (Fig. 7c,f). In ST 1, the higher basal area is associated with a larger d.b.h. for beech, trees that are a better host for beech scale population build-up (Houston and O'Brien 1983; Mize and

Lea 1979; Wiggins et al. 2004). In ST 2, the high basal areas were attributable to higher beech densities, a factor that should also favour build-up of scale and *Neonectria* populations. However, mean disease rating and severity did not differ between low- and high-mortality plots within ST 2. If basal area is related to beech mortality, it is attributable to its impact on recent scale/drought interactions and not long-term BBD development. Other site measure parameters such as elevation and age cannot explain why mortality varied across this region. Additional site factors associated with vulnerability to drought stress, such as soil type, probably play a role in explaining differing levels of beech mortality in northern Maine but were not part of this study.

4.4 Plausible stresses associated with beech mortality

Multiple factors occurred and offer plausible explanations for Maine's beech mortality: Drought occurred at the same time weather conditions (warm winters, dry falls) favoured scale outbreaks, and *Neonectria* infections became established on stressed trees. A similar situation resulting in 48% beech mortality occurred in western Pennsylvania during droughts from 2001 to 2005 (Mackenzie 2006). Beech in western Pennsylvania suffered from high scale populations associated with the killing front prior to 2001, indicating that a spike in beech mortality is associated with drought and BBD in both Pennsylvania and Maine. However, because severe drought stress only coincided with beech scale outbreaks, it is unclear whether drought alone can cause enough stress to allow infections by *Neonectria* followed by beech mortality. Finally, higher beech mortality is associated with another factor, higher beech basal area.

The fate of Maine's northern hardwood forests is largely dependent on the reoccurrence of beech in stands exhibiting dieback and mortality. Although advanced beech regeneration was present in most study plots from 2005 to 2006 (Kasson 2007), whether additional sprouts arose in the aftermath of the most recent mortality is unknown. If the 2001–2002 drought period resulted in mortality of beech root systems to the extent that beech failed to resprout, then the prevalence of diseased trees within the affected stands may decrease over time. Mackenzie (2006) observed that canopy gaps left by BBD-killed beech in Pennsylvania were filled quickly by expanding crowns of non-beech canopy trees, suggesting that stands with higher species diversity and uneven age structure may favour the displacement of beech in the canopy. However, if beech trees do resprout from surviving root systems, then a cycle of BBD involving prolonged defect accumulation followed by eruptive episodes of mortality as seen in stand type 2 could continue.

Concerning global climate change, Dukes et al. (2009) predict more widespread effects on forest composition and structure, including increased dispersal and survival of *C. fagisuga*, consistent with our observations. Our study supports these predictions and indicates a potential for additional mortality episodes if lethal winter temperatures and other climatic constraints become rarer.

The results of this study demonstrate that the following stresses are plausible explanations for beech mortality in northern Maine: (1) A scale outbreak stressed trees from 2000 to 2003. This conclusion is supported by (a) reports of outbreaks in adjacent areas of Canada, (b) conditions for a scale outbreak, i.e. lack of killing temperatures <−34°C and August–October precipitation < 10 cm, occurred during this period and (c) beech increment decreases were significantly more severe than those found in associated species during this period. (2) A record drought from 1999 to 2002 severely impacted the trees as indicated by (a) a decrease in increments in both beech and associated species starting in 1999 and (b) beech died or stopped producing increment immediately after 1999. (3) *Neonectria* infected weakened trees and hastened mortality as indicated by the presence of tarry spots and perithecia on dying and recently killed trees. Despite mortality being consistently high across all bioregions, BBD had two simultaneous killing phases across northern Maine from 1999 to 2003. The first was an expanding killing front along the Maine–Quebec border, a region not previously affected by BBD, presumably due to the high frequency of winter temperatures lethal to *C. fagisuga.* The second was widespread mortality further east in stands that had been affected by BBD for many years (i.e. aftermath forests) (Houston 1975). Even though BBD has been in Maine for decades, recent combinations of warmer winters and droughts are associated with unprecedented levels of beech tree mortality.

Even though field sampling and measurements began after the mortality had started, dendrochronology could be used to quantify temporal relationships between weather, stresses and tree increments, and the results provided the basis for identifying plausible explanations for a dieback/mortality event.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Plot-level factors for 38 beech mortality plots in northern Maine, USA.

Table S2. Marker years used by plot for cross dating.

Table S3. Between and within subjects tests, repeated measures analysis ANOVAS for GC_x (1990–2004).