2008

# Using Dendrochronology to Understand the Response of Eastern Hemlock to Past Stresses and its Current Status in Southern Maine

Sophia DeMaio

## Recommended Citation

DeMaio, Sophia, "Using Dendrochronology to Understand the Response of Eastern Hemlock to Past Stresses and its Current Status in Southern Maine" (2008). *Electronic Theses and Dissertations*. 427.
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# USING DENDROCHRONOLOGY TO UNDERSTAND THE RESPONSE OF EASTERN HEMLOCK TO PAST STRESSES AND ITS CURRENT STATUS IN SOUTHERN MAINE

By

Sophia DeMaio

B.S. Bates College, 2003

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Forestry)

The Graduate School

The University of Maine

May, 2008

Advisory Committee:

William Livingston, Associate Professor of Forest Resources, advisor

Laura Kenefic, Faculty Associate, Research Forester, U.S. Forest Service

Jennifer Pontius, Research Ecologist, U.S. Forest Service

Jeremy Wilson, Assistant Professor of Forest Management

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# USING DENDROCHRONOLOGY TO UNDERSTAND THE RESPONSE OF EASTERN HEMLOCK TO PAST STRESSES AND ITS CURRENT STATUS IN SOUTHERN MAINE

By Sophia DeMaio

Thesis Advisor: Dr. William H. Livingston

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
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May, 2008

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is an ecologically important species that is threatened across its range by the non-native hemlock woolly adelgid (HWA, *Adelges tsugae* (Annand) (Hemiptera: Adelgidae)). In order to understand potential impacts of HWA in southern Maine, we conducted a tree-ring study of 36 sites in southern Maine (York and Cumberland counties) to evaluate how stress events affected eastern hemlock increments, especially after the 1999-2002 drought.

The primary objectives were to: 1) create a master chronology and identify reduced growth events 2) model abiotic factors associated with differences in drought response among plots and 3) evaluate the impact of the 1999-2002 drought on growth trends across the southern Maine hemlock population.

Reduced growth events coincided with records of drought and defoliation by hemlock looper (*Lambdina fiscellaria* (GUEN.) and gypsy moth *Lymantria dispar* (L.). Hemlock growth for the master chronology was also associated with 1) previous year's June and July temperatures, 2) both previous and current summer precipitation, and 3) both maximum and minimum February temperatures.

A predictive model for the 2003 drought year showed that plots with higher expressed population signals (and adjustment of interseries correlation for sample size), shallower O soil horizons, lower average February maximum temperatures, higher B soil horizon aluminum saturation, and greater stand densities had the largest decreases in mean growth, as expressed by the percent growth change of increments over a 3 year period. The plots with the most negative percent growth change in 2003 had the most positive percent growth change in 2005. The 2005 recovery was positively related to average plot age and calcium in the B soil horizon.

The low number of trees (59 of 503) experiencing decreased growth in 2005 supports the observation from the master chronology that hemlock trees in this study are typically healthy and able to quickly recover following drought stress. These findings support the consideration of management strategies that increase hemlock vigor leading to greater growth potential and enhanced ability of trees to recover from stress.

# DEDICATION

In loving memory of my grandmother
Sarah F. Tomaino
(who never really approved of coring trees)

### Forest

The forest floor in glittering laurel
Is mushroom black
Roofed by a tent of tilting light
Beyond these thresholds of night
It is noon in the clearings

I sit by the swamp walk
I am swamp myself
Probed and sipped by mosquitoes
Full of unvirginal fluids

I like it here. My place
Mud-foot, frog-haunch, fern-skin
Tonight I'll be back
Let me in, let me in.

*Sarah F. Tomaino*

# ACKNOWLEDGEMENTS

I am extremely grateful to my advisor, Bill Livingston, for offering to advise me and his patience and commitment throughout this process. He and his daughter Amanda helped me get started in the field. Committee members Jennifer Pontius, Laura Kenefic, and Jeremy Wilson brought their insight and enthusiasm to the project, and helped me make it presentable. Thanks to Bob Seymour, Shawn Fraver and Al White for introducing me to the study of tree rings, Ivan Fernandez and Bruce Hoskins for answering soil questions, and Bill Halteman for statistical explanations. Big thanks to Louis Morin, Gail Belanger, Cindy Paschal, Dolores Stone and the rest of the crew at Nutting Hall–you have helped me in so many ways over the past 3 years.

This project would not have been possible without the generous support and guidance of the Maine Forest Service. Special thanks to Dave Struble, Don Ouellette, Allison Kanoti, Wayne Searles, and Charlene Donahue. I would also like to thank all of the landowners and managers who were interested in the project and allowed me to work on their land. Special thanks to Norman Forbes of the Department of Inland Fisheries and Wildlife, who offered the assistance of his 4 wheel drive and spent a day digging soil pits. Thanks to John Brissette and the U.S. Forest Service who allowed me to stay in the house in Lyman and Justin Waskiewicz, Fred Beaudry, and the turtle crew who shared accommodations and experience. Ed, Al, and all of the kind strangers who offered general assistance during the field season, you were more important than you'll ever know!

I can’t imagine anybody I’d rather spend a summer working with than Abby Pearson. The project greatly benefited from her interest, knowledge organization, and humor. She even got her mom, Cindy Finnamore, out working with us! Thank you to Catherine Amy Kropp, who helped in the forest when I needed her friendship and assistance most, and mounted cores through the winter. I also appreciate the fine workmanship of Mike Puleo who sanded the cores.

Thanks to Mom (digging in a poncho), Dad (editor and nursemaid), Lucia (big sister-always), and Scott (comisserator). The Roach and Underwood families have been a constant source of friendship and kid-energy. Fellow students have given me helpful input on Photoshop, photosynthesis, and calculations in between. They’ve also been there for friendship and fun. Thanks to the Flying Trouts bicycle gang for their camaraderie during the last few years and Jamie Weaver who coached me through the thesis out on the PEF. I have been lucky to live and work with so many amazing people during my time at the University of Maine and I thank you all!

Finally, I am very grateful that I was able to spend a summer in the hemlock forests of southern Maine.

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# Chapter 1

# INTRODUCTION

## Background

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is a species of ecological importance that is threatened across its range by the non-native hemlock woolly adelgid (HWA, *Adelges tsugae* (Annand) (Hemiptera: Adelgidae)). HWA currently exists across one-half of eastern hemlock's native range, but its spread is much slower in northern New England (Evans and Gregoire 2007) where cold winter temperatures periodically decrease populations and limit the spread of the insect (Paradis et al. 2007). HWA began to infest natural stands along the southern border of Maine in 2003 (Maine Forest Service 2007). It has been suggested that the slower spread in this region will give forest managers more time to take advantage of management options for limiting the spread and severity of HWA infestations (Fajvan 2007).

Other stresses affecting hemlock in southern Maine include drought and defoliation. There are published records of several droughts in the region since 1940 (Lombard 2004). Drought has been shown to cause hemlock mortality on its own (Balio et al. 2004) and in combination with insect activity (Maine Forest Service 2002, Mayer et al. 2002). There are also records of defoliating insects known to affect hemlock in this region, primarily hemlock looper and gypsy moth (Trial 1994, Trial and Devine 1994, Bradbury, 1990, Bradbury, 1991, Bradbury, 1992, Bradbury 1993, Bradbury 1994).

In order to manage eastern hemlock effectively in the presence of HWA, drought, defoliators, and other stresses, we must understand how hemlock has been affected by past stress events. This thesis uses tree-ring analysis of hemlock in southern Maine to evaluate the species' past response to stresses and its current growth trends prior to HWA infestation.

## Ecology and Importance

Eastern hemlock grows from the Great Lakes region to Nova Scotia as well as through New England, along the Appalachian Mountains to northern Georgia and Alabama and in other outlying populations (Godman and Lancaster 1990) (Figure 1). In Maine there are about 161,000 acres of the white pine/hemlock forest type and 625,000 acres of the hemlock forest type (McWilliams et al. 2005). Based on recent Forest Inventory and Analysis data, hemlock accounts for approximately 17,000 million cubic feet of volume in Maine forests. The highest basal area of hemlock occurs in a band just inland and parallel to the coast (McWilliams et al. 2005) (Figure 1).

Hemlock grows in a wide range of site conditions across its range (Godman and Lancaster 1990). In New Hampshire, eastern hemlock basal area was highest on poorly drained soils, rock, outwash and wet compact tills (Leak 1978).

Stable microclimates develop under dense hemlock crowns (Godman and Lancaster 1990), characterized by cool damp conditions, slow rates of nitrogen cycling, and low soil nutrient status (Jenkins et al. 1999). Eastern hemlock is the only shade tolerant conifer in many parts of its range (Beaty 1984) and influences structure of mixed stands through vertical and horizontal stratification, which enhance wildlife habitat (Kelty 1989, Yamasaki et. al. 2000). The milder conditions, shade, and forest structure facilitated by hemlock are favored by wildlife throughout the year (Reay 2000, Yamasaki et al. 2000, Tingley et al. 2002).

The shade produced by hemlock forests also influences soil moisture and stream temperatures, thus supporting a number of amphibians, fish, and freshwater invertebrates (Allison et al. 2005, Ross 2003, Snyder 2005) and impacting streamflows and runoff (Ford and Vose 2007)

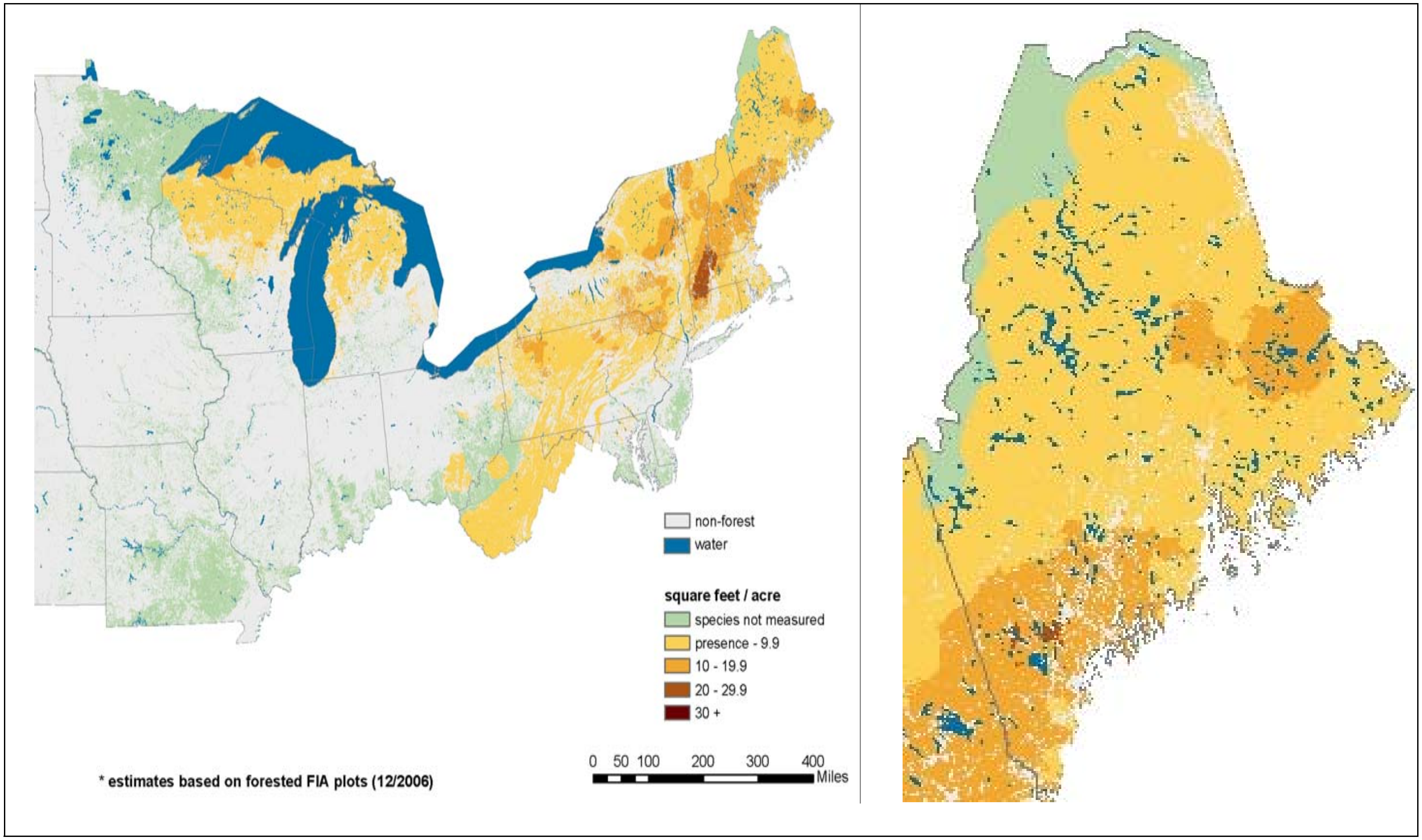

**Figure 1. Eastern hemlock distribution in the eastern U.S. and Maine.**
Measured in basal area per acre. Image created by the Northern Research Station Forest Inventory and Analysis (http://www.nrs.fs.fed.us/fia/).

## Dendrochronology

Dendrochronology is the study of annual tree ring growth (Stokes and Smiley 1996). Yearly ring growth is related to both external resources and conditions in the tree. External factors include water, temperature, light, carbon dioxide, oxygen and soil minerals, which affect temperature, water availability, and carbon building materials within trees (Fritts 1976). Therefore the availability of resources for growth depends on climate, site, and stand conditions as well as genetics. One aspect of dendrochronology, dendroclimatology, relates differences in yearly growth to climatic factors in order to improve understanding of the past, present, and future relationship between climate and tree growth (Fritts et al. 1965, Cook and Cole 1991, Oberhuber et al. 1998, Linderholm 2001).

Because shading and competition were thought to be the major factors limiting tree growth in the northeast, dendrochronology developed later in this region (Fritts 1976). Eastern hemlock was one of the first species in the northeast to be used for climate-tree ring studies (Cook 1990). Hemlocks were first cross-dated by Douglas in 1919 (Cook 1919). Lyon (1935) related tree growth to April-August rainfall and suggested the use of small ring widths to extend and improve records of physiological drought. Cook and Jacoby (1977) also related tree ring growth to water availability with Palmer Drought Severity Index values for May of the previous year to August of the current year. They also suggested that ring growth could be used to reconstruct past droughts. Cook and Cole (1991) found associations between average monthly temperatures and ring widths that appeared to be independent of site conditions. They reported that precipitation growth responses, however, were dependent on site hydrology.

Dendroecology, another application of dendrochronology for understanding ecosystem processes, has been used to document the disturbance history and succession of hemlock in relation to other tree species (Abrams and Orwig 1996, McLachlan et al. 2000). Dendroecology also was used to compare heavily and lightly HWA infested trees in an old growth stand in Pennsylvania. The trees that were growing at lower rates prior to infestation became more severely infested by HWA (Davis et al. 2007). A study at the Delaware Water Gap National Recreation Area showed that HWA infestation level and crown variables including live crown ratio, crown density, foliar transparency, and branch dieback were most closely associated with growth decline as measured by three consecutive years of declining growth (Rentch et al. In Review).

Both dendroclimatology and dendroecology are important for understanding the factors historically affecting a tree population, as well as the current growth status of that population. This study uses both dendroclimatology and dendroecology to investigate stress history and current status of southern Maine’s hemlock population.

## Objectives

This study had three primary objectives. The first objective was to identify reduced growth events for hemlock in southern Maine and identify their causes from historical records.

The second objective was to identify abiotic factors associated with increment growth response following the 1999-2002 drought, including variations in site, climate, and/or average tree characteristics.

The third objective of this study was to evaluate the effect of the 1999-2002 drought on growth trends occurring in the southern Maine hemlock population.

## Chapter 2

## METHODS

### Plot Locations

Polygons were selected at random from maps of conservation lands in York and Cumberland counties by soil series (Maine Geographic Information System 2007) where aerial photos indicated the presence of conifers. A forest stand within a polygon was sampled if hemlocks dominated (dominant or codominant >12.5 cm DBH, >8 $m^2$/ha in hemlock). This resulted in 36 sample plots of 0.081 ha each.

Most of the sites are on conservation lands owned or managed by the state of Maine and federal governments (Figure 2). Some of the lands are in public parks with limited cutting, while others are under conservation easements where logging activities continue to occur. Climate throughout the region is characterized by warm summers and cold winters with precipitation spread evenly throughout the year. Plots have diverse land-use and disturbance histories. Though this was not explicitly studied, evidence of past farming and fire were indicated by the presence of rock walls and charcoal at some sites. Defoliation by gypsy moth and hemlock looper was also variable across this region (Trial 1994, Trial and Devine 1994, Bradbury 1990-1994).

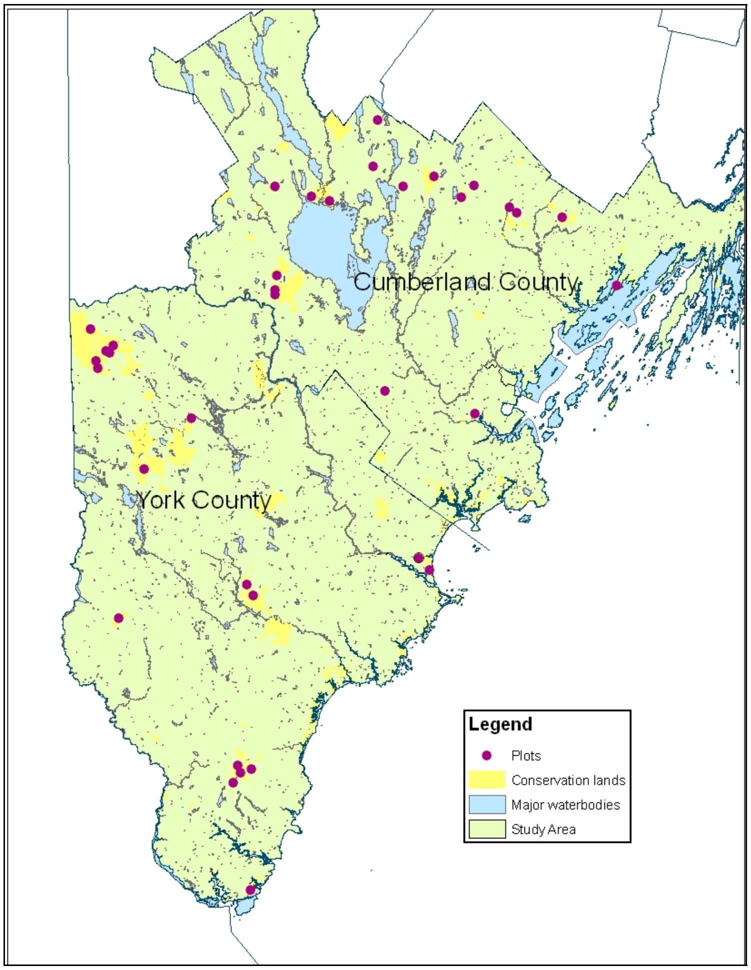

**Figure 2. Plot locations in southern Maine**

## Plot and Tree Measurements

At each site we recorded primary aspect along with slope (%) in each of the four cardinal directions using a Suunto clinometer. Species, crown class, and diameter at breast height (1.4 meters above the ground) were recorded for all trees greater than 12.5 cm DBH within each 0.081 ha plot. Height and lowest live branch were also measured for all dominant and codominant hemlocks using a sonic hypsometer. Live crown ratio (LCR) was calculated from these measurements: LCR = (height - height to lowest live branch) / height * 100).

Percent dieback and other indicators of tree health including presence of logging damage, frost cracks, fire scars, and fungus were recorded.

### Soil Measurements

A soil pit was dug in the center of each plot to below the maximum rooting depth or restrictive layer. All horizons were described for depth, texture, and percent course fragments. Samples of the upper O, B, and C horizons were collected, dried, shattered, and sieved through 4 mm (organic horizons) and 2 mm (mineral horizons) sieves. Soil samples were analyzed for pH, percent loss on ignition (% LOI), percent nitrogen (N), percent carbon (C), exchangeable acidity, and cations calcium (Ca), potassium (K), phosphorus (P), aluminum (Al), iron (Fe), manganese (Mn), sodium (Na), and zinc (Zn) using the Forest Soils Protocol (Roberge and Fernandez 1986).

Calculations of additional soil parameters relevant to plant growth included cation exchange capacity (CEC), percent base saturation (%Base), percent aluminum saturation (%Al), carbon to nitrogen ratio (C/N), and the ratio of calcium to aluminum (Ca/Al) based on concentrations (meq/100g).

### Tree Cores

One core was extracted from each dominant and codominant hemlock in plots using a 4mm increment borer. Trees were cored at breast height perpendicular to the slope to avoid compression wood. Then the clearest surface of the trunk was cored to reduce branch interference and ring-shake. If less than twelve dominant and co-dominant hemlocks were available within the plot, overstory hemlocks on the perimeter of the plot were included. Cores were dried, mounted, and sanded up to 800 grit. Tree rings were then marked and visually crossdated using WinDendro (Guay et al. 1992) and statistically cross-dated using COFECHA (Holmes 1983). Age at breast height was estimated for each plot based on cores that either contained pith or where a pith locator could be used (Applequist 1958).

Basal area increment (BAI) has been used as a measure of tree growth in dendrochronological studies to account for total accumulation of wood during a given year (Phipps 1984, LeBlanc 1990, Duchesne et al. 2002). To calculate basal area increment (BAI) an estimate of the breast height radius was obtained by subtracting the bark width from half of the DBH to obtain the radius of the wood. Bark measurements were estimated using a linear regression of known hemlock bark thicknesses from central Maine: $Y = 2.08135+(0.50616 * X)$ where X is DBH in centimeters and Y is bark thickness in millimeters (adjusted $r^2 = 0.79$, 88 degrees of freedom) (unpublished data from Laura Kenefic, U.S. Forest Service, Northern Research Station, Orono, ME).

The radius of the wood ($r_w$) was estimated as DBH / 2 – Y. Total BA at the breast height cross-section was calculated as $\pi * (r_w)^2$. Using radial increments (r) for each calendar year (n), BAI for a calendar year was calculated:

$BAI_n = \text{Total BA} - \pi * (r_w - (r_n + r_{n+1 \ldots} r_{2005}))^2 - (BAI_{n+1} + BAI_{n+2} \ldots BAI_{2005})$

## Climate Data

Palmer Drought Severity Index values were obtained from the National Climatic Data Center (NOAA Satellite and Information Service 2008 http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp). Yearly values were averaged for Maine climate zones 2 and 3 covering the inland and coastal sections of southern Maine.

Estimates for monthly precipitation, average maximum temperature, and average minimum temperature were obtained for each plot using the PRISM database (Spatial Climate Analysis Service 2008 http://prism.oregonstate.edu/). The continuous climate data provided by PRISM has 4 km resolution and is derived from climate station values, a digital elevation model, incorporation of coastal affects, and other climactic influences (Daly et al. 2004).

## Chronology Development

Ring-widths were standardized using a 30 year smoothing spline in the program ARSTAN (Holmes et al. 1986). Cook (1985) introduced cubic smoothing splines to better fit actual growth trends and to minimize ring trends related to age-size, local, and stand-wide disturbances (Cook, 1987) without eliminating short-term year to year variation. A thirty-year period was used because that was the minimum age of any core. Flexibility was set at a 50% cutoff wavelength (Holmes et al. 1986).

A residual chronology (RES) was also calculated in ARSTAN, using autoregressive modeling of residuals from the standard chronology, which removes persistent trends and shows the common yearly growth relationships by chronology (Cook and Holmes 1986). Residuals indicate how far an increment varies from the average, so negative residuals indicate abnormally low growth in a corresponding year which can be compared to historical drought and insect reports. Published drought records were only available after 1940 (Lombard 2004, Maloney and Bartlett 1991); therefore, most of the discussion was limited to that time period.

ARSTAN was used to modify the RES chronology to reincorporate the autocorrelation in yearly growth presumably due to climate (Cook and Holmes 1986). The modified chronology (ARSTAN) was used in the climate analysis.

### Climate Analysis

DendroClim 2002 (Biondi and Waikul 2004) was used to identify climatic variables associated with year to year variations in tree growth. This program uses principle components regression, where eigenvectors derived from climate variables are predictors used in stepwise linear regression (Biondi and Waikul 2004). Confidence intervals for climatic correlation and response variable coefficients were then bootstrapped to estimate coefficients (Biondi and Waikul 2004).

To evaluate growth trends against climate values, a master chronology of all 503 cores was created and standardized in ARSTAN. The climate values for the study area were the averages of all the plot PRISM values for each year since 1895. Two separate models were estimated using DendroClim 2002 where the dependent variable in each model was the ARSTAN chronology and the independent variables were: 1) Monthly minimum temperatures and monthly precipitation and 2) maximum monthly temperatures and monthly precipitation. Initial analyses for each growth increment in the master chronology included 18 months of temperature averages from April of the previous year to September of the current year, and the corresponding 18 months of monthly precipitation.

Bootstrapping (1000 times, samples of 300 cores) in DendroClim 2002 was used to create confidence intervals for each correlation and response coefficient. This is an advantage over other climate analysis programs such as PRECON, which only bootstraps response functions (Biondi and Waikul, 2004). Monthly correlation values were used to confirm response coefficients as suggested by Blasing et al (1984). Only monthly climatic variables with significant correlation *and* response coefficients were reported in the results and used in plot-based models.

To examine consistencies in growth trends through time in the master chronology, ARSTAN growth was also analyzed in progressive 60 year intervals from the beginning of the PRISM climate record in 1895. This interval was chosen because 60 years was the shortest interval that could be analyzed for the significant months of June of the previous year to August of the current year.

Plot chronologies were created using the same standardization techniques and Dendroclim 2002 was also run independently at each plot with corresponding PRISM data to determine whether plots had similar significant climate response coefficients throughout the study region.

## Plot-level Models

We calculated percent growth change (PGC) in basal area increments to compare growth trends among plots following the 1999-2002 drought. This has been done in studies measuring canopy disturbance (Moesswilde 1995, Nowacki and Abrams 1997) and tree declines for fir (*Abies balsamea*) (Kanoti 2006) and American beech (*Fagus grandifolia*) (Kasson 2007).

Prior studies measured percent growth change in a given year using 10 year increment averages (Moesswilde 1995, Nowacki and Abrams 1997).
To evaluate how trees in a plot responded to drought, the PGC was modified to emphasize short-term growth trends following a stress event (Kanoti 2006, Kasson 2007), such that the current year's value (n) was compared to the average of the previous 2 years:

$\text{PGC} = (\text{BAI}_n - (\text{Average}\ (\text{BAI}_{(n-1)} + \text{BAI}_{(n-2)})) / \text{Average}\ (\text{BAI}_{(n-1)} + \text{BAI}_{(n-2)}) * 100.$

The impact of drought on tree growth was estimated using the PGC in 2003 (PGC03) the year following the most severe drought conditions in southern Maine (Lombard 2004). Because 2003 was a low growth year for most trees, using the PGC in 2003 for all cores minimized the chance of using a response variable associated with other tree or plot-level stresses. PGC in 2005 (PGC05) was used to measure how well trees recovered increment growth after the drought stress because 2005 was a year with a high PDSI following the drought and most trees showed increased growth. Four plots located at Mt. Agamenticus in York County were excluded because reported infestation by hemlock looper

(Dearborn and Granger 2002) appeared to be affecting measurements of drought response in this area (Figure A.1).

A decline model was calculated using PGC03 as the response variable, and a recovery model was calculated using PGC05 as a response variable. Models were developed using JMP IN 5.1 statistical software (SAS Institute, Cary, North Carolina) unless otherwise noted.

Independent variables used in the stepwise regression model included variables found to be significant in our climate-growth analysis or previous studies, as well as plot measurements considered influential to growth. Climate variables included: minimum and maximum February temperature, July precipitation of the current year, previous June and July maximum temperatures and average June-August precipitation in the previous and current years of growth. Distance from the coast and elevation were also included for their possible effects on temperature and tree growth. The following soil chemistry data for both the O and upper B horizons included: Ca, %N, pH, % loss on ignition, CEC, % base, % Al, C/N ratio and Ca/Al ratio. Soil variables were $\log_{10}$ transformed when needed to fit the assumptions of normal distribution and equal variance. Site variables included for their possible affect on water availability were: degrees from the southern aspect, slope of the aspect, distance from surface water (obtained from a GPS and GIS map), rooting depth, and categorical measures of soil texture and landscape position. To account for affects of competition the following variables were included: stand density, stand basal area, %hardwood basal area, and %hemlock basal area. Plot average measurements for cored trees were also included: age, height, DBH and %LCR.

Basic chronology statistics were also included in the 2003 and 2005 stepwise regressions to understand how past growth patterns influenced the drought and recovery models. These included mean sensitivity (MS) and expressed population signal (EPS). Mean sensitivity is a measure of the year to year variation in ring widths within a plot (Fritts et al. 1965). Because sensitivity tends to increase near the limits of tree growth (Fritts et al. 1965) mean sensitivity may represent the relative environmental stress among plots (Oberhuber et al. 1998). EPS was included in the stepwise regression as a measure of the common growth signal expressed among trees within each plot, described as the “potential climate signal” (Wigley et al. 1984):
$\mathrm{EPS} = n * r / (n * r + (1 - r))$ where $n$ is the sample size and $r$ is the interseries correlation (the measure of correlation in growth response among trees). PGC03 was also included in the PGC05 model as a measure of recent growth response among trees in a plot to the regional drought event.

Regression models for drought (PGC03) and recovery (PGC05) were developed using a mixed stepwise regression analysis with values to enter and leave at 0.15 and 0.05 respectively. Robustness of the chosen variables was tested using bootstrap analysis in Systat (1000 runs, 25 samples) (SYSTAT 12, SYSTAT Software Inc., San Jose, CA). When variables were not found to be robust using bootstrap analysis (95% confidence intervals of coefficients included

0), they were removed from the stepwise regression and the process was repeated.

Significant variables for the PGC2003 model were included in stepwise regression analysis of PGC at episodes of decreased growth following 1970: 1976, 1979, 1980, 1991 and 1994 to examine which variables were significant in other years of decreased growth.

## Identifying Recent Growth Trends

Basal area increments can be used to infer health status of individual trees. In a study of white oak (*Quercus alba*) and red spruce, LeBlanc (1990) and Duchesne et al. (2002) used negative slopes in growth as an indicator of decline. Similar to Duchesne et al. (2002), we used negative PGC in 2005 in addition to significantly low BAI to identify declining trees. Means and standard deviations were calculated for BAI05 to identify trees and plots most at risk for decline. Trees with both decreasing growth in 2005 (negative PGC) and BAI05 below 1 standard deviation were considered to be in the poorest health.

# Chapter 3

# RESULTS

## Plot Characteristics

Average plot basal area was 39.5 $m^2$/ha (Table 1) and ranged from 18.93 $m^2$/ha to 67.39 $m^2$/ha. Southern Maine hemlocks were similar DBH to average size of same-aged eastern hemlocks in Michigan and New York (Godman and Lancaster (1990). Stand density ranged from 333.59 trees/ha to 852.51 trees/ha. Proportion of basal area in hemlock ranged from 18.93% to 87.65%. The stands with the highest stocking had the highest proportion of basal area in hemlock were correlated with taller, larger DBH, and older trees (Table 2). Average age of dominant and codominant hemlocks ranged from 63.08 to 133.09 years. Percent hardwood was negatively correlated with height and DBH of dominant and codominant hemlocks (Table 2).

Sites were located 10 to 54 km from the coast (Figure 3). Lowest February temperature and highest summer precipitation were in the western portion of the study area (Table 3). February minimum temperature ranged from -12.68$^0$C to -7.82$^0$C across the plots and summer precipitation ranged from 7.77 cm to 9.83 cm. Coastal and southern sites tended to have milder February temperatures and inland sites had warmer July temperatures. Maximum July temperature varied from 25.75$^0$C to 26.14$^0$C. Northern sites had the coolest maximum July temperatures.

Elevation ranged from sea level to 78 m in the southern portion of the study area. The majority of plots had western aspects (N=15); there were 7 plots each with north, east and south aspects. Seventeen plots were flat, and 18 were on plots with slopes greater than 10% (Only 3 plots were located on slopes steeper than 15%). One plot was located in a gully.. There were no discernable regional patterns to slope or aspect.

**Table 1. Averages of plot characteristics**

| | **Mean ± se** |
|---|---|
| **Stand density (stems/ha)** | 562 ± 21.17 |
| **Plot basal area ($m^2$/ha)** | 39.5 ± 1.92 |
| **Hemlock basal area ($m^2$/ha)** | 24.09 ± 1.57 |
| **Hardwood basal area ($m^2$/ha)** | 9.48 ± 0.78 |
| **Mean DBH (cm)** | 27.64 ± 0.69 |
| **Elevation (m)** | 43.82 ± 2.62 |
| **Distance from surface water (m)** | 265.31± 34.76 |
| **Percent slope (%)** | 7.42 ± 1.40 |
| **Rooting depth (cm)** | 59.5 ± 2.87 |
| **Minimum February temperature (1996-2005 average, $^0$C)** | -10.19 ± 0.050 |
| **Maximum July T (1996-2005 average, $^0$C)** | 26.31 ± 0.013 |
| **Summer precipitation (1996-2005 average, cm)** | 8.99 ± 0.013 |
| **Distance from the coast (m)** | 24,400 ± 2,766 |

**Table 2 Pearson's correlations for response variables, plot variables, and chronology statistics across plots.** **PGC03** and **PGC05** are the percent growth changes from the previous two years in 2003 and 2005. **BA** is the plot basal area, **hardwood BA** is the basal area of hardwood, **hemlock BA** is the basal area of hemlock. **Age** is average tree age at breast height, **DBH** is average diameter at breast height, and **HT** is average tree height. **IC** is the interseries correlation. **EPS** is the expressed population signal. Correlations above 0.3 are indicated in bold.

| | **PGC03** | **PGC05** | **Plot BA** | **hemlock BA** | **hardwood BA** | **Age** | **PLCR** | **DBH** | **HT** | **IC** | **EPS** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **PGC03** | **1** | | | | | | | | | | |
| **PGC05** | **-0.3** | **1** | | | | | | | | | |
| **Plot BA** | -0.21 | **0.34** | **1** | | | | | | | | |
| **hemlock BA** | **-0.39** | **0.33** | **0.77** | **1** | | | | | | | |
| **hardwood BA** | 0.23 | -0 | 0.09 | -0.25 | **1** | | | | | | |
| **Age** | -0.03 | **0.55** | **0.35** | **0.44** | -0.06 | **1** | | | | | |
| **PLCR** | 0.12 | 0.2 | -0.2 | -0.27 | **0.41** | -0.07 | **1** | | | | |
| **DBH** | -0.23 | **0.67** | **0.54** | **0.6** | -0.03 | **0.67** | 0.15 | **1** | | | |
| **HT** | -0.21 | **0.51** | **0.6** | **0.62** | **-0.3** | **0.62** | -0.27 | **0.69** | **1** | | |
| **IC** | -0.16 | **0.39** | **0.3** | 0.24 | 0.04 | 0.04 | -0.08 | 0.21 | 0.14 | **1** | |
| **EPS** | -0.24 | 0.28 | **0.35** | **0.4** | -0.16 | 0.04 | **-0.32** | 0.11 | 0.18 | **0.89** | **1** |

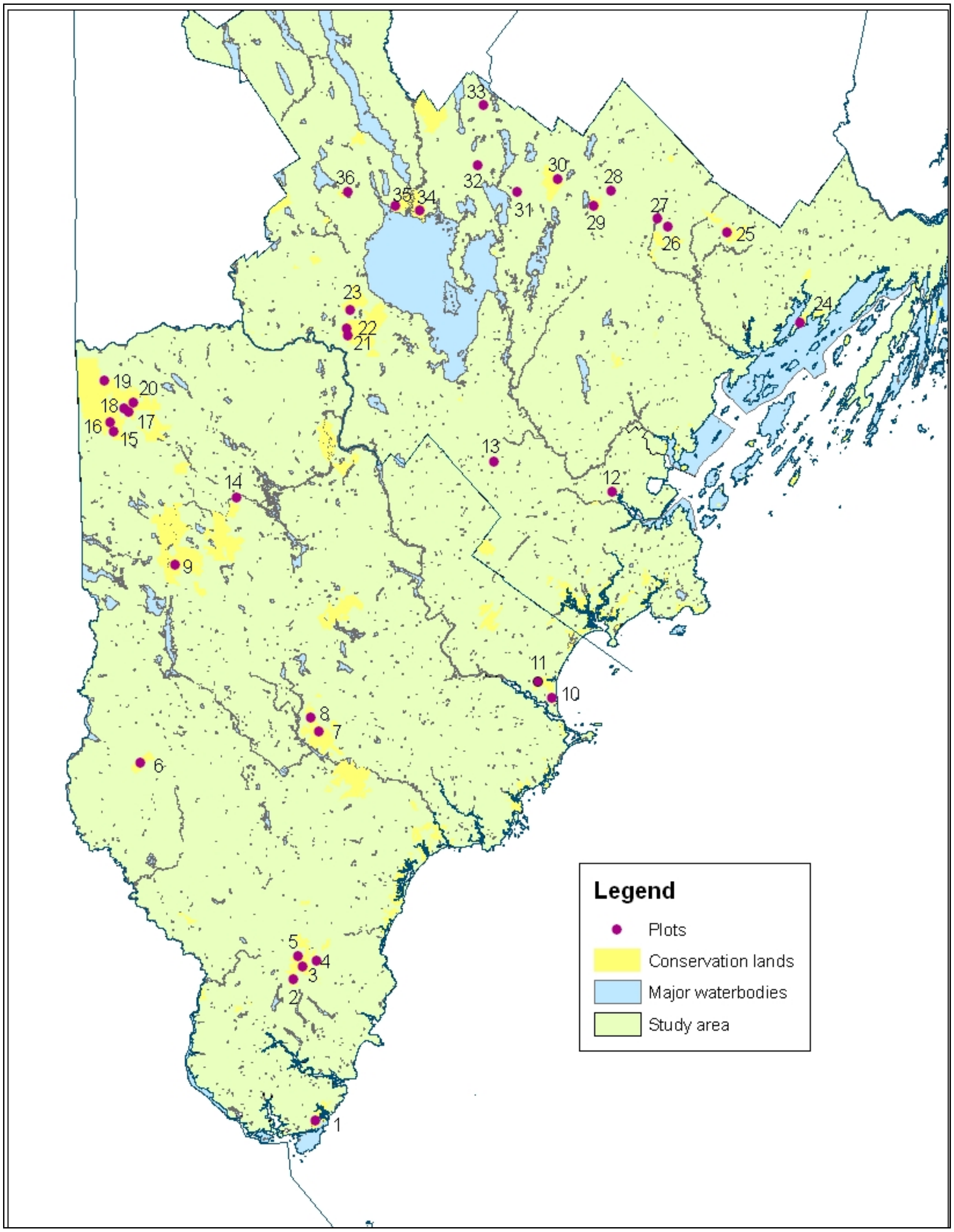

**Figure 3. Numbered plot locations in York and Cumberland Counties, Maine.**

## Table 3. Measurements by plot.

| Plot | Stand Density (trees/ha) | Average DBH ± se (cm) | Plot basal area ($m^2$/ha) | Hemlock basal area (%) | Hardwood basal area (%) | Age ± se (years) | Slope of aspect (%) |
|---|---|---|---|---|---|---|---|
| 1 | 655 | 24.6 ± 1.09 | 47.27 | 58.98 | 31.1 | 119 ± 4 | 1 |
| 2 | 507 | 26.06 ± 3.00 | 23.16 | 56.3 | 40.31 | 119 ± 5 | 10 |
| 3 | 642 | 27.78 ± 1.30 | 42.16 | 39.24 | 53.36 | 66 ± 9 | 10 |
| 4 | 815 | 25.56 ± 1.74 | 34.85 | 24.93 | 52.76 | 84 ± 7 | 6 |
| 5 | 482 | 25.23 ± 1.42 | 29.53 | 33.29 | 48.9 | 118 ± 6 | 12 |
| 6 | 334 | 26.22 ± 1.69 | 41.82 | 55.1 | 18.67 | 100 ± 2 | 0 |
| 7 | 593 | 39.42 ± 1.53 | 67.39 | 46.65 | 3.18 | 124 ± 3 | 6 |
| 8 | 383 | 21.71 ± 2.53 | 36.36 | 40.49 | 34.45 | 78 ± 4 | 2 |
| 9 | 432 | 28.4 ± 1.69 | 32.87 | 81.59 | 18.41 | 124 ± 9 | 29 |
| 10 | 531 | 29.53 ± 1.84 | 33.23 | 75.28 | 5.29 | 74 ± 5 | 2 |
| 11 | 840 | 22.17 ± 1.41 | 34.12 | 65.62 | 34.38 | 99 ± 4 | 2 |
| 12 | 494 | 30.03 ± 2.44 | 50.72 | 46.84 | 19 | 89 ± 4 | 34 |
| 13 | 457 | 27.95 ± 2.36 | 50.5 | 53.78 | 18.49 | 98 ± 7 | 10 |
| 14 | 507 | 23.04 ± 2.39 | 27.42 | 69.31 | 19.64 | 79 ± 7 | 9 |
| 15 | 593 | 27.08 ± 1.91 | 22.61 | 75.48 | 24.52 | 98 ± 1 | 9 |
| 16 | 741 | 25.62 ± 2.07 | 28.81 | 84.64 | 15.36 | 97 ± 4 | 9 |
| 17 | 469 | 23.86 ±1.80 | 24.33 | 65.27 | 34.73 | 129 ± 8 | 6 |
| 18 | 704 | 23.22 ± 1.62 | 27.66 | 53.32 | 44.11 | 77 ± 5 | 2 |
| 19 | 395 | 25.34 ± 1.32 | 35.38 | 69.94 | 30.06 | 93 ± 8 | 1 |
| 20 | 593 | 22.3 ± 1.49 | 30.56 | 30.4 | 38.52 | 63 ± 4 | 1 |
| 21 | 729 | 27.14 ± 1.41 | 41.4 | 57.92 | 27.99 | 110 ± 7 | 1 |
| 22 | 494 | 21.95 ± 0.89 | 24.38 | 56.03 | 18.25 | 93 ± 2 | 1 |
| 23 | 469 | 32.68 ± 2.24 | 42.95 | 77.16 | 19.87 | 117 ± 8 | 2 |
| 24 | 593 | 27.29 ± 1.48 | 39.54 | 59.15 | 35.09 | 124 ± 3 | 15 |
| 25 | 432 | 33.19 ± 1.08 | 47.84 | 87.65 | 6.28 | 112 ± 8 | 30 |
| 26 | 630 | 28.88 ± 1.21 | 56.74 | 65.48 | 27.06 | 104 ± 4 | 0 |
| 27 | 655 | 32.64 ± 1.27 | 44.28 | 77.97 | 10.94 | 99 ± 2 | 0 |
| 28 | 482 | 30.1 ± 1.11 | 49.63 | 66.93 | 21.64 | 122 ± 8 | 5 |
| 29 | 593 | 34.24 ± 2.85 | 55.52 | 68.23 | 25.6 | 126 ± 11 | 8 |
| 30 | 556 | 33.86 ± 0.80 | 45.38 | 58.48 | 9.05 | 86 ± 7 | 10 |
| 31 | 507 | 22.43 ± 1.77 | 18.94 | 66.72 | 33.28 | 70 ± 3 | 3 |
| 32 | 482 | 28.8 ± 1.56 | 40.14 | 79.55 | 15.4 | 125 ± 7 | 4 |
| 33 | 593 | 26.65 ± 1.3 | 31.93 | 40.46 | 36.15 | 116 ± 11 | 11 |
| 34 | 395 | 29.24 ± 1.27 | 56.66 | 70.46 | 24.67 | 112 ± 10 | 1 |
| 35 | 853 | 33.54 ± 2.12 | 52.66 | 52.41 | 18.03 | 133 ± 5 | 3 |
| 36 | 605 | 30.67 ± 1.87 | 52.89 | 78.15 | 7.97 | 104 ± 8 | 12 |

## Soils

Soils were primarily coarse textured sands and loams (27 out of 36 plots). Silty clays and clay loams were found at the remaining sites. Most plots were well or somewhat excessively drained, with glacial till or outwash parent material (n=33). Rooting depths ranged from 22 to 92 cm (59.5±17.49 cm). Only 4 sites had rooting depths of 30 cm or less due to compact till, bedrock or water levels. Six soil pits contained standing water at the time of excavation.

B Horizon Ca averaged 54.9 ± 57.8 mg/kg (Table 4) with one plot below 10 mg/kg (7.7 mg/kg) and one plot above 100 mg/kg ( 301 mg/kg). B horizon Ca had a high positive correlation with other B horizon values including Ca/Al ratio, percent base saturation, CEC, N, and %LOI (Table 5). B horizon Ca was negatively correlated with %Al.

**Table 4. Soil chemistry, O and B soil horizons.**
**%LOI** is percent loss on ignition. **CEC** is the cation exchange capacity. **C/N ratio** is the ratio of carbon to nitrogen. **%Al** and **%Base** saturation are the percent of total ions in aluminum and base cations respectively. **Ca/Al ratio** is the ratio of exchangeable calcium to aluminum. Means are given ± se.

| | **O Horizon** | **B Horizon** |
|---|---|---|
| **pH** | 3.6 ± 0.01 | 4.9 ± 0.03 |
| **Acidity (meq/100g)** | 11.1 ± 0.11 | 2.7 ± 0.28 |
| **%LOI (550$^0$C)** | 82.7 ± 0.34 | 8.2 ± 0.72 |
| **C (% at 1350$^0$C)** | 43.81 ± 0.18 | 3.38 ± 0.38 |
| **N (% at 1350$^0$C)** | 1.37 ± 0.01 | 0.15 ± 0.02 |
| **Ca (mg/kg)** | 1722 ± 32.31 | 54.90 ± 9.63 |
| **K (mg/kg)** | 585.5 ± 3.75 | 29.2 ± 4.67 |
| **Mg (mg/kg)** | 374.5 ± 4.56 | 11.1 ± 3.5 |
| **Na (mg/kg)** | 114.4 ± 2.43 | 24.2 ± 3.00 |
| **P (mg/kg)** | 86 ± 0.82 | 1.2 ± 0.17 |
| **Al (mg/kg)** | 351.6 ± 7.31 | 195.0 ± 23.38 |
| **Fe (mg/kg)** | 43.81 ± 0.18 | 3.38 ± 0.38 |
| **Mn (mg/kg)** | 49.03 ± 0.58 | 13.13 ± 1.78 |
| **Na (mg/kg)** | 114.36 ± 2.44 | 24.18 ± 3.00 |
| **Zn (mg/kg)** | 29.28 ± 0.42 | 1.31 ± 0.25 |
| **CEC (meq/100g)** | 24.9 ± 0.13 | 3.2 ± 0.33 |
| **C/N ratio** | 32.1 ± 0.10 | 23.4 ± 0.47 |
| **%Al saturation** | 16.2 ± 0.32 | 66.6 ± 2.2 |
| **%Base saturation** | 53.7 ± 0.48 | 16.7 ± 1.62 |
| **Ca/Al ratio** | 4.06 ± 0.17 | 0.15 ± 0.03 |

**Table 5. Pearson's correlations for soil parameters, B soil horizon**
**%LOI** is percent loss on ignition. **CEC** is the cation exchange capacity. **C/N** is the ratio of carbon to nitrogen. **%Al** and **%Base** are the percent of total cations in aluminum and base cations respectively. **Ca/Al** is the ratio of exchangeable calcium to aluminum. Correlation values at or above 0.30 are indicated in bold.

| | **Ca** | N | **C/N** | **PH** | %LOI | CEC | **Ca/Al** | **%Al** | %Base |
|---|---|---|---|---|---|---|---|---|---|
| **Ca** | **1** | | | | | | | | |
| **N** | **0.42** | 1 | | | | | | | |
| **C/N** | -0.15 | -0.24 | **1** | | | | | | |
| **PH** | 0.17 | -0.12 | -0.07 | **1** | | | | | |
| **%LOI** | **0.39** | **0.93** | -0.06 | -0.01 | 1 | | | | |
| **CEC** | **0.61** | **0.71** | -0.03 | **-0.39** | **0.65** | 1 | | | |
| **Ca/Al** | **0.80** | 0.03 | -0.25 | **0.42** | 0 | 0.08 | **1** | | |
| **%Al** | **-0.39** | 0.03 | 0.27 | **-0.48** | 0.01 | 0.14 | **-0.66** | **1** | **0.6** |
| **%Base** | **0.78** | 0.10 | -0.27 | **0.51** | 0.09 | 0.06 | **0.95** | **-0.60** | 1 |

## Plot Chronology Statistics

The chronology had an interseries correlation of 0.436 with a mean sensitivity of 0.223 (Table 6). COFECHA results showed intercorrelations within sites between 0.343 and 0.790 with an average plot intercorrelation of 0.55 ± 0.09. Only two plots had values below 0.40 but still above the 99% critical value (0.328). Average mean sensitivity at the plot level was 0.22 ± 0.02 Most of the mean sensitivity values were in the mid-range, though four plots had mean sensitivities just below the 0.20 threshold, indicating low sensitivity (Grissino-Mayer 2001). Interseries correlation was positively correlated with PGC05, plot basal area, average height, and DBH. It was negatively correlated with PGC03 (Table 2).

**Table 6. Master chronology statistics**
**Master length** is the length of the oldest core in the chronology. **Mean length** is the average length of core segments. Mean length underestimates age because many cores did not contain pith and ages were estimated (Applequist 1958). Means are given ± standard error.

| | |
|---|---|
| **N** | 503 |
| **Interseries correlation** | 0.44 |
| **Expressed population signal (EPS)** | 0.997 |
| **Mean sensitivity** | 0.223 |
| **Master length** | 199 |
| **Mean length** | 86.7 |
| **DBH (cm, n=503)** | 37.4 ± 0.4 |
| **Age (years, n=428)** | 102.5 ± 1.3 |
| **Height (m, n=502)** | 21.6 ± 0.2 |
| **Percent live crown (n=502)** | 69.7 ± 0.8 |

## Tree Ring Chronologies and Reduced Growth Events

The master chronology showed that since 1940, 12 years have had chronology growth patterns at or below -1 standard deviation (Figure 4). These included: 1941, 1948, 1950, 1956, 1964, 1966, 1968, 1976, 1979,1980, 1991, 1994 and 2003. Most of these growth reductions corresponded with drought events. The master chronology was related to the average PDSI (Pearson's r = 0.38) (Figure 5). Corresponding low flow intervals occurred in 1938-43, 1947-1950, 1955-59, 1963-69, 1978, and 1999-2003 (Lombard 2004). The only low-flow interval recorded for this area of the state that is not apparent in the tree ring chronologies is the 1995 drought. In fact, growth trends appeared to be slightly above average in 1995 and 1996 (Figure 4).

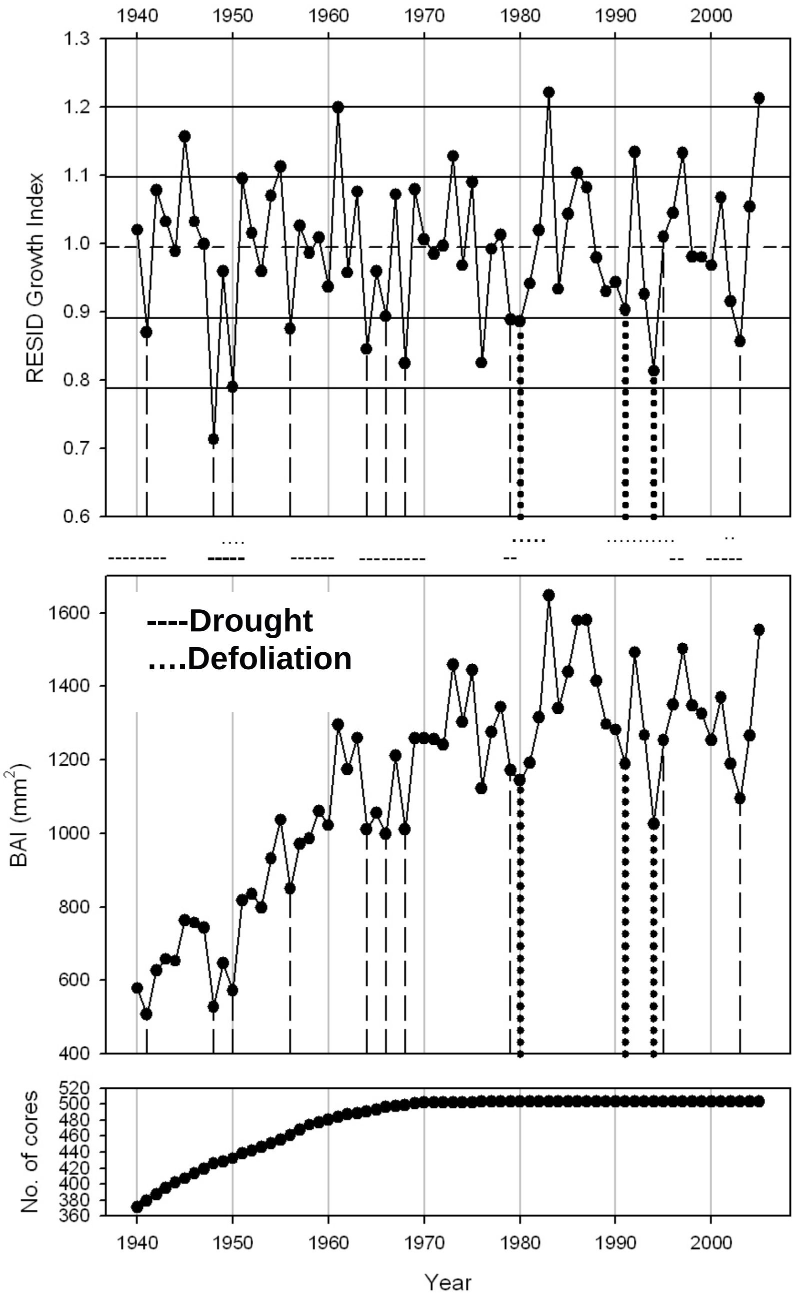

**Figure 4. Master chronology standardized growth index (RESID) and basal area increment (BAI), 1940-2005.**
The standardized chronology is the residuals from a 30-year smoothing spline with the autocorrelation removed (RESID). The horizontal dashed line in the RESID graph indicates the mean. Solid horizontal lines represent 1 and 2 standard deviations above and below the mean. Vertical dashed and dotted drop lines represent low growth events corresponding with drought and defoliation events. Dashed and dotted lines below the RESID graph indicate periods of drought and defoliation. Vertical gray lines mark decades.

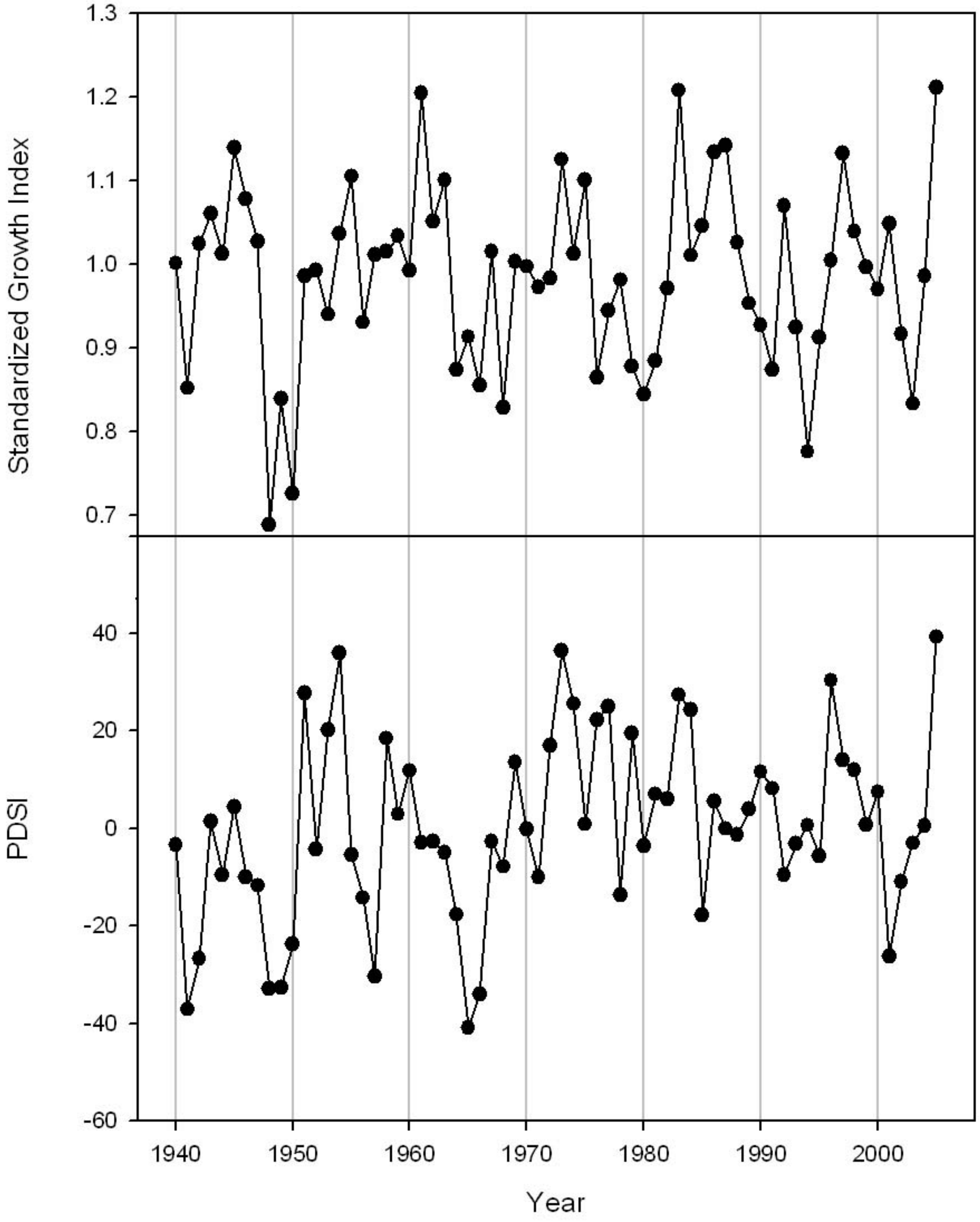

**Figure 5. Standardized growth index and Palmer Drought Severity Index (PDSI), 1940-2005.**

Growth index was calculated for the chronology using a 30 year smoothing spline. PDSI is the yearly average for PDSI zones 2 (inland) and 3 (coastal). Vertical grey lines mark decades.

In addition to the growth reductions corresponding with drought intervals, growth reductions occured in 1976, 1980, 1991 and1994 (Figure 4). The most recent events correspond with a major hemlock looper outbreak in northern New England from 1989 through the early 1990s (Trial and Devine 1994). These dates also correspond with a gypsy moth outbreak recorded in Maine Forest Service condition reports from 1989-1994 (Bradbury 1990-1994). An earlier gypsy moth outbreak occurred from 1979-82 (Bradbury 1992), overlapping with effects from the 1978 drought and corresponding with the 1979 and 1980 growth reductions. There is no record of a drought or defoliation event occurring in 1975 or 1976. Published records of defoliation events prior to 1980 are lacking, but there was a gypsy moth defoliation around 1950 (Dave Struble, Maine Forest Service, personal communication). Therefore, the growth reductions in 1948 and/or 1950 were likely exacerbated by defoliation.

Growth reductions seen in the master chronology did not occur at all plots (Figure 6). In addition to expressing the most severe reduction in growth, the 1947-1950 drought was the most widespread, affecting growth at 32 out of 36 plots. The 1956, 1966, 1979, 1980, and 2003 growth reductions that were apparent in the master chronology occured across more than 11 plots. Growth decreases in 1956, 1966, 1979 and 1980, which were among the least severe of the decreases were observable at 7 or 8 plots (Figure 6).

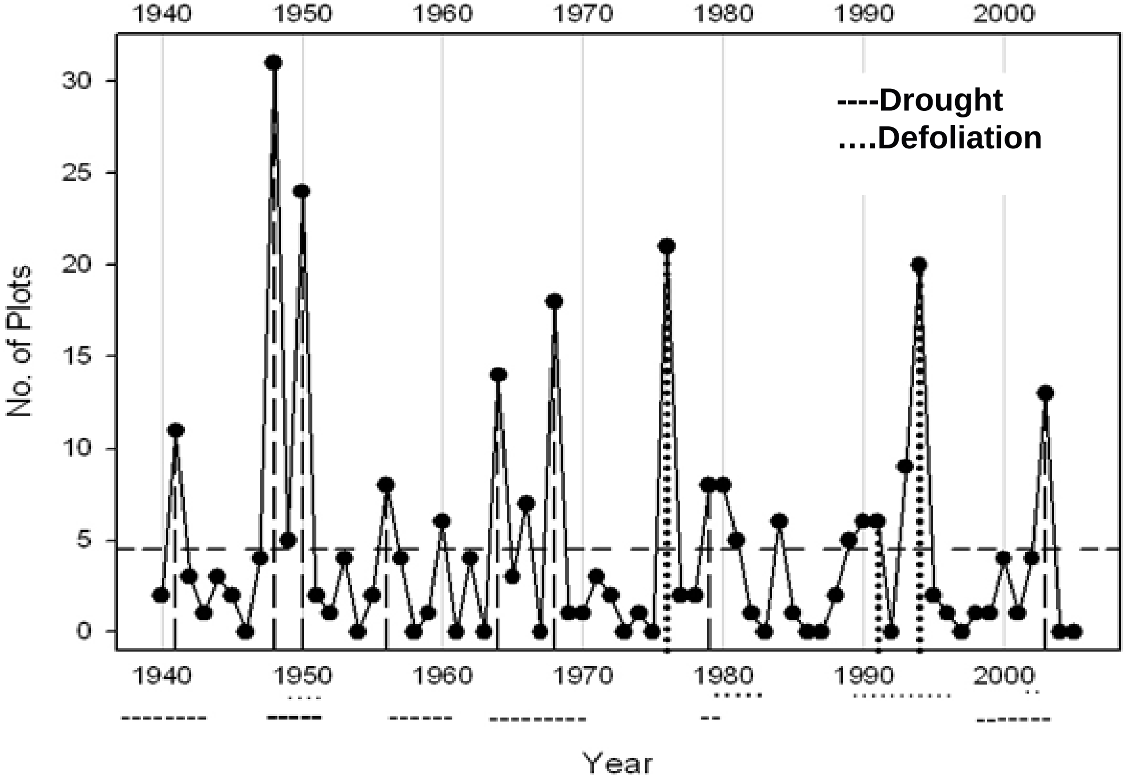

**Figure 6. Number of plots with growth below 1 standard deviation, 1940-2005.**
Vertical dashed and dotted lines drop lines indicate periods of drought and defoliation. Horizontal dashed and dotted lines below the graph indicate periods of drought and defoliation. The horizontal dashed line indicates the mean number of plots with standardized growth below 1 standard deviation, 1940-2005. Vertical gray lines mark decades.

## Climate Analysis

Significant climatic response coefficients were found at the population level using DendroClim 2002 (Biondi and Waikul 2004). When average precipitation and maximum temperature were run with ARSTSTAN values for the master chronology, climatic variables with significant coefficients at the .05 level were maximum temperatures in the June (-0.18), July (-0.16), and February (0.19) prior to increment growth. Precipitation in the current July was also significant (0.15).

Relationships between climate and the master chronology were also seen through time using forward evolutionary intervals. Moving intervals showed that higher February temperatures have been related to better growth since 1955. Positive coefficients occured for November and March from 1955 to 1996. There were positive relationships with July and August precipitation, but only until the early 1970s. Coefficients for June and July temperatures were significant from the early 1980s and 1990s respectively to 2005 (Table 7).

**Table 7. Significant climate coefficients for 60-year moving intervals with maximum temperature and precipitation.**
Year indicated is the final year included in interval. Capital letters indicate temperature (T) and precipitation (P) for monthly climate variables from the previous year. Lowercase letters indicate current year climate variables.

| Year | JUN T | JUL T | NOV T | feb t | mar t | JUL P | AUG P | jul p | aug p |
|---|---|---|---|---|---|---|---|---|---|
| **1955** | | | 0.214 | 0.224 | 0.193 | 0.181 | 0.185 | | 0.198 |
| **1956** | | | 0.209 | 0.228 | | | 0.199 | | 0.195 |
| **1957** | | | 0.213 | 0.238 | 0.194 | | 0.189 | | 0.19 |
| **1958** | | | 0.226 | 0.237 | 0.189 | | 0.189 | | 0.196 |
| **1959** | | | 0.224 | 0.24 | 0.192 | 0.18 | 0.183 | | 0.198 |
| **1960** | | | 0.228 | 0.237 | 0.201 | 0.183 | 0.189 | | 0.216 |
| **1961** | | | 0.254 | 0.265 | 0.205 | 0.189 | | | 0.191 |
| **1962** | | | 0.254 | 0.26 | 0.205 | 0.193 | | | 0.188 |
| **1963** | | | 0.256 | 0.241 | 0.212 | 0.194 | 0.165 | | 0.187 |
| **1964** | | | 0.245 | 0.232 | 0.205 | 0.192 | | | 0.198 |
| **1965** | | | 0.243 | 0.24 | 0.208 | 0.187 | | | 0.198 |
| **1966** | | | 0.243 | 0.229 | 0.208 | 0.198 | | | 0.198 |
| **1967** | | | 0.257 | 0.222 | 0.202 | 0.185 | 0.169 | | 0.186 |
| **1968** | | | 0.265 | 0.227 | 0.199 | 0.173 | 0.153 | 0.157 | 0.2 |
| **1969** | | | 0.252 | 0.228 | 0.195 | 0.165 | | 0.166 | 0.195 |
| **1970** | | | 0.247 | 0.224 | 0.195 | | | 0.165 | 0.191 |
| **1971** | | | 0.252 | 0.23 | 0.198 | | 0.156 | 0.172 | 0.196 |
| **1972** | | | 0.248 | 0.228 | 0.197 | 0.172 | 0.156 | 0.173 | 0.194 |
| **1973** | | | 0.233 | 0.231 | 0.205 | 0.17 | | 0.175 | 0.191 |
| **1974** | | | 0.234 | 0.234 | 0.211 | 0.174 | | 0.168 | 0.194 |
| **1975** | | | 0.233 | 0.237 | 0.206 | | | 0.178 | 0.206 |
| **1976** | | | 0.186 | 0.204 | 0.202 | | | | 0.179 |
| **1977** | | | 0.19 | 0.201 | 0.181 | | | 0.16 | 0.18 |
| **1978** | | | 0.197 | 0.201 | 0.178 | | | | 0.176 |
| **1979** | | | 0.191 | 0.201 | 0.179 | | | | 0.172 |
| **1980** | | | 0 | 0.211 | | | | | 0.17 |
| **1981** | | | 0.174 | 0.178 | | | | | 0.178 |
| **1982** | | | 0.17 | 0.186 | | | | | 0.167 |
| **1983** | -0.159 | | 0.175 | 0.188 | 0.171 | | | | 0.173 |
| **1984** | -0.166 | | 0.179 | 0.192 | 0.174 | | | | 0.174 |
| **1985** | -0.164 | | 0.18 | 0.196 | 0.175 | | | | 0.179 |
| **1986** | -0.174 | | 0.179 | 0.186 | 0.179 | | | | 0.185 |
| **1987** | -0.173 | | 0.176 | 0.193 | 0.177 | | | | 0.175 |
| **1988** | -0.169 | | 0.171 | 0.191 | 0.175 | | | | 0.176 |
| **1989** | -0.173 | -0.141 | 0.162 | 0.192 | 0.178 | | | | 0.164 |
| **1990** | -0.175 | | 0.173 | 0.18 | 0.166 | | | | 0.168 |
| **1991** | -0.175 | | 0.165 | 0.169 | 0.173 | | | | |
| **1992** | -0.172 | | 0.168 | 0.167 | | | | | |
| **1993** | -0.167 | -0.138 | 0.158 | 0.17 | | | | | |
| **1994** | -0.174 | -0.139 | 0.157 | 0.176 | 0.168 | | | | |
| **1995** | -0.167 | | 0.157 | 0.185 | 0.166 | | | | |
| **1996** | -0.16 | | | 0.182 | | | | | |
| **1997** | -0.164 | -0.137 | | 0.201 | | | | | |
| **1998** | -0.168 | -0.144 | | 0.19 | | | | 0.153 | |

Table 7 continued

| Year | JUN T | JUL T | NOV T | feb t | mar t | JUL P | AUG P | jul p | aug p |
|---|---|---|---|---|---|---|---|---|---|
| **1999** | -0.167 | -0.146 | | 0.198 | | | | 0.155 | |
| **2000** | -0.172 | -0.148 | | 0.192 | | | | | |
| **2001** | -0.175 | -0.153 | | 0.198 | | | | | |
| **2002** | -0.185 | -0.141 | | 0.189 | | | | | |
| **2003** | -0.175 | -0.141 | | 0.196 | | | | 0.152 | |
| **2004** | -0.17 | -0.148 | | 0.198 | | 0.163 | | 0.157 | |
| **2005** | -0.164 | -0.16 | | 0.193 | | 0.154 | | | |

When average minimum monthly temperatures and precipitation were analyzed with the master chronology, coefficients for minimum temperatures in the previous July (-0.23), and current-year February (0.18), were significant as well as precipitation for previous July (0.22) and August (0.16) and current July (0.17).

Analysis using moving intervals showed that increment growth was consistently associated with higher February temperatures, higher March temperatures prior to 1996, higher previous July precipitation, and higher current June, July, or August precipitation. Lower minimum July temperature was also associated with higher increment growth from 1963 to 2005 (Table 8).

**Table 8. Significant climate coefficients for 60-year moving intervals with minimum temperature and precipitation.**

Year indicated is the final year included in the interval. Capital letters indicate temperature (T) and precipitation (P) for monthly climate variables from the previous year. Lowercase letters indicate current year climate variables.

| Year | JUL T | NOV T | feb t | mar t | JUL P | AUG P | jun p | jul p | aug p |
|---|---|---|---|---|---|---|---|---|---|
| **1955** | | | 0.182 | 0.254 | 0.219 | | 0.213 | | 0.237 |
| **1956** | | | 0.19 | 0.244 | 0.213 | 0.188 | 0.21 | | 0.236 |
| **1957** | | | 0.2 | 0.25 | 0.219 | | 0.222 | | 0.23 |
| **1958** | | | 0.203 | 0.243 | 0.21 | 0.189 | 0.221 | | 0.235 |
| **1959** | | | 0.2 | 0.251 | 0.216 | | 0.225 | | 0.233 |
| **1960** | | | 0.202 | 0.269 | 0.228 | 0.192 | 0.221 | | 0.259 |
| **1961** | | 0.166 | 0.217 | 0.251 | 0.232 | | | | 0.232 |
| **1962** | | | 0.215 | 0.255 | 0.241 | | | | 0.229 |
| **1963** | -0.176 | | 0.197 | 0.258 | 0.245 | | | | 0.242 |
| **1964** | -0.194 | | 0.188 | 0.258 | 0.245 | | | | 0.239 |
| **1965** | -0.203 | | 0.191 | 0.249 | 0.236 | | | | 0.246 |
| **1966** | -0.183 | | 0.182 | 0.242 | 0.247 | | | 0.175 | 0.236 |
| **1967** | -0.187 | | 0.171 | 0.245 | 0.24 | | | 0.174 | 0.223 |
| **1968** | -0.195 | | 0.177 | 0.233 | 0.233 | | | 0.195 | 0.237 |
| **1969** | -0.192 | | 0.185 | 0.235 | 0.232 | | | 0.2 | 0.233 |
| **1970** | -0.197 | 0.155 | 0.178 | 0.231 | 0.226 | | | 0.209 | 0.234 |
| **1971** | -0.204 | | 0.179 | 0.233 | 0.233 | | | 0.215 | 0.234 |
| **1972** | -0.193 | | 0.176 | 0.228 | 0.235 | | | 0.209 | 0.23 |
| **1973** | -0.19 | | 0.181 | 0.237 | 0.236 | | | 0.209 | 0.23 |
| **1974** | -0.177 | | 0.181 | 0.247 | 0.235 | | | 0.208 | 0.229 |
| **1975** | -0.18 | | 0.184 | 0.242 | 0.227 | | 0.184 | 0.214 | 0.234 |
| **1976** | -0.21 | | 0.158 | 0.235 | 0.207 | | 0.19 | 0.182 | 0.206 |
| **1977** | -0.199 | | 0.168 | 0.223 | 0.184 | | | 0.2 | 0.197 |
| **1978** | -0.204 | | 0.16 | 0.213 | 0.185 | | 0.186 | 0.198 | 0.194 |
| **1979** | -0.202 | | 0.168 | 0.203 | 0.181 | | 0.196 | 0.183 | 0.181 |
| **1980** | -0.218 | | 0.174 | 0.202 | | | | 0.185 | 0.179 |
| **1981** | -0.23 | | | 0.192 | | | 0.189 | 0.171 | 0.186 |
| **1982** | -0.237 | | 0.159 | 0.187 | | | 0.189 | 0.182 | 0.186 |
| **1983** | -0.236 | | 0.152 | 0.189 | | | | | 0.184 |
| **1984** | -0.235 | | | 0.2 | | | | | 0.192 |
| **1985** | -0.233 | | 0.154 | 0.198 | | | | | 0.203 |
| **1986** | -0.225 | | 0.152 | 0.192 | 0.166 | | 0.182 | 0.167 | 0.201 |
| **1987** | -0.229 | | 0.153 | 0.2 | 0.165 | | 0.195 | | 0.195 |
| **1988** | -0.235 | | 0.155 | 0.199 | 0.181 | | 0.19 | | 0.19 |
| **1989** | -0.239 | | 0.156 | 0.199 | | | 0.189 | | 0.186 |
| **1990** | -0.239 | | 0.149 | 0.202 | 0.166 | | 0.191 | | 0.186 |
| **1991** | -0.243 | | | 0.184 | 0.16 | | 0.193 | | |
| **1992** | -0.249 | | 0.147 | 0.18 | 0.153 | | 0.201 | | |
| **1993** | -0.247 | | 0.15 | 0.176 | 0.157 | 0.174 | 0.201 | | |
| **1994** | -0.249 | | 0.169 | 0.168 | 0.162 | 0.161 | 0.214 | | |
| **1995** | -0.246 | | 0.174 | 0.159 | | 0.165 | 0.211 | | |
| **1996** | -0.222 | | 0.182 | | 0.162 | | 0.199 | 0.172 | |
| **1997** | -0.212 | | 0.201 | | 0.188 | | 0.199 | 0.172 | |
| **1998** | -0.218 | | 0.188 | | 0.186 | | 0.169 | 0.179 | |

Table 8 continued

| Year | JUL T | NOV T | feb t | mar t | JUL P | AUG P | jun p | jul p | aug p |
|---|---|---|---|---|---|---|---|---|---|
| **1999** | -0.217 | | 0.196 | | 0.193 | | 0.164 | 0.173 | |
| **2000** | -0.227 | | 0.185 | | 0.19 | | | 0.165 | |
| **2001** | -0.244 | | 0.19 | | 0.212 | | 0.16 | 0.174 | |
| **2002** | -0.235 | | 0.183 | | 0.216 | | | 0.182 | |
| **2003** | -0.232 | | 0.181 | | 0.234 | | | 0.193 | |
| **2004** | -0.24 | | 0.186 | | 0.236 | | 0.159 | 0.199 | |
| **2005** | -0.233 | | 0.176 | | 0.225 | 0.163 | | 0.185 | |

Significant response coefficients for climatic variables varied across plots. Coefficients ranged from ± 0.14 to 0.3, values comparable to the regional analysis (Table A.1). For runs with both minimum and maximum temperature, 14 plots showed responses to previous summer temperature, 12 to winter temperature, 14 to previous summer precipitation, and 9 to current summer precipitation (Table 9). Higher previous summer temperature was associated with a negative growth response, while higher previous summer precipitation, winter temperature, and current summer precipitation were associated with positive growth responses.

Based on consistent relationships between growth and climate variables through time and across plots, the following climatic variables (monthly averages) were included in plot models: Current minimum and maximum February temperatures, previous maximum June and July temperatures, current July precipitation and average June-August precipitation of the current and previous years.

**Table 9. Climatic response across plots.**
Capital headings indicate temperature (**T**) and precipitation (**P**) for monthly climate variables from the previous year. Lowercase headings indicate current year climate variables. The nature of the response is indicated as positive (**+**) or negative (**-**), or **mixed**.

| Variable | No. Plots Responding | Correlation |
|---|---|---|
| **JUNE T** | 13 | - |
| **JULY T** | 19 | - |
| **AUGST T** | 3 | - |
| **november t** | 2 | + |
| **december t** | 3 | + |
| **february t** | 17 | + |
| **mar. t** | 5 | mixed |
| **may t** | 3 | - |
| **june t** | 2 | - |
| **september t** | 2 | + |
| **JULY P** | 11 | + |
| **AUGUST P** | 9 | + |
| **december p** | 4 | + |
| **march p** | 4 | mixed |
| **june p** | 10 | + |
| **jul p** | 11 | + |

## Plot-level Models

The stepwise model for decline following the drought, PGC03, returned the following variables: expressed population signal (EPS), depth of the organic soil horizon, maximum February temperature of the current year, % Al saturation in the B soil horizon, and stand density (Figure 7):

PGC03 = 168.34 - (278.40 * EPS) + (1.80 * O horizon depth) + (3.26 * maximum February T) - (0.25 * B % Al saturation) - (0.024 * stand density) (Table 10).

All variables were robust in the bootstrap analysis.

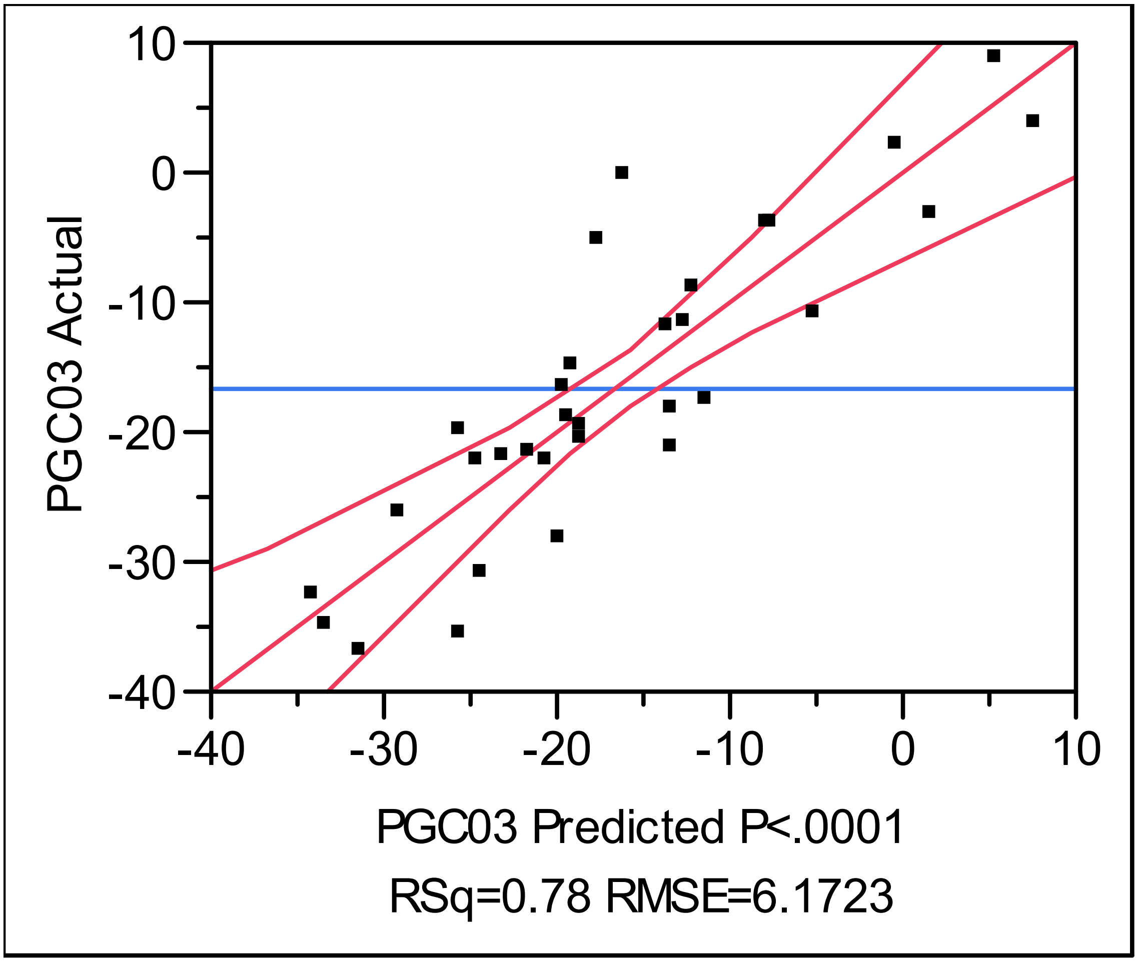

**Figure 7. PGC03 predictive model**

**PGC03** is the percent growth change in 2003 relative to the previous two years. Independent variables include: expressed population signal (EPS), depth of the O soil horizon, maximum average February temperature, % aluminum saturation in the B soil horizon, and stand density. The horizontal line indicates the mean. Curved lines are 95% confidence intervals.

## Table 10. Model statistics, PGC03

**PGC03** is the percent growth change in 2003 relative to the previous two years. Independent variables include: expressed population signal, depth of the O soil horizon, current maximum February temperature, % aluminum saturation in the B soil horizon, and stand density. **CI** is the confidence interval. **VIF** is the variance inflation factor.

| **Summary of Fit** | | | | | |
|---|---|---|---|---|---|
| **$r^2$** | 0.78 | | | | |
| **$r^2$ Adj** | 0.73 | | | | |
| **Root Mean Square Error** | 6.17 | | | | |
| **Mean of Response** | -16.54 | | | | |
| **N** | 32 | | | | |
| **Analysis of Variance** | | | | | |
| **Source** | **DF** | **Sum of Squares** | **Mean Square** | **F Ratio** | |
| **Model** | 4 | 3425.33 | 685.066 | 17.98 | |
| **Error** | 26 | 990.54 | 38.098 | **Prob > F** | |
| **Total** | 31 | 4415.87 | 0 | <.0001 | |
| **Press Statistic** | 1431.86 | | Press RMSE | 6.69 | |
| **Parameter Estimates** | | | | | |
| **Term** | **Estimate** | **Std Error** | **t Ratio** | **Prob>\|t\|** | **VIF** |
| **Intercept** | 168.34 | 57.62 | 2.92 | 0.007 | |
| **Expressed population signal** | -278.4 | 50.46 | -5.52 | <.0001 | 1.1 |
| **Depth of the O soil horizon** | 1.8 | 0.38 | 4.68 | <.0001 | 1.38 |
| **Current February maximum T** | 3.26 | 1.06 | 3.06 | 0.0051 | 1.18 |
| **B soil horizon % Al saturation** | -0.25 | 0.09 | -2.75 | 0.011 | 1.24 |
| **Stand density (stems/hectare)** | -0.024 | 0.01 | -2.45 | 0.021 | 1.22 |
| **Bootstrap Estimates** | **Estimate** | **Std Error** | **Lower 95% CI** | **Upper 95% CI** | |
| **Expressed population signal** | 165.5 | 69.729 | 51.102 | 345.375 | |
| **Depth of the O soil horizon** | -276.404 | 63.383 | -424.603 | -168.074 | |
| **Current February maximum T** | 1.816 | 0.458 | 0.759 | 2.602 | |
| **B soil horizon % Al saturation** | 3.342 | 1.275 | 0.522 | 5.604 | |
| **Stand density (stems/hectare)** | -0.269 | 0.107 | -0.466 | -0.046 | |
| **Expressed population signal** | -0.024 | 0.012 | -0.048 | -0.001 | |

The stepwise model for PGC05 included variables: Percent growth change in 2003, summer precipitation in 2004, age, height, distance from the coast and log10 of B horizon Ca (Figure 8). After bootstrap analysis summer precipitation, height and distance from the coast dropped out and the final model was:

PGC05 = -55.850 - (0.784 * PGC03) + (0.410 * Age) +(21.98 * $\text{Log}_{10}$ B Ca) (Table 11).

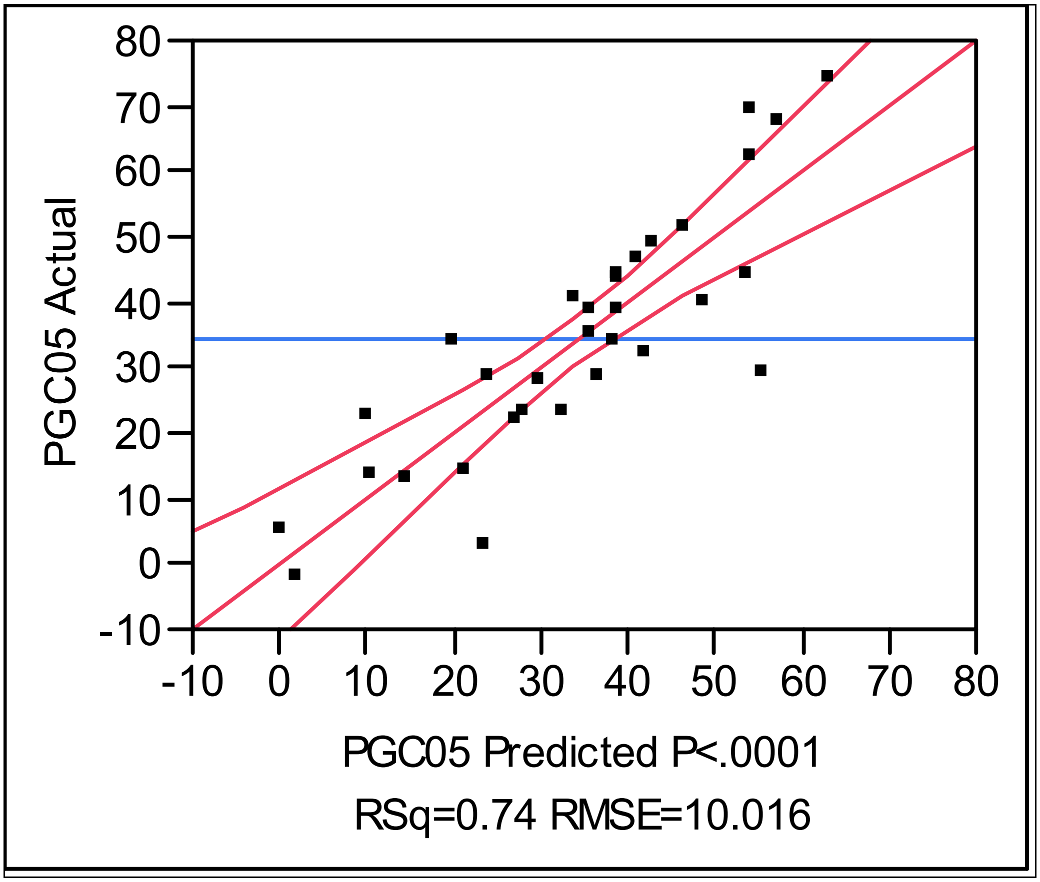

**Figure 8. PGC05 predictive model**

**PGC05** is the percent growth change in 2005 relative to the previous two years. Independent variables include: percent growth change in 2003 (**PGC03**), average age, and B soil horizon calcium (B Ca) ($\log_{10}$ transformed). The horizontal line indicates the mean. Curved lines are 95% confidence intervals.

**Table 11. Model statistics, PGC05**

**PGC05** is the percent growth change in 2005 relative to the previous two years. Independent variables include: percent growth change in 2003 (**PGC03**), average **Age**, and transformed B soil horizon calcium (**B Ca $\log_{10}$**). **CI** is the confidence interval. **VIF** is the variance inflation factor.

**Summary of Fit**

| | |
|---|---|
| **$r^2$** | 0.74 |
| **$r^2$ Adj** | 0.71 |
| **Root Mean Square Error** | 10.02 |
| **Mean of Response** | 34.11 |
| **N** | 32 |

**Analysis of Variance**

| Source | DF | Sum of Squares | Mean Square | F Ratio |
|---|---|---|---|---|
| **Model** | 3 | 8055.31 | 2685.1 | 26.76 |
| **Error** | 28 | 2809.22 | 100.33 | **Prob > F** |
| **Total** | 31 | 10864.53 | | <.0001 |
| **Press Statistic** | 3578.02 | Press RMSE | 10.57 | |

**Parameter Estimates**

| Term | Estimate | Std Error | t Ratio | Prob>\|t\| | VIF |
|---|---|---|---|---|---|
| **Intercept** | -55.84 | 11.98 | -4.66 | <.0001 | |
| **PGC03** | -0.77 | 0.15 | -5.03 | <.0001 | 1.03 |
| **Age** | 0.41 | 0.1 | 4.29 | 0.0002 | 1.03 |
| **B Ca ($\log_{10}$)** | 22.15 | 4.96 | 4.47 | 0.0001 | 1.02 |

**Bootstrap Estimates**

| | Estimate | Std Error | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|
| **Intercept** | -55.850 | 12.599 | -80.213 | -31.661 |
| **PGC03** | -0.784 | 0.193 | -1.173 | -0.392 |
| **Age** | 0.410 | 0.091 | 0.227 | 0.587 |
| **B Ca ($\log_{10}$)** | 21.979 | 4.993 | 12.33 | 32.913 |

The PGC03 model variables were not useful for predicting the three recent low growth years associated with insect outbreaks (1994, 1991, 1980). Significant models with EPS occurred in 1976 and 1979, no other variables came into the models:

PGC1976 = 185.74 - 204.99 EPS ($r^2 = 0.16$, $p < 0.0089$)

PGC1979 = 174.87 - 203.82 EPS ($r^2 = 0.16$, $p < 0.0083$)

## Tree Recovery and Decline Following the Recent Drought

Relatively few trees show declining growth from 2003-2005 as indicated by negative PGC05 (N=59), and only 19 trees had both negative PCG05 values and BAI below 1 standard deviation (Table 12). These trees were spread among 11 plots. Seven of the 18 trees in Ferry Beach State Park in Saco met these criteria, and that was the only plot with a negative average percent growth change in 2005.

**Table 12. Tree contingency table, PGC05**

**PGC05** is the percent growth change in 2005 relative to the previous two years. **BAI05** is the basal area increment in 2005. **SD** is the standard deviation.

| | **BAI05<1SD (580.79 $mm^2$)** | **Mid BAI05** | **BAI05>1SD (2527.91 $mm^2$)** | **Total** |
|---|---|---|---|---|
| **PGC05<0** | 19 | 36 | 4 | 59 |
| **PGC05>0** | 35 | 342 | 67 | 444 |
| **Total** | 54 | 378 | 71 | 503 |

# Chapter 4

# DISCUSSION

## Reduced Growth Events

Major causes of reduced growth for hemlock in southern Maine appear to be climate, particularly drought, and defoliation; 11 out of 12 identified events were associated with these stresses. Several studies show that increment growth of eastern hemlock is sensitive to drought conditions (Lyon 1936, Cook and Jacoby 1977, Cook and Cole 1991 and others) This sensitivity has even been used to extend drought records (Cook and Jacoby 1977). In our study, decreased growth in the master chronology consistently occured during or directly following drought events (Figure 4).

The only published drought event since 1940 affecting this area that did not result in decreased radial growth was the 1995 drought. The 1995 drought had a recurrence interval of 10 to 25 years in our study area, compared to the 35-year drought from 1999-2002 (Lombard 2004). However, white pine (*Pinus strobus*) decline in this region has been attributed to the 1995 drought in stands where agricultural land abandonment led to dense stands of white pine growing on sites with restricted rooting depths (Fries 2002, Granger 2005). There were signs of past agricultural use, such as rock walls, at a few of our hemlock sites but rooting depths did not appear to be restricted at these sites.

The 1995 drought occurred after a growth minimum in 1994 that coincided with heavy defoliation in 1993 involving gypsy moth and hemlock looper (Bradbury 1994, Trial 1994). Hemlock that became dominant and co-dominant in the stands were capable of recovering from a defoliation event followed by a drought event in 1993-1996 as can be seen in average basal area increment growth (Figure 4). A similar response was seen at Mt. Agamenticus in 2002-2003.

Other studies have also showed reduced hemlock growth corresponding with gypsy moth (Nowacki and Abrams 1997) and eastern hemlock looper (Trial 1994, Trail and Devine 1994). Decreased growth of hemlock in our study corresponded with a hemlock looper outbreak from 1989-1993 and gypsy moth outbreaks in 1950, 1979-1982 and 1989-1994. When trees are defoliated late in the season and energy is put into refoliation, energy reserves are decreased by 30-50% and the tree is more susceptible to secondary stresses (McManus et al. 1992). Though not the preferred host for gypsy moth, hemlock is more likely to be killed than hardwoods and complete defoliation will kill 90% of hemlock trees (McManus et al. 1992).

The trees in our study appeared to have experienced energy and growth reductions due to defoliation, but not at levels that caused trees to permanently decline. Low growth associated with defoliation was usually more severe than that associated with drought and occurred for multiple years at some sites (Figure A.1). Therefore, the association of looper and gypsy moth outbreaks with the 1994 increment decrease being the most severe event in the chronologies in the last 50 years is consistent with observations from other studies. The declines in 1948 and 1950 also coincided with gypsy moth defoliation in addition to drought (Figure 4).

## Climate Variables

The climate models for eastern hemlock indicated low summer precipitation and high summer temperature were associated with decreased increment growth. Both factors are associated with water stress (Fritts 1976). High summer temperatures are expected to exacerbate water stress in trees due to increased evapotranspiration (Cook and Cole 1991). This agrees with the negative relationship in our climate models between maximum June and July temperatures and increment growth.

In addition to climatic factors associated with water availability, both higher minimum and maximum February temperatures were associated with higher growth in our study. There is no clear explanation for this phenomenon, though other studies in New York, Ontario, and Pennsylvania have shown similar results (D’Arrigo 2001, Tardif 2001, Gove and Fairweather 1978). Two possible explanations are a decrease in winter injury caused by low winter temperatures (DeHayes et al. 2001), and/or photosynthesis that can occur with warmer winter temperatures (Hadley 2000). Winter injury has been noted in red spruce (DeHayes et al. 2001) which can lose some cold tolerance by March. However hemlock has been shown to maintain cold tolerance to -61$^0$C (Sakai and Weiser 1973) and is probably less vulnerable to the same winter stresses. A 2003 report (Maine Forest Service 2003) noted slight to moderate browning of hemlock on knolls and shallow soils, which they attributed to drought and/or winter injury.

Another explanation for the relationship between low growth and low February temperatures is that cold conditions reduced carbon stores. Studies have shown that hemlock can fix carbon at temperatures above -$5^0$C (Hadley and Schedlbauer 2002) and 10-30% of carbon is accumulated in winter months (Hadley 2000) in central Massachusetts. Therefore the positive association with higher February temperatures could be related to less winter injury or more photosynthesis during winter months. These possibilities should be further investigated.

As seen in New York (D'Arrigo 2001) March conditions do appear important in some sites in this study (Table A.1) and during some time periods (Table 7, Table 8) . The positive association between March temperatures and growth has been explained by warm winter temperatures speeding snowmelt and increasing photosynthesis (D'Arrigo 2001).

## Plot-level Models

Similar to the climate analysis, plots with higher maximum February temperatures declined less in the 2003 drought model. Again, the mechanism for greater growth in plots with higher Februaries is not well understood, but maximum rather than minimum February temperature entered into the model supporting the increased photosynthesis with warmer winter temperatures hypothesis.

Neither summer precipitation or temperature, both of which were found to be important in the climate analysis presumably because of their influence on water availability, entered into the plot-level models. Cook and Cole (1991) found that correlations between precipitation and growth were inconsistent across plots and depended on site hydrology. They found that chronologies from well-drained sites were most closely correlated with precipitation. Most of our plots were well-drained, however water-availability at our sites may have been limited by other factors, including stand density and depth of the organic soil horizon, which also came into the drought model.

The negative association between stand density and growth change during drought fits with explanations of resource availability and competition. For example, stand density was positively associated with white pine decline in southern Maine (Fries 2002). A study is currently underway to evaluate silvicultural thinning of fully stocked hemlock stands prior to hemlock woolly adelgid infestation (Fajvan 2007). Decreasing stand density by thinning increases availability of resources such as sunlight, water, and nutrients to remaining trees, potentially increasing individual tree and stand vigor (Gottschalk 1993). An early study showed that hemlock on thinned stands were better able to survive drought than unthinned stands (Stickel 1933).

Percent aluminum saturation in the B soil horizon was also found to be a significant predictor of PGC03. Plots with higher Al saturation declined more during the drought. The greater amount of Al absorbed by roots, the greater the possibility of Al causing toxicity and stress to tree roots (Cronan and Grigal 1995). Percent Al in our study had a high negative correlation with the calcium to aluminum ratio (Pearson’s r = -0.66) (Table 5), which has been used as a measure of aluminum toxicity in fine roots (Vanguelova et al. 2007). In addition, Al can displace other cations at exchange sites, including calcium and magnesium which are essential for tree growth (Cronan and Grigal 1995). Percent aluminum saturation in our study was negatively correlated with calcium (Pearson's r = -0.39) (Table 5).

The PGC03 model also showed less decline at sites with thicker organic horizons. Al has been found to be less soluble and mobile in hemlock stands than other forest types, attributed to thick, carbon-rich organic soil layers that develop under eastern hemlock forests (Dijkstra and Fitzhugh 2003). Complexes of Al with organic compounds reduce dissolved Al, causing less displacement of Ca and other divalent cations and less uptake of Al by tree roots (Dijkstra and Fitzhugh 2003). Depth of the organic soil horizon may also contribute to availability of water and nutrients for growth, as surface organic matter is important for erosion control, water infiltration, and conservation of nutrients (Franzluebbers 2002).

The factor with the largest effect on the model was the expressed population signal (Table 10). Because this measure is based on interseries correlation, a measure of the similarity of growth response among trees, plots where growth is limited by climate would be expected to have high expressed population signals as in the arid southwestern United States where crossdating was developed (Fritts 1976). The 0.46 interseries correlation for the 503 trees across plots indicates that growth is being largely affected by regional climate patterns. However, climate may be more limiting at some sites than others. The average maximum June and July temperatures in recent years (1996-2005) were climatic factors most positively correlated with EPS (0.25), suggesting the possibility that maximum summer temperatures may be limiting hemlock growth in this region, especially at warmer plots; this association could be further explored.

Within-site factors also appear to be affecting growth at some sites more than others, resulting in lower expressed population signals. These factors could include microsite differences affecting rooting and availability of light, nutrients, and water that would cause larger variation in increment growth among trees. Another factor possibly influencing EPS is past defoliation. Defoliation stress can occur unevenly across some plots causing increased variation in tree growth due to some trees being more defoliated than others and making more resources available for less affected trees. The expressed population signal is positively correlated with hemlock basal area (Table 2). Since hemlock modifies its local environment (Godman and Lancaster 1990), within-plot conditions would be expected to be less variable in stands with high hemlock basal area.

The association between EPS and decreased growth during drought in the PGC03 drought model fits with the premise of dendroclimatology; trees that are strongly affected by regional climate factors will show a strong common growth signal (Fritts 1976). Differences in regional signal strength would be emphasized in a drought year like 2003, which may also help explain why PGC03 is predictive of PGC2003.

A look at the last 5 low growth events in our chronology showed that EPS alone was a significant predictor of variation in PGC among plots for years following droughts (2003, 1979) but not for years associated with defoliation

(1994, 1991, 1980). Low growth in 1976 was significantly predicted by EPS, suggesting that the growth decrease in 1976 was related to climatic conditions. Although 1976 was not indicated as a drought year, there was a large drop in PDSI in 1995 (Figure 5). It seems logical that the “potential climate signal” would be a good predictor of decline after drought, but not defoliation. This variable could be tested in other studies, both where hemlock stands have and have not experienced defoliation.

The recovery model also supports the observation that plots that are strongly affected by climate will show a strong common signal; PGC in 2003 is the most powerful predictor for PGC05. Plots having the most negative response in 2003 after drought had the most favorable response in 2005 when conditions were favorable for eastern hemlock growth (Figure 9).

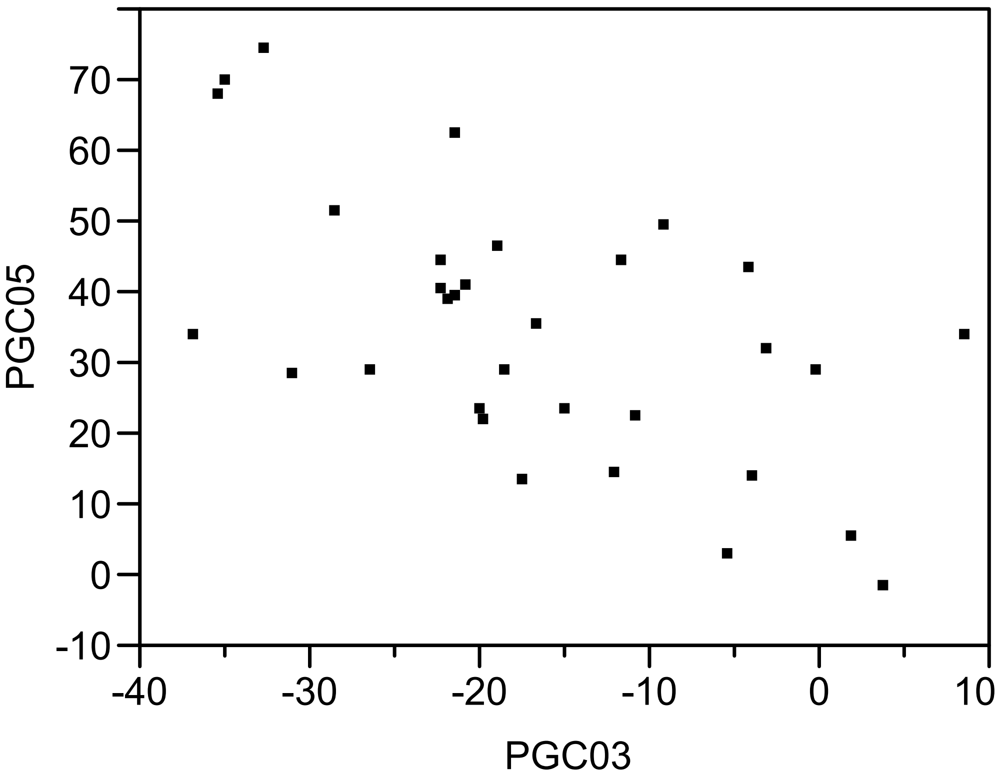

**Figure 9. Relationship Between PGC03 and PGC05 plot means.**

The recovery model also included soil Ca in the B horizon, which could be positively related to PGC05 for several reasons. Ca is needed for growth and stress response in plants (McLaughlin and Wimmer 1999), controlling protein synthesis, cell division, membrane and stomatal function and plant metabolism (McLaughlin and Wimmer 1999, DeHayes et al. 1999). Exchangeable Ca in soil is the most plant-available form of the nutrient (Szillery 1998). Possitive correlations between Ca and other soil nutrients and negative correlations between Ca and Al (Table 5) also might help account for its presence in the model. The one declining plot, at Ferry Beach State Park, had the lowest levels of Ca (7.7 mg/kg) and a highest Ca/Al ratio (0.025); possibly Al toxicity

(Vanguelova et al. 2007) or Ca limitations are detrimental to growth or stress response at this site.

Age is the final variable in the PGC05 model, with older trees showing higher rates of recovery (PGC05). This could be due to larger root systems and a greater competitive advantage of older trees, as age is highly correlated with height and diameter for the dominant and codominant hemlocks in our study (Table 2). Another explanation is that the greatest variation in ring widths occurs near the base of the tree (Larson 1963), so basal area increment does not necessarily estimate volume production. During unfavorable conditions, BAI is likely to underestimate volume production, especially for trees with much of their growth above breast height (Bouriaud et al. 2005), therefore the percent growth change measurement in 2005 is likely to overestimate recovery for older/larger trees. There were no indications that trees are over mature or that older trees should be harvested. This is consistent with the long lifespans of eastern hemlock on good sites (Godman and Lancaster 1990).

In summary, growth changes for plot models are best predicted by measures of regional growth signal. The mechanisms behind this variable are not well understood, but EPS appears to be influenced by factors affecting in-plot variability, particularly hemlock basal area; higher concentrations of hemlock may create more similar plot conditions, leading to higher EPS. Limiting climatic conditions, such as maximum July temperature, may also contribute to EPS.

Differences in plot characteristics that affect water availability and nutrient status also came into plot-level models. Stand density, organic matter, and percent aluminum appeared more important than differences in precipitation for explaining water-availability. This was consistent with Cook and Cole's (1991) finding that site conditions influenced precipitation response. The only temperature variable that came into the models was February temperature in the drought model.

## Study Implications

A major influence on the PGC models in this study was attributed to regional growth response as expressed by EPS and PGC03 in the PGC05 model. Including these measures in our models helped us to explore other variables associated with PGC growth response for hemlock stands in southern Maine. It will be worthwhile to test whether these variables can be used for modeling growth decline and recovery in hemlock stands in other regions, including stands infested with HWA.

There were few visual signs of decline when stands were visited in the summer of 2006, which did not allow us to evaluate factors related to hemlock decline at our sites as in other studies (Davis et. al 2007, Rentch et al. In review) Even a method for characterizing declining trees based on increment growth yielded too few declining trees for a useful comparison of declining versus healthy plots. Tree rings are currently being analyzed from Pontius' New England stands. Comparing how tree growth responded to past stresses and HWA infestation using both tree rings and visual signs of decline should help us better understand the usefulness of BAI models and how hemlock in southern Maine will respond to impending HWA infestation.

Other factors associated with vulnerability could also be compared among locations to understand susceptibility. For example, a preliminary comparison of soil chemistry in southern Maine and New England shows that Maine sites have higher Ca and lower N than Pontius' sites. Studies have shown that Ca is toxic to aphids and limits population levels, making trees better able to tolerate infestation (Harada et al. 1996, Verma 1985). Calcium in the upper B horizon was higher and more variable in our study (54.9 ± 9.64, n=36) than in a study of infested and uninfested hemlock stands throughout New England (21.97 ± 5.12, n = 51) (Pontius 2008 Unpublished Data). Forty-two of Pontius' 51 plots with soil data had Ca values lower than the median value at our plots (35.10 mg/kg. In addition, Ca/Al ratios in the B soil horizon were higher in southern Maine than at the New England sites (0.15 ± 0.03 v. 0.022 ± 0.0056), potentially indicating a lower probability of rootlet mortality due to Al toxicity (Vanguelova et al. 2007).

Lower foliar N is a factor associated with lower hemlock vulnerability to HWA infestations (Pontius 2006). Aphids are more successful on high N foliage (Carrow and Betts 1973, McClure 1980) and N fertilization increased HWA populations (McClure 1991) and made hemlocks more susceptible to HWA (McClure 1992). Nitrogen concentrations in the upper B horizon were much lower and less variable at our plots (0.15 ± 0.018%, n=36) than Pontius' New England sites (3.93 ± 1.25% n=51). Thirty-three of Pontius' 51 sites had N values above the median value (0.12%) at our site. Foliar concentrations of Ca and N in Maine hemlock stands need to be evaluated. If higher Ca and lower N in soils are also expressed in the foliage, hemlock in Maine would likely be less vulnerable to HWA than regions to the south.

The low proportion of declining trees in 2005 indicates that the population of hemlock trees in southern Maine is relatively healthy and able to recover from stress on the scale of recent drought and defoliation events. Plots where trees declined the most in 2003 recovered the most in 2005 (). The study suggests that hemlock in this area are not predisposed to decline and have adjusted to drought and defoliation events as experienced over the last 60 years.

The effects of climate change on hemlock vigor and stressors are complex and could have a large range of impacts on HWA populations and resulting damage in Maine. Currently we see that a major future stress for Maine's hemlock, HWA, has spread slower (Evans and Gregoire 2007) and been more limited by cold winter temperatures in the northern part of its range (Paradis et al. 2007) compared to regions farther south. In addition, hemlocks in southern Maine are able to recover from periods of reduced growth due to drought and defoliation, and soil factors could favor reduced tree vulnerability to HWA compared to other regions.

Management that takes into account hemlock ecology, silviculture and local stand conditions could be used to further improve the ability of southern Maine hemlocks to resist decline from HWA. Silvicultural thinning is being investigated as a preemptive management strategy to increase hemlock vigor and resistance to HWA-induced decline (Favjan 2007). Thinning will reduce basal area in fully stocked hemlock stands and should increase crown conditions and growth rates, both of which have been shown to decrease damage due to HWA (Davis et. al 2007, Rentch et al. In Review).

In addition practices that have been shown to negatively impact individual hemlocks and hemlock ecosystems, such as overthinning (more than 30% of the stand) (Godman and Lancaster 1990), root damage (Godman and Lancaster 1990) and presalvage and salvage harvests (Kizlinski et al. 2002, Orwig and Kizlinski 2002) should be avoided.

Hemlocks in southern Maine will likely respond in a similar manner to infested hemlocks in adjacent regions where stands have shown resistance to HWA infestation but have been highly influenced by the level of infestation (Pontius 2006). Therefore continued regulatory measures and improvement of biological controls are also important for maintaining southern Maine’s ecologically important hemlock population.

# Chapter 5

# CONCLUSION

Hemlock increment growth in this study was sensitive to climatic variation and insect defoliation. Low growth years were related to published drought and defoliation events (hemlock looper, gypsy moth). Climatic factors associated with higher growth throughout the chronology included higher previous and current summer precipitation, especially during the month of July, lower previous June and July maximum temperatures, and higher February temperatures.

Increment decline and recovery after the 1999-2002 drought were related to local plot conditions including climate, soil, and tree factors. The strongest relationship with growth decrease and recovery after drought were measures of previous growth response. In 2003 expressed population signal, a measure of common growth signal within a plot, was associated with more a negative percent growth change. Negative percent growth change in 2003 was associated with positive percent growth change in 2005. Expressed population signal was the only predictor of percent growth change in the decline period following other climatic stress events.

Additional factors which were associated with smaller decreases in growth during the decline year were depth of the organic soil layer, maximum February temperature, percent aluminum saturation in the B soil horizon and stand density. For the recovery model, age and soil calcium in the B horizon were associated with larger growth increases.

Overall, hemlock in this region recovered quickly from drought and defoliation events over the past 60 years. The population’s ability to respond positively to favorable growth conditions indicates that if management techniques are successful in increasing tree vigor (Fajvan 2007), such strategies could be used in Maine to increase the ability of hemlock to tolerate HWA infestation. Such management could help maintain this ecologically important species in areas where the insect is not yet established.

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# APPENDIX

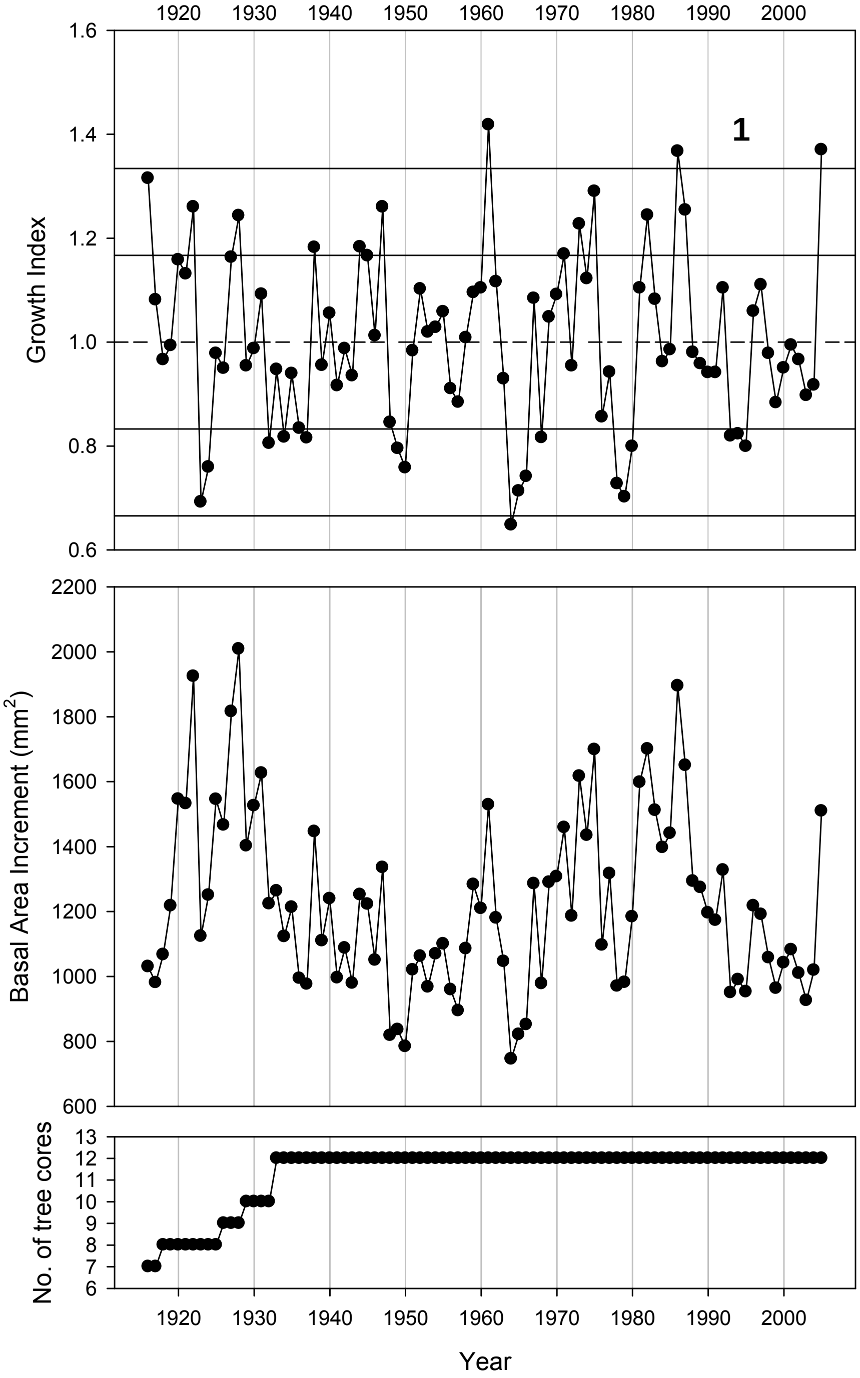
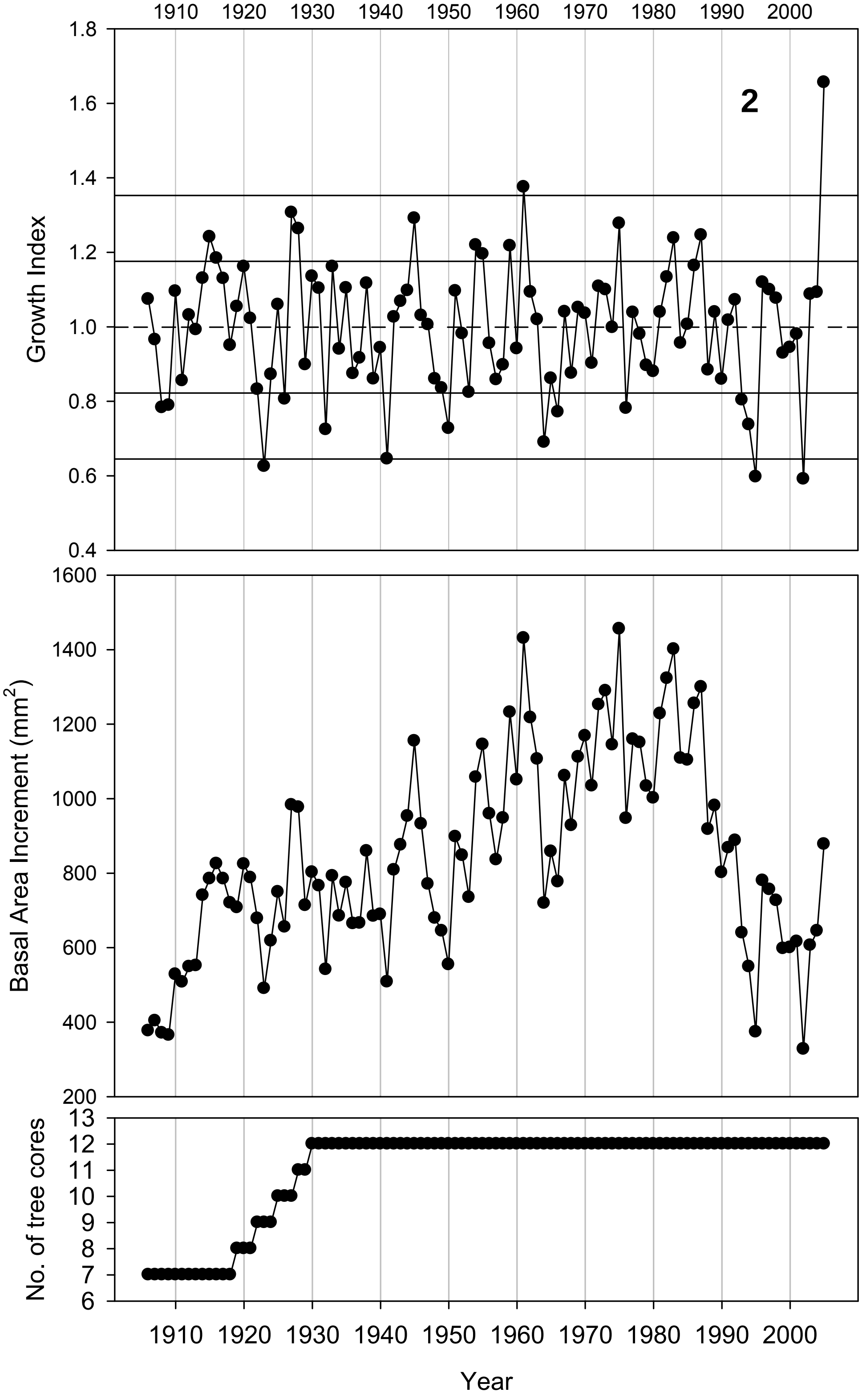


**Figure A.1. Standardized growth index (RESID) and basal area increment (BAI) by plot.** The standardized chronology is the residuals from a 30-year smoothing spline with the autocorrelation removed. The dashed line indicates the mean. Solid horizontal lines show 1 and 2 standard deviations above and below the mean. Vertical gray lines mark decades. Plot number is in the upper right corner. Bottom plot shows the number of trees represented, with a minimum of 7.



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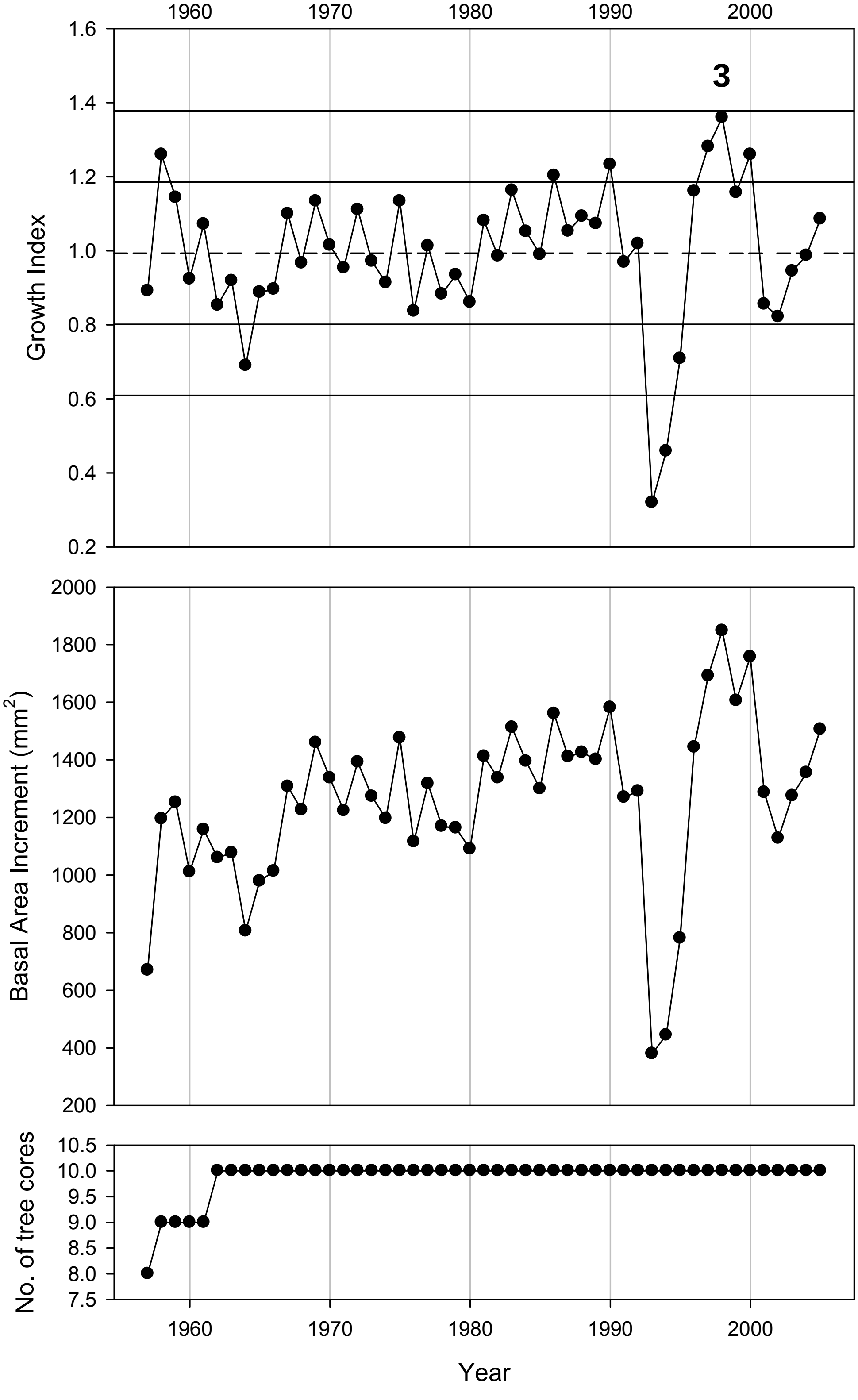

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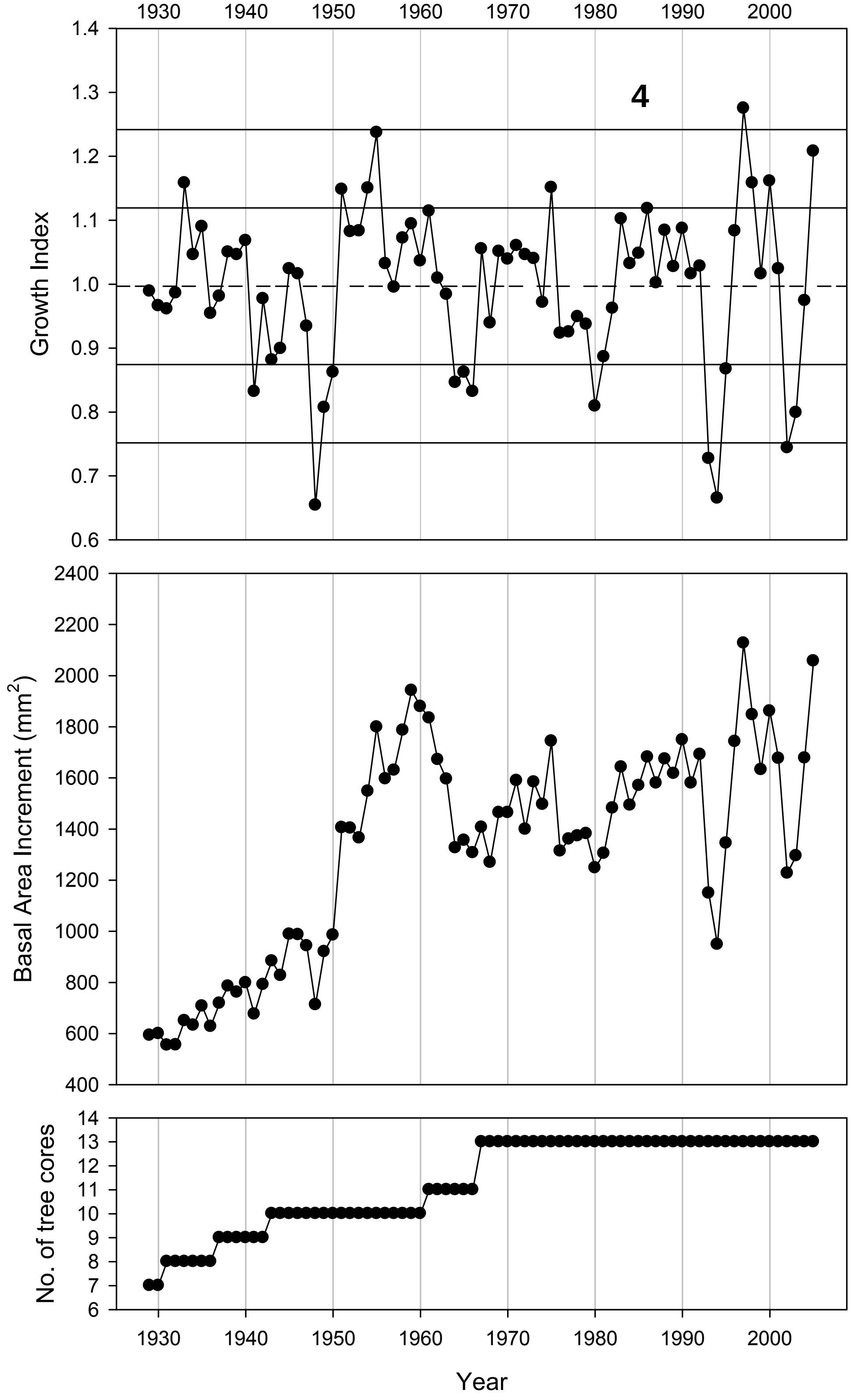

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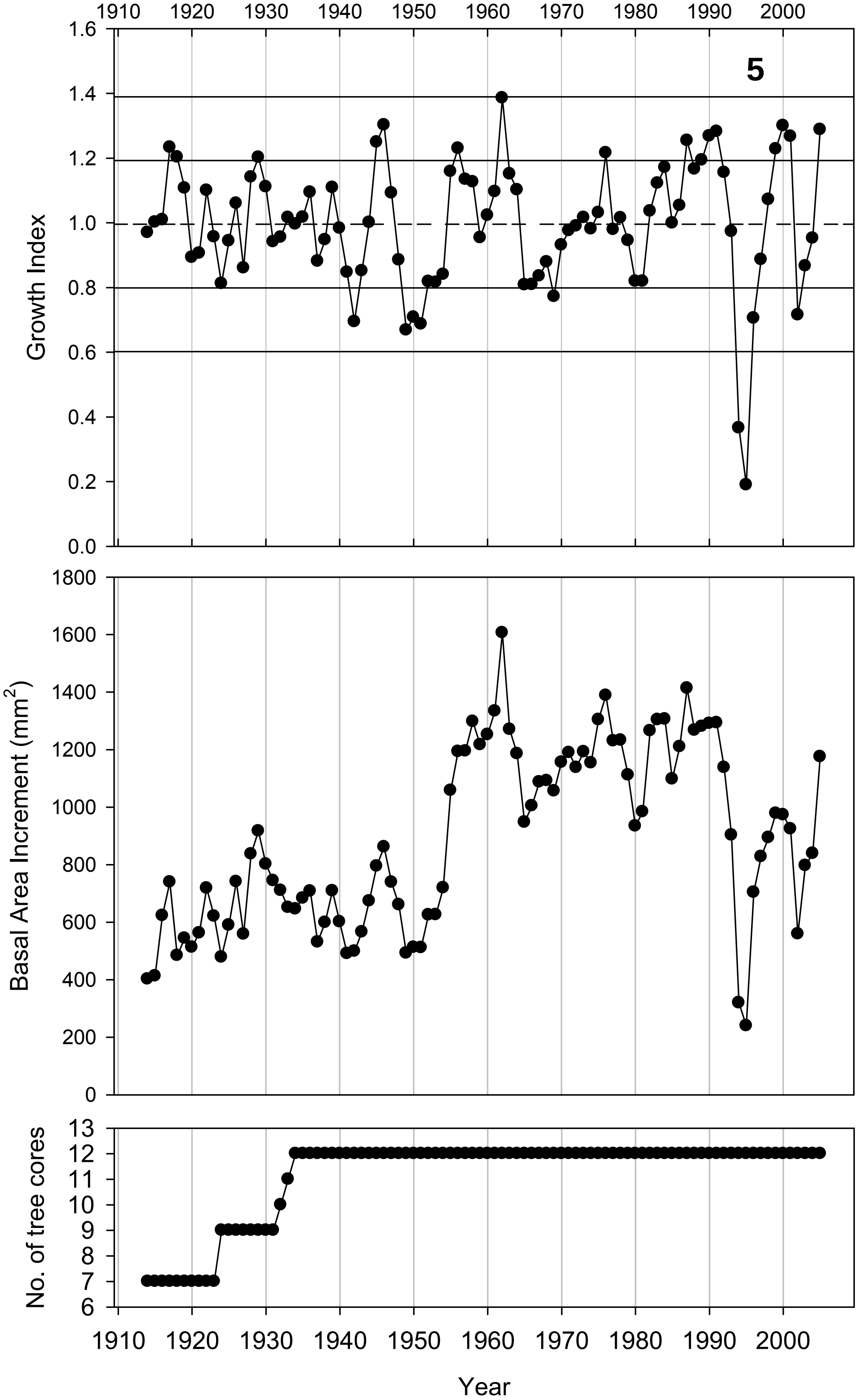

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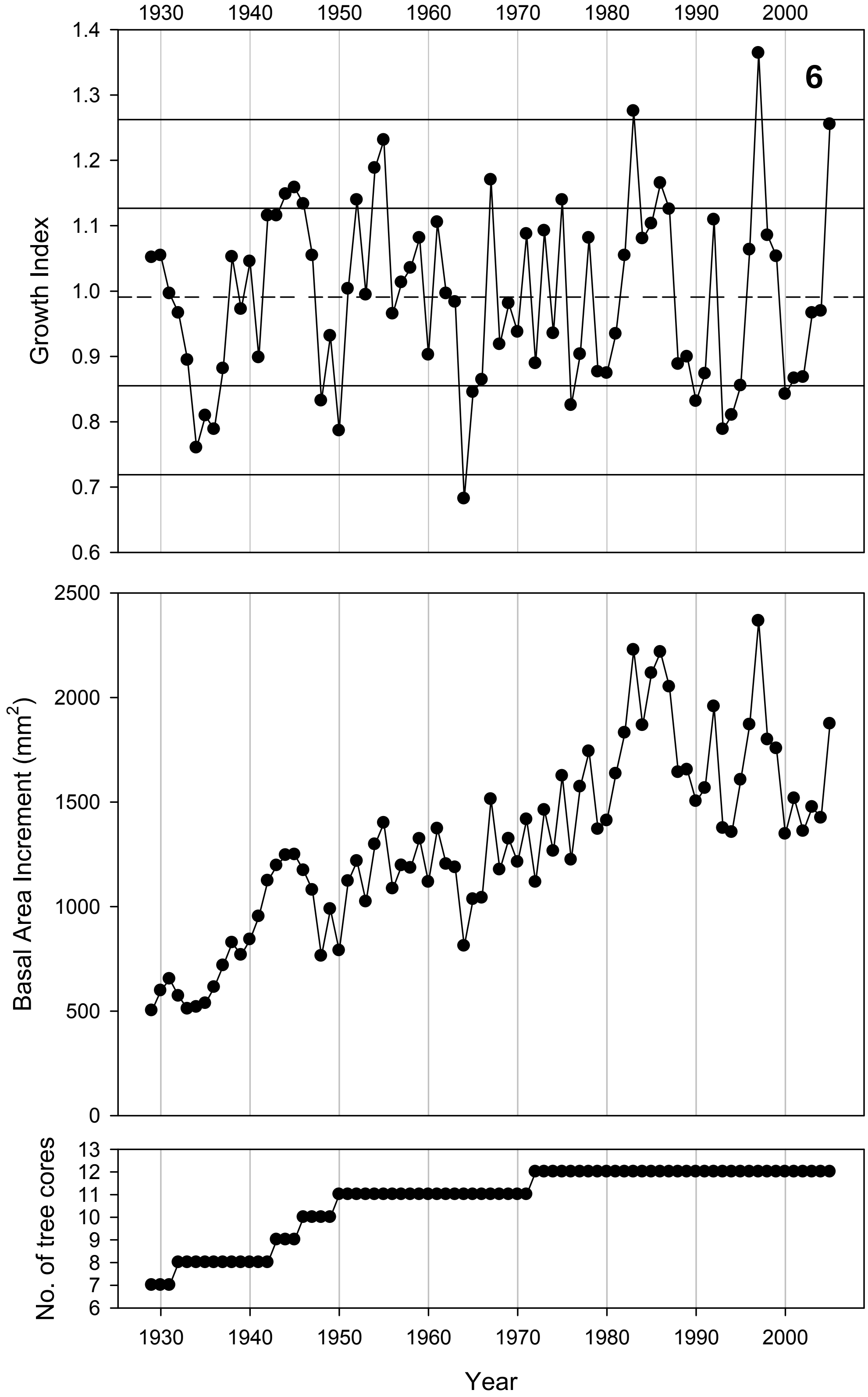

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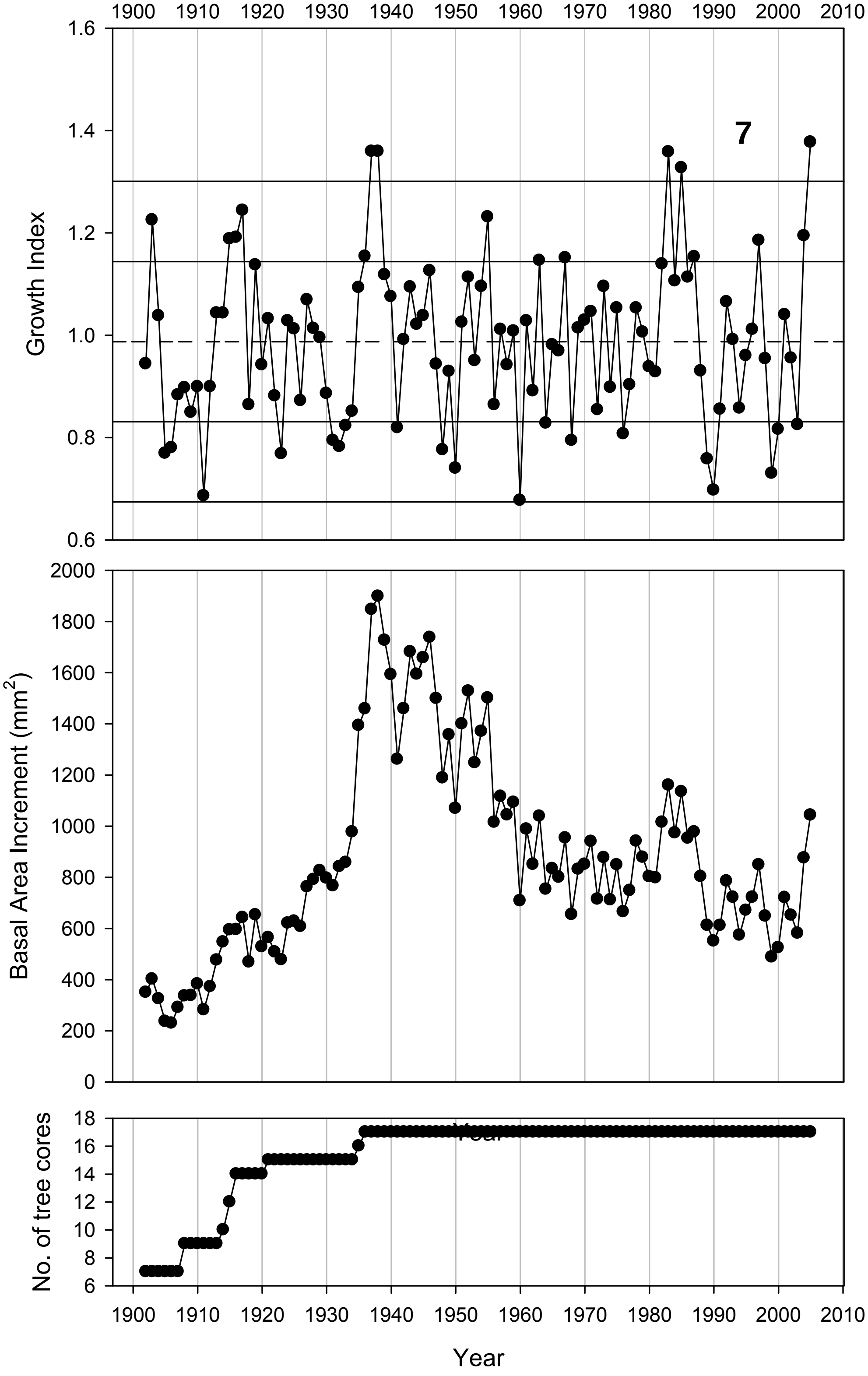

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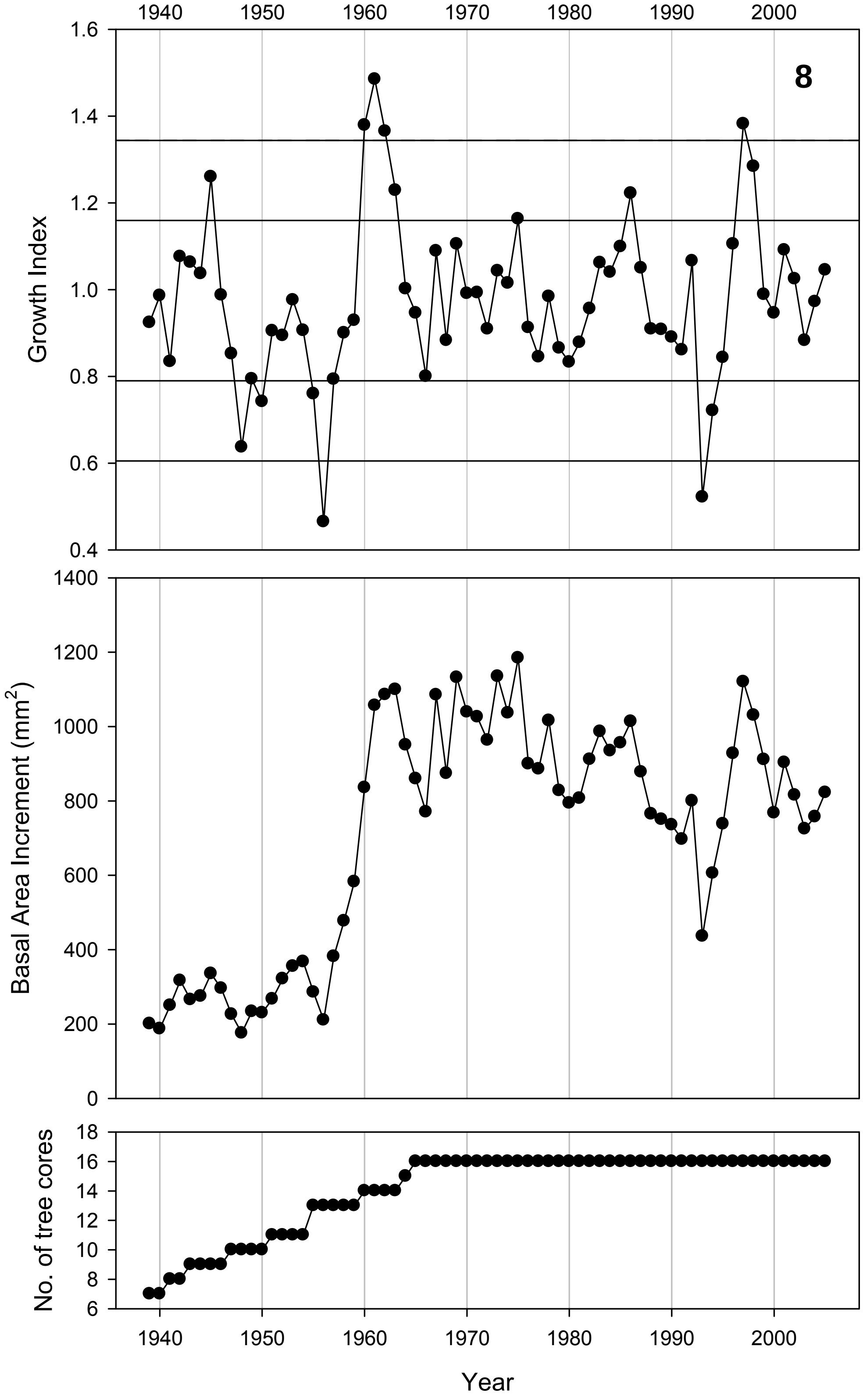

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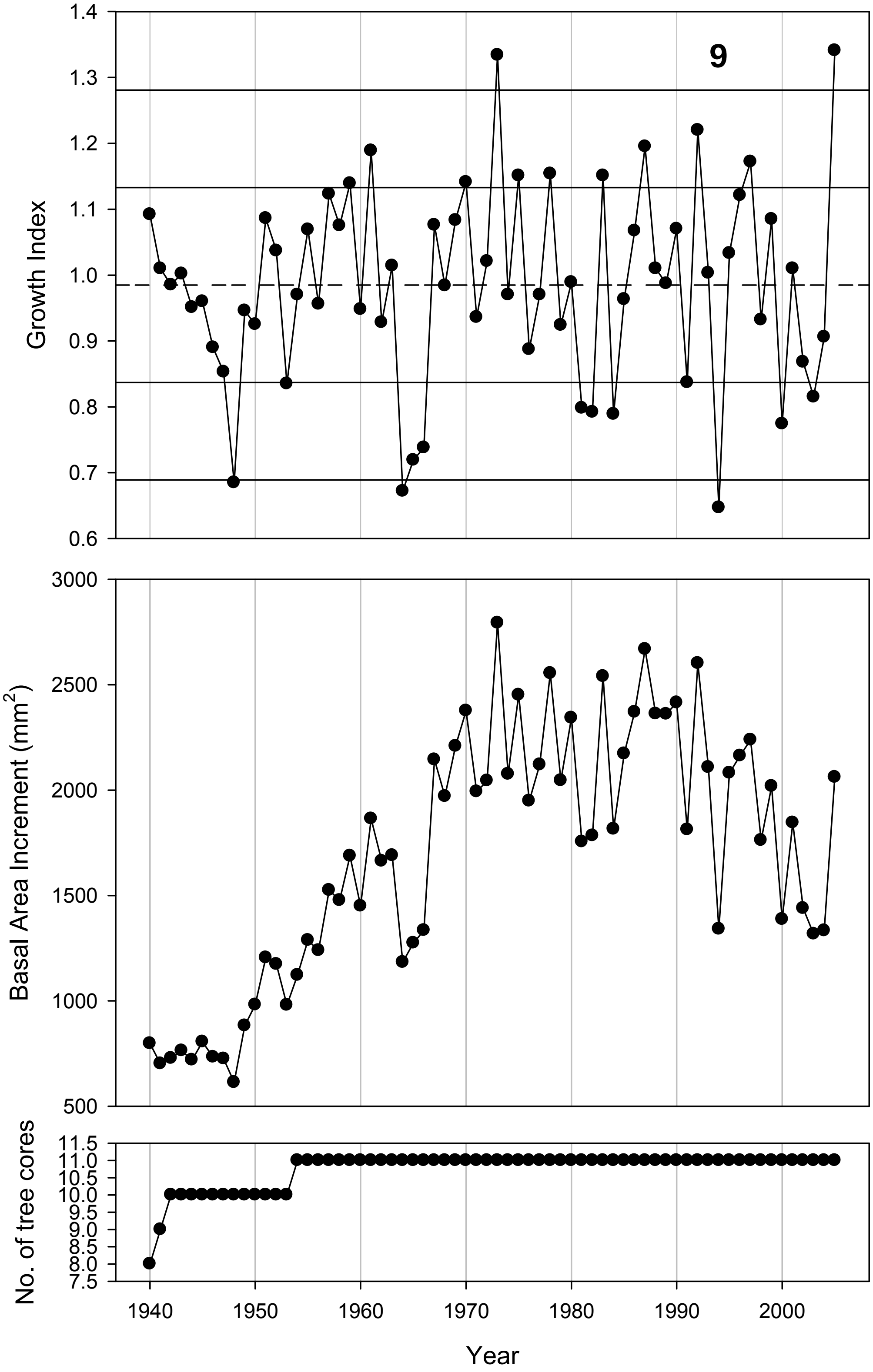

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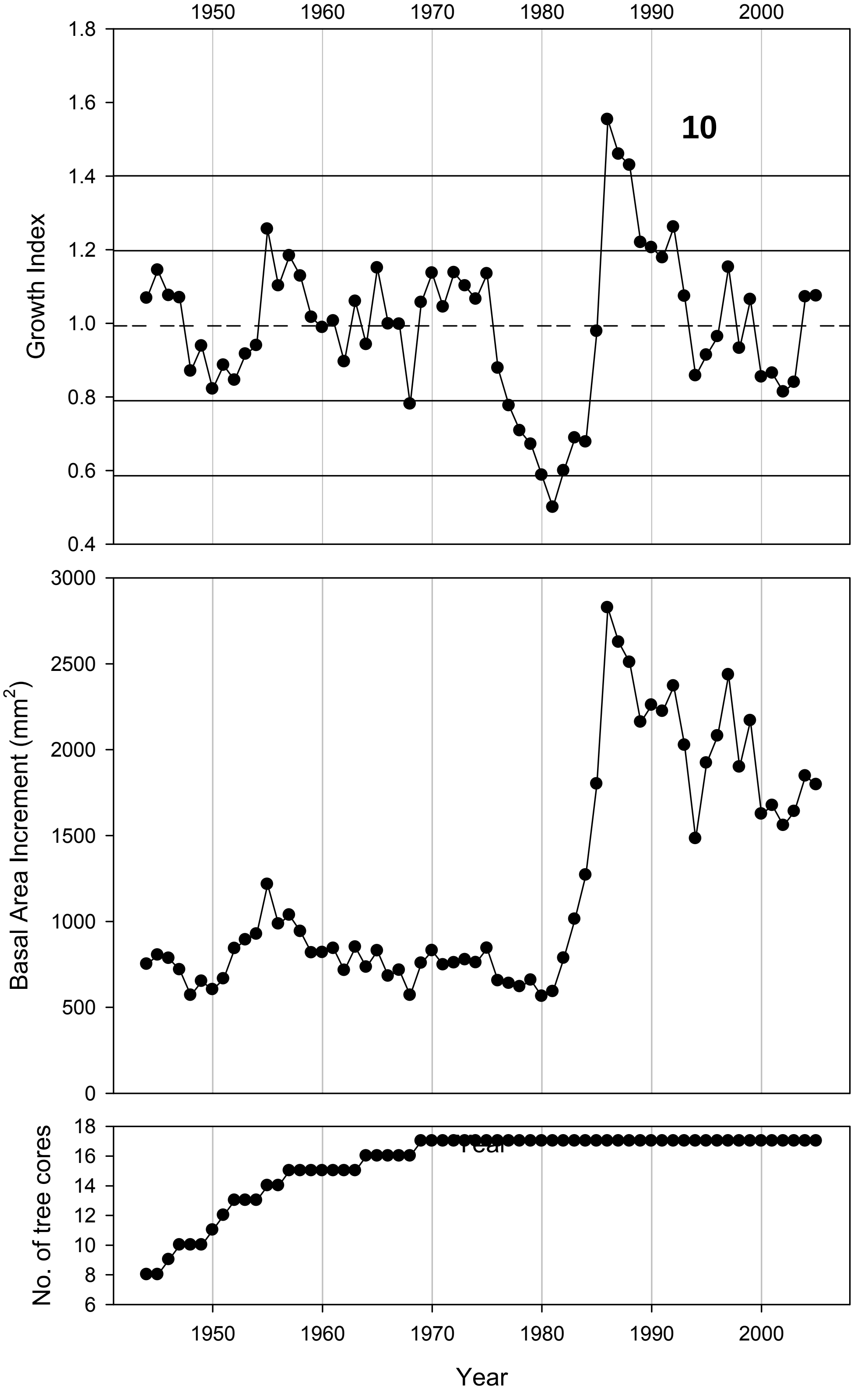

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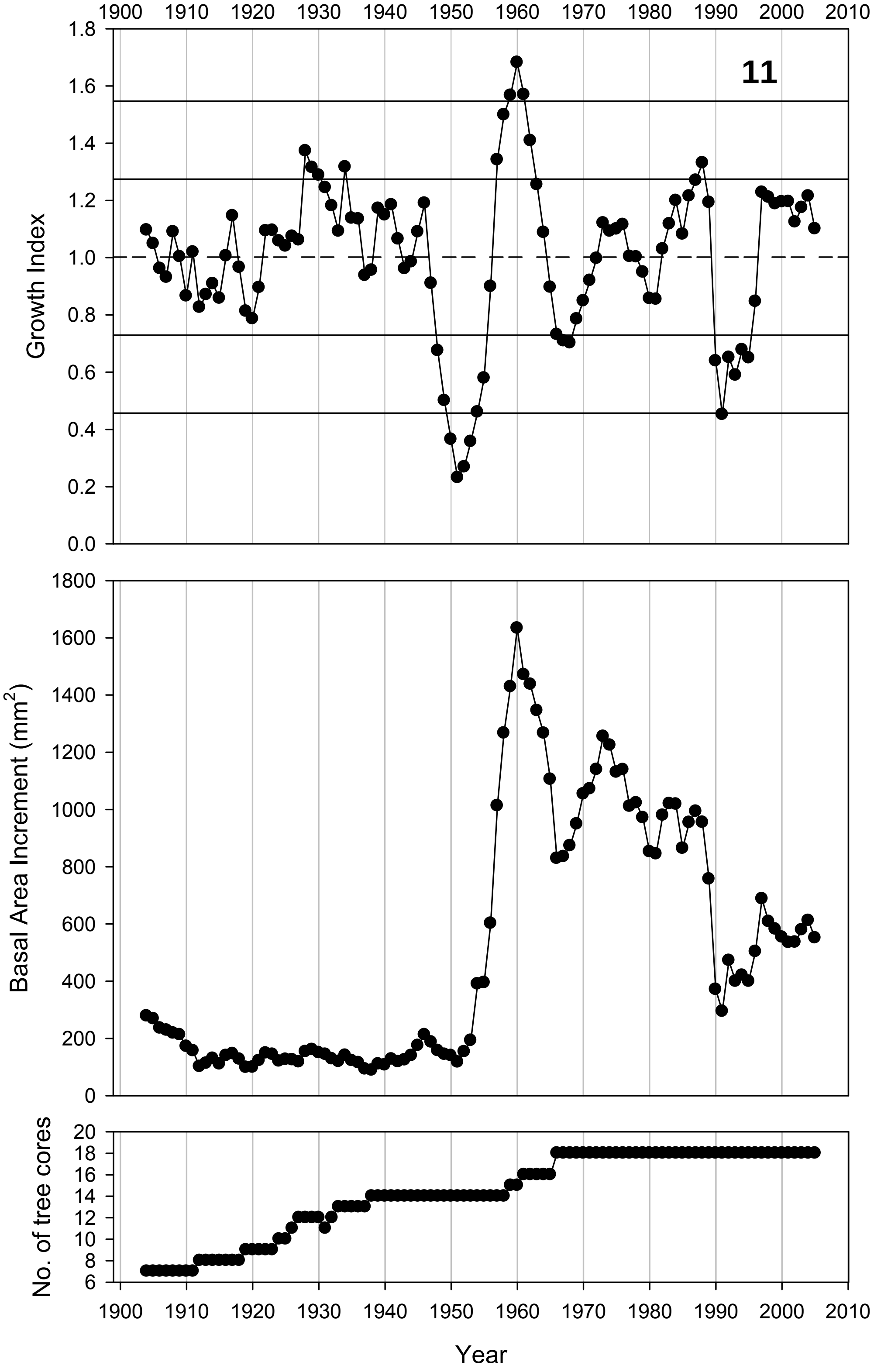

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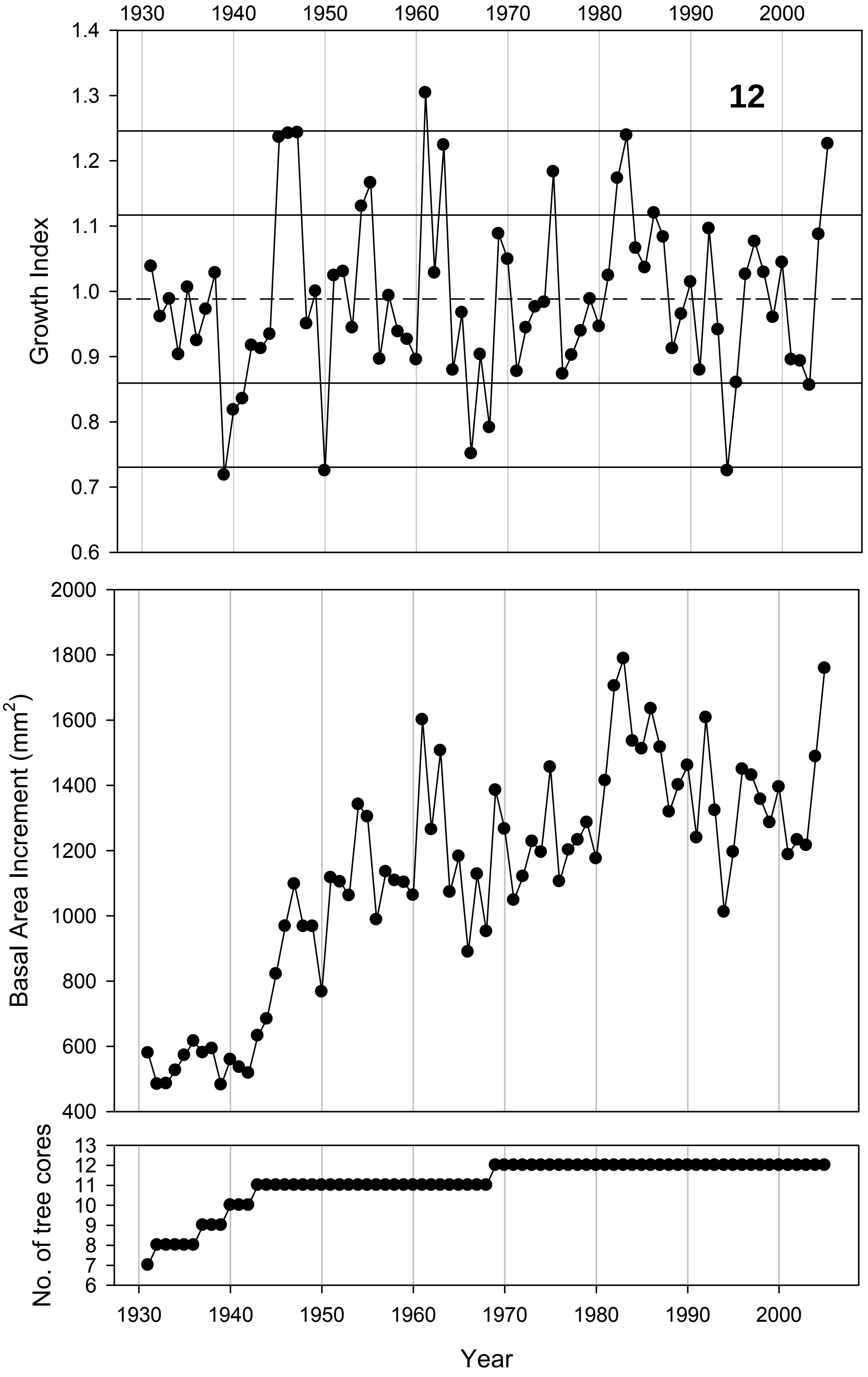

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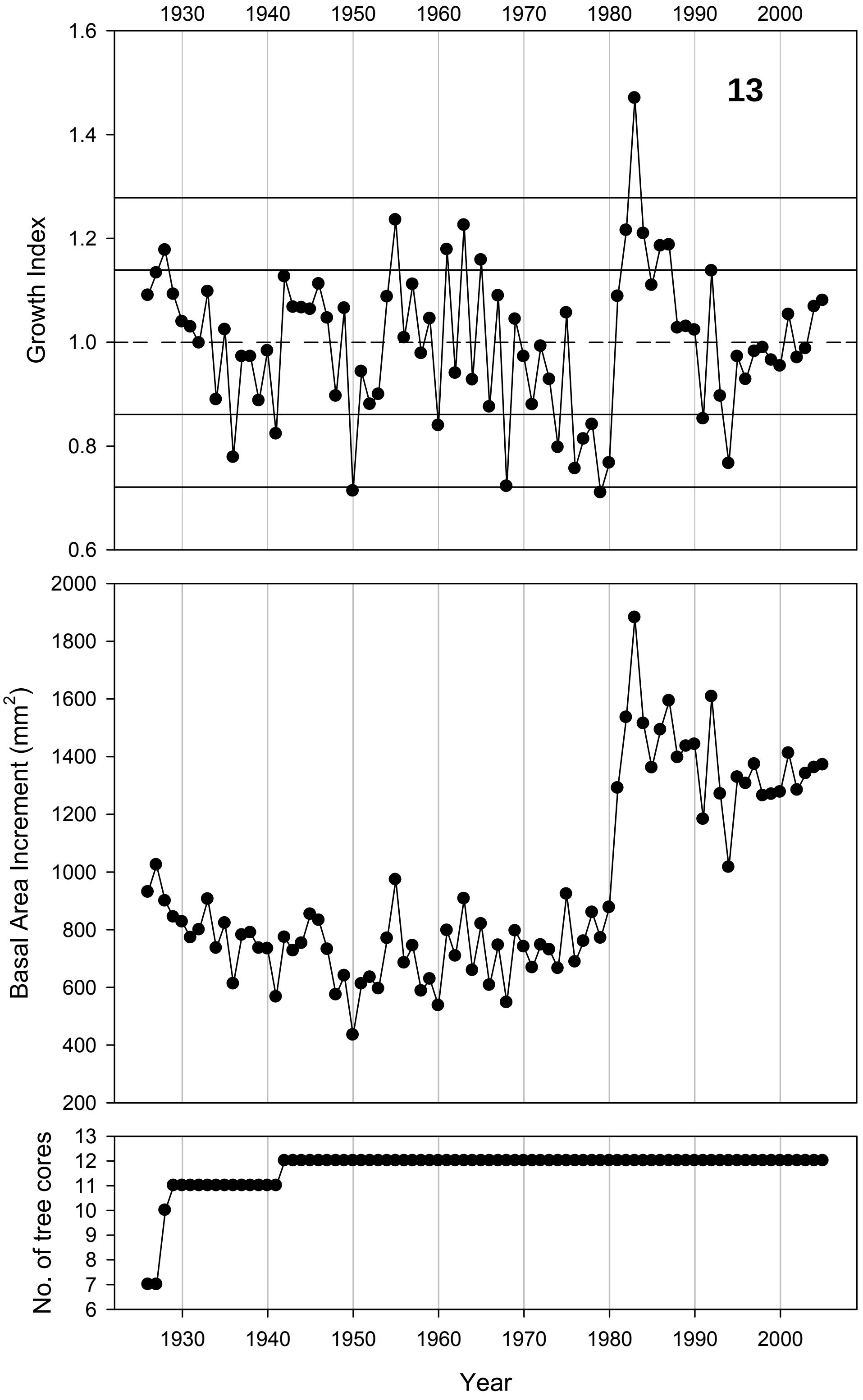

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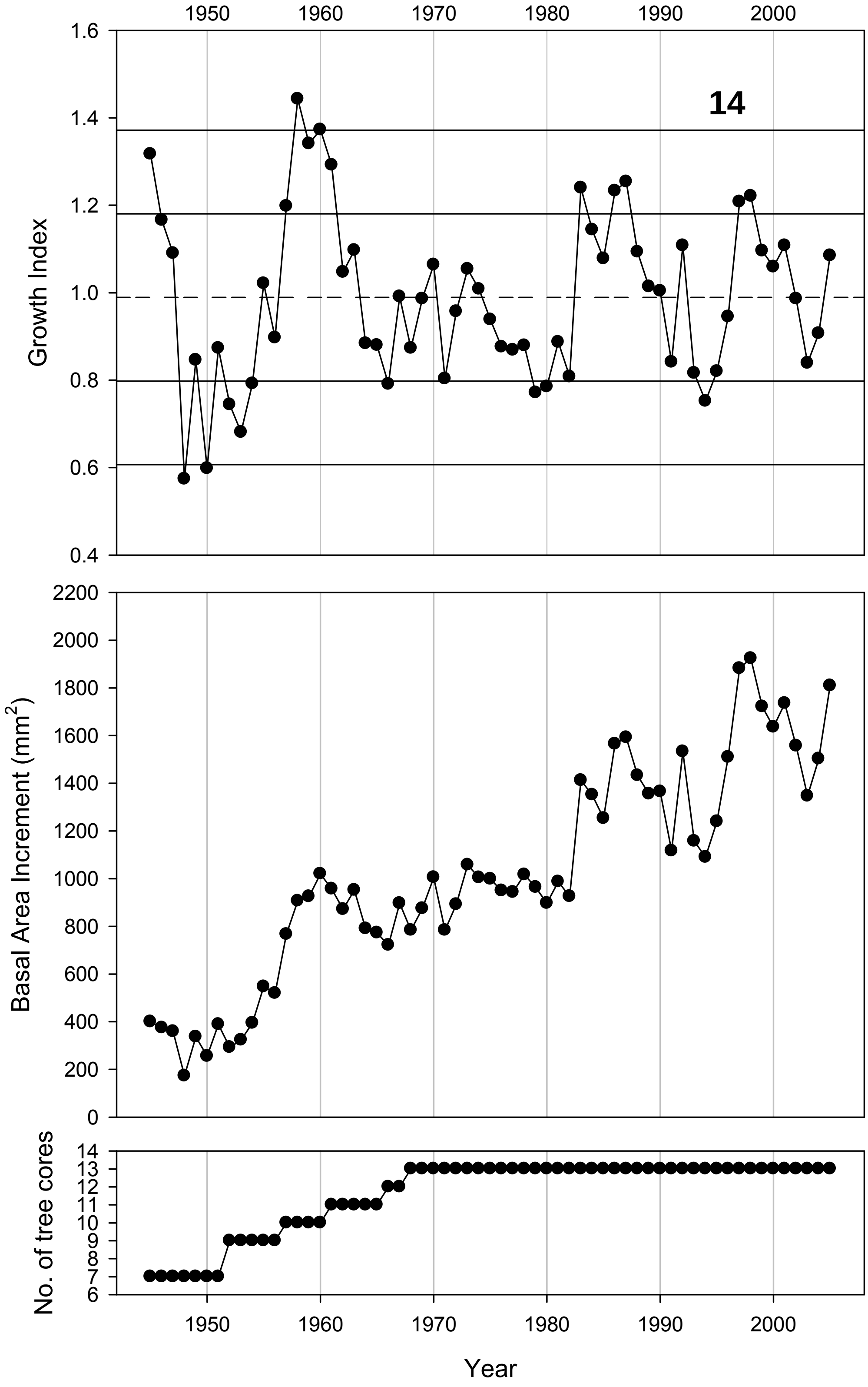

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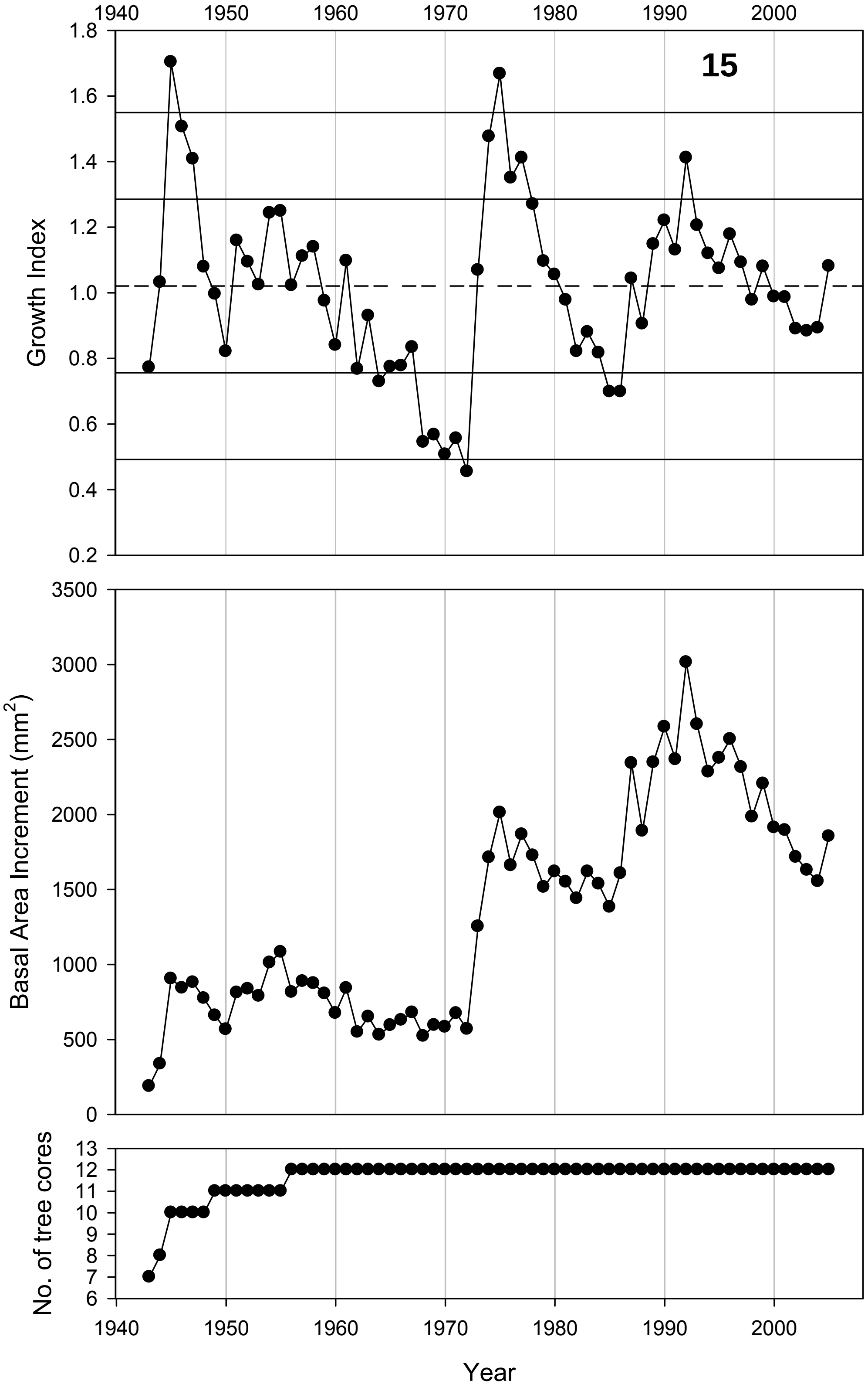

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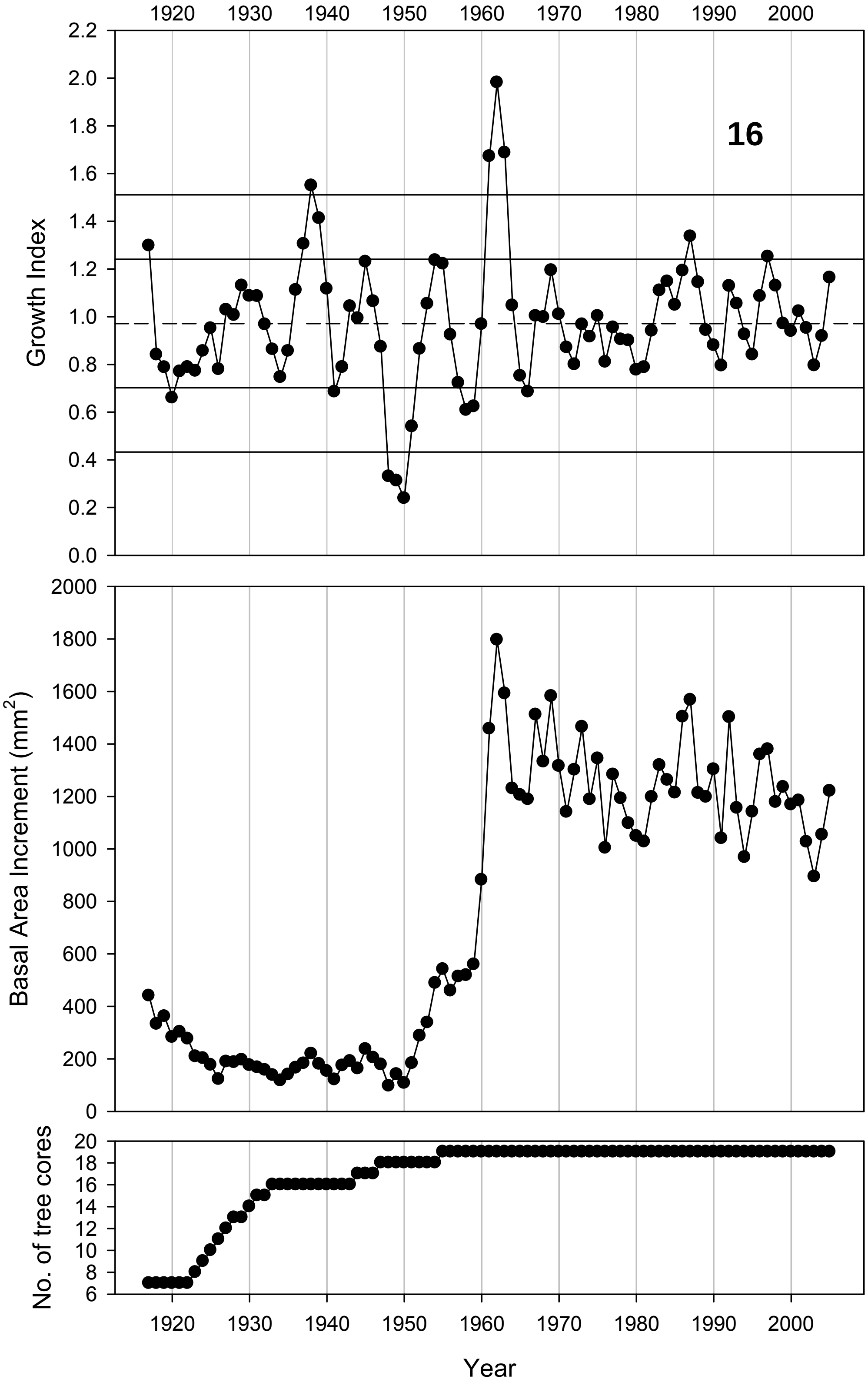

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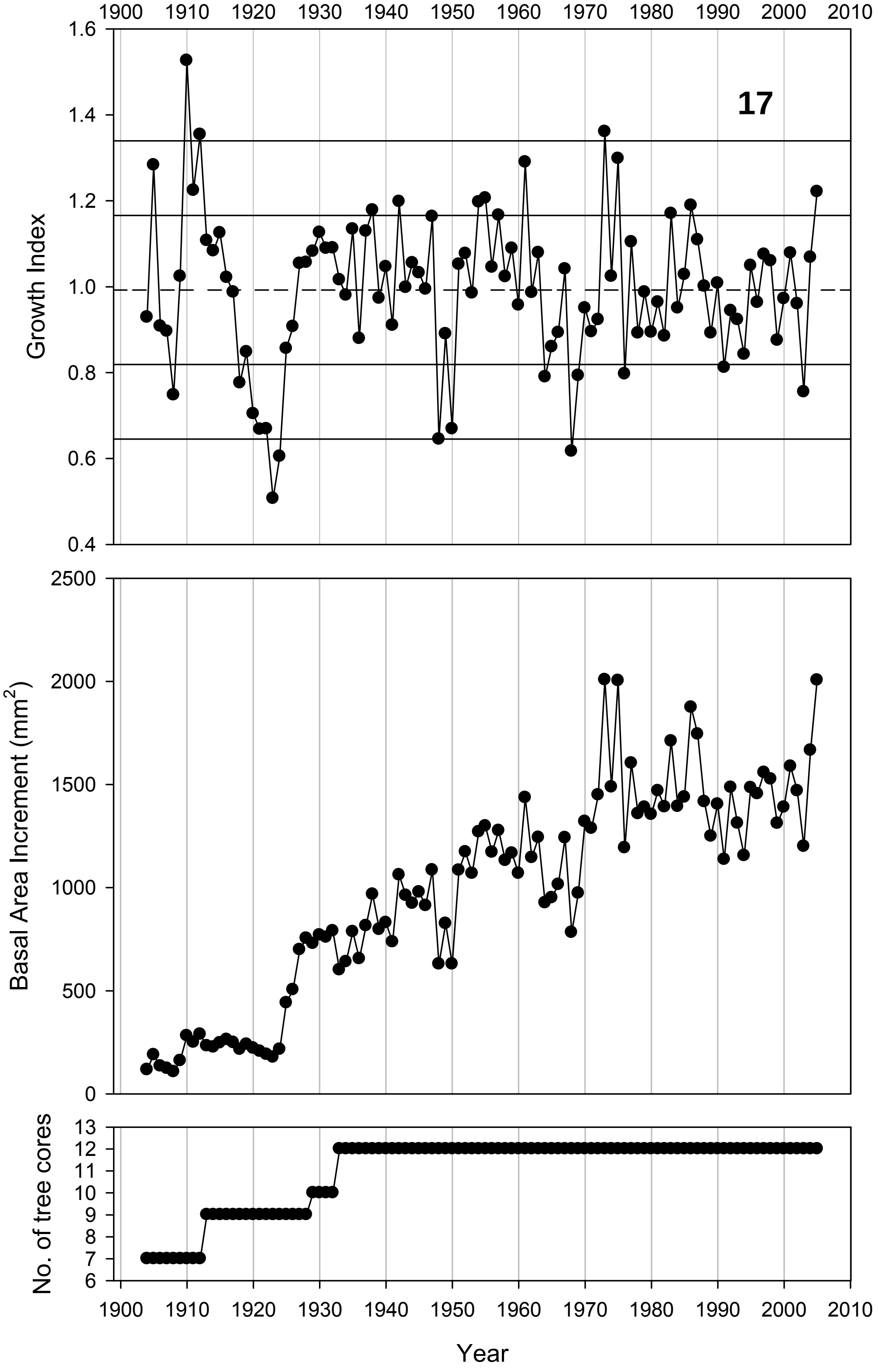

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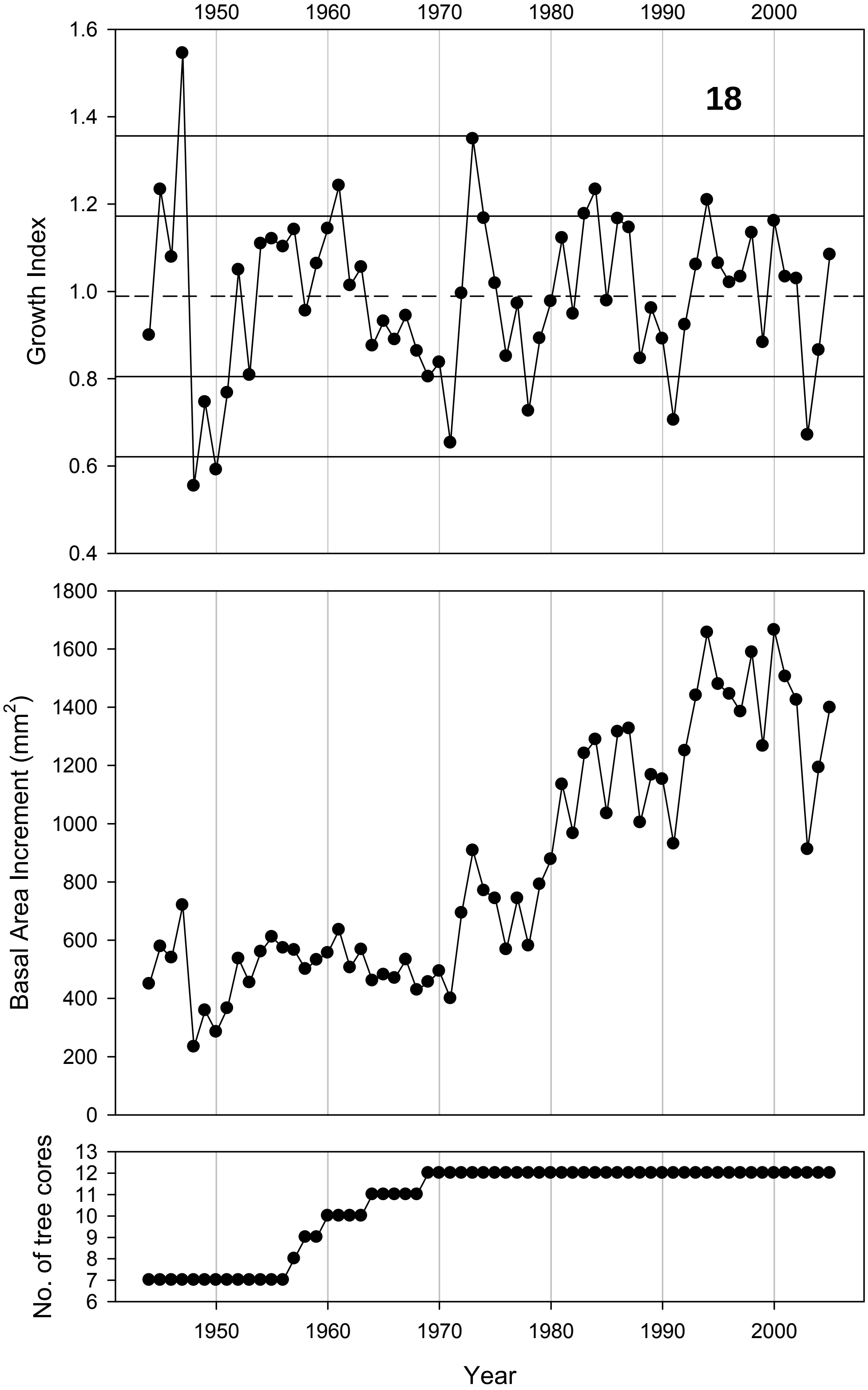

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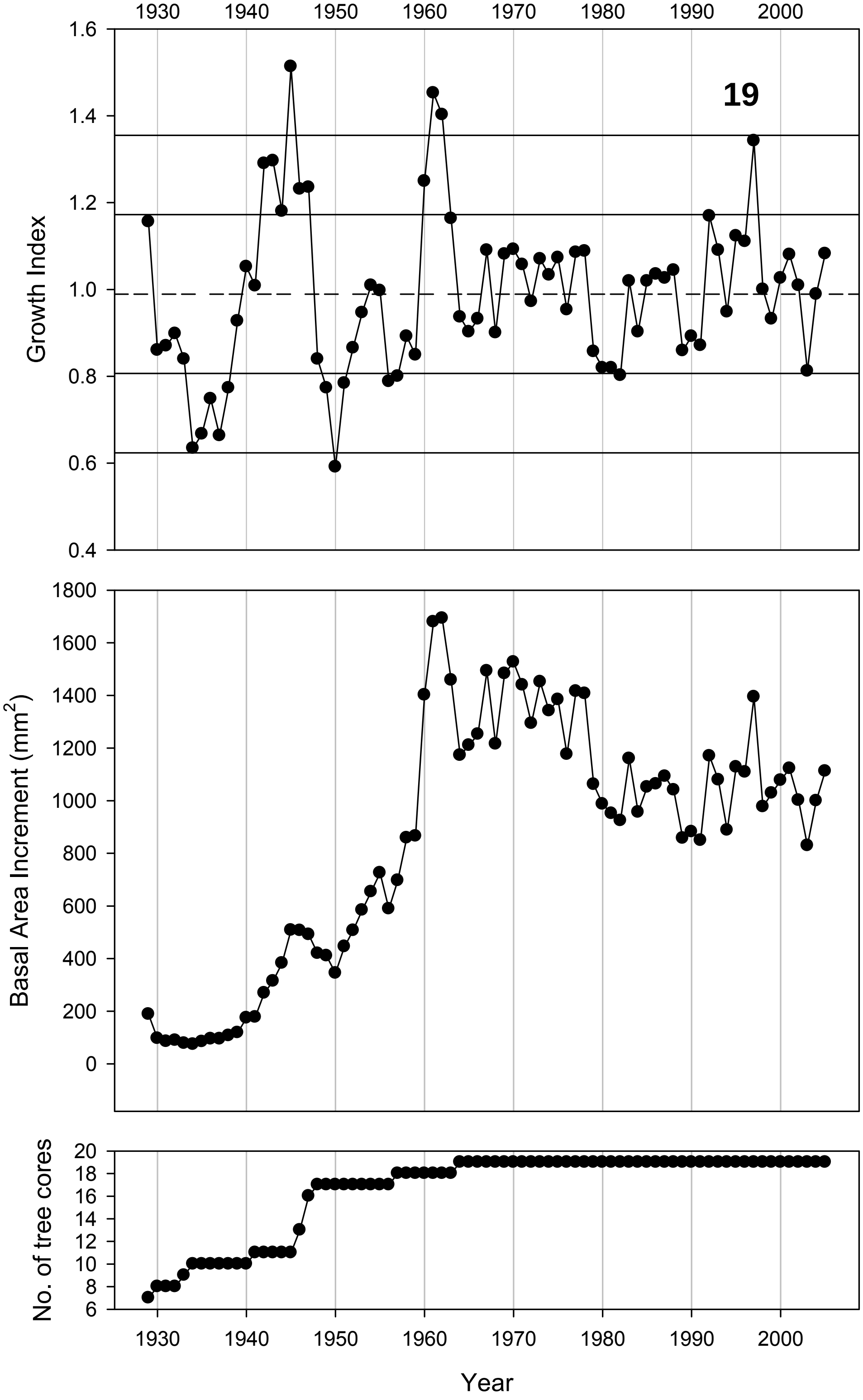

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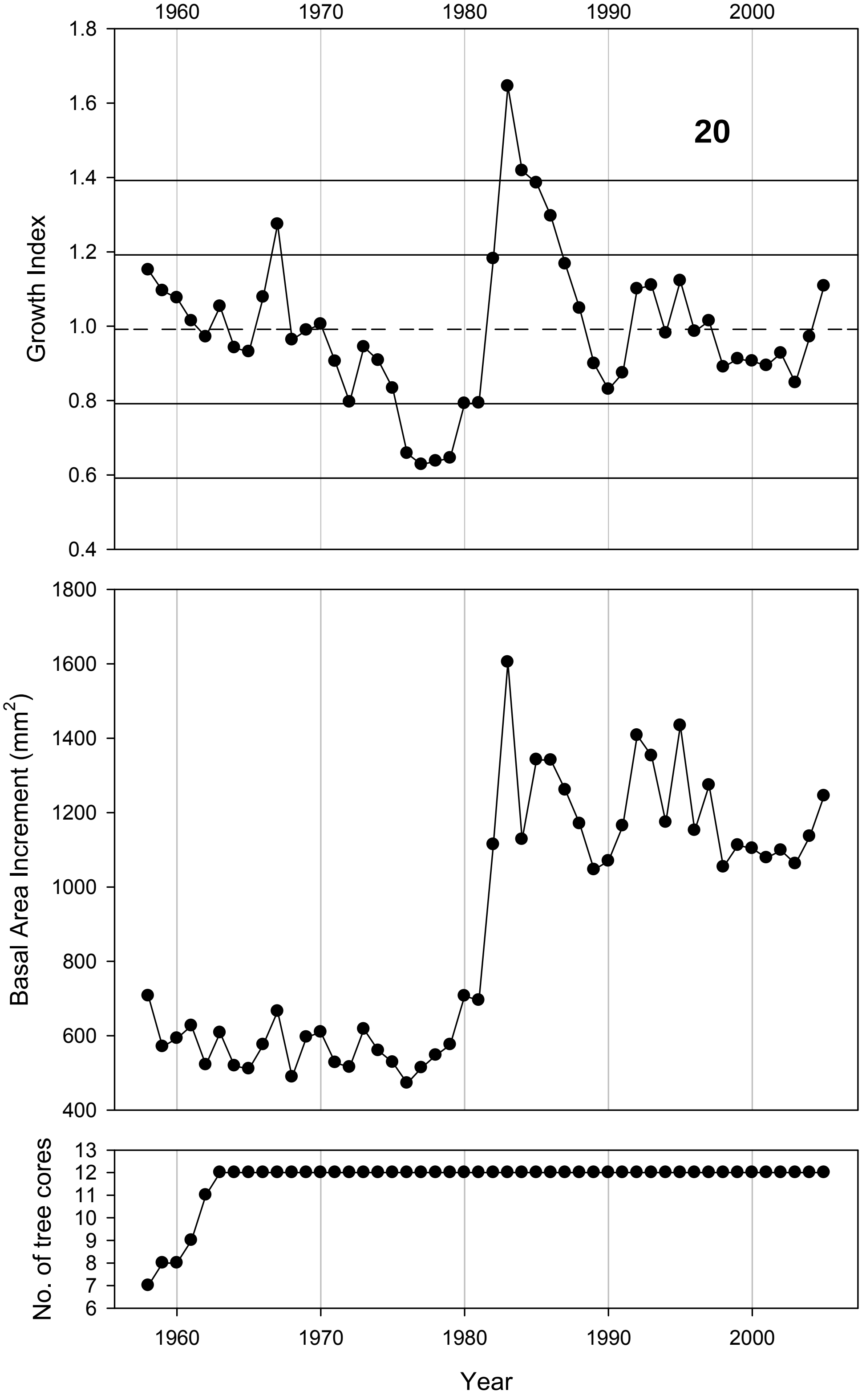

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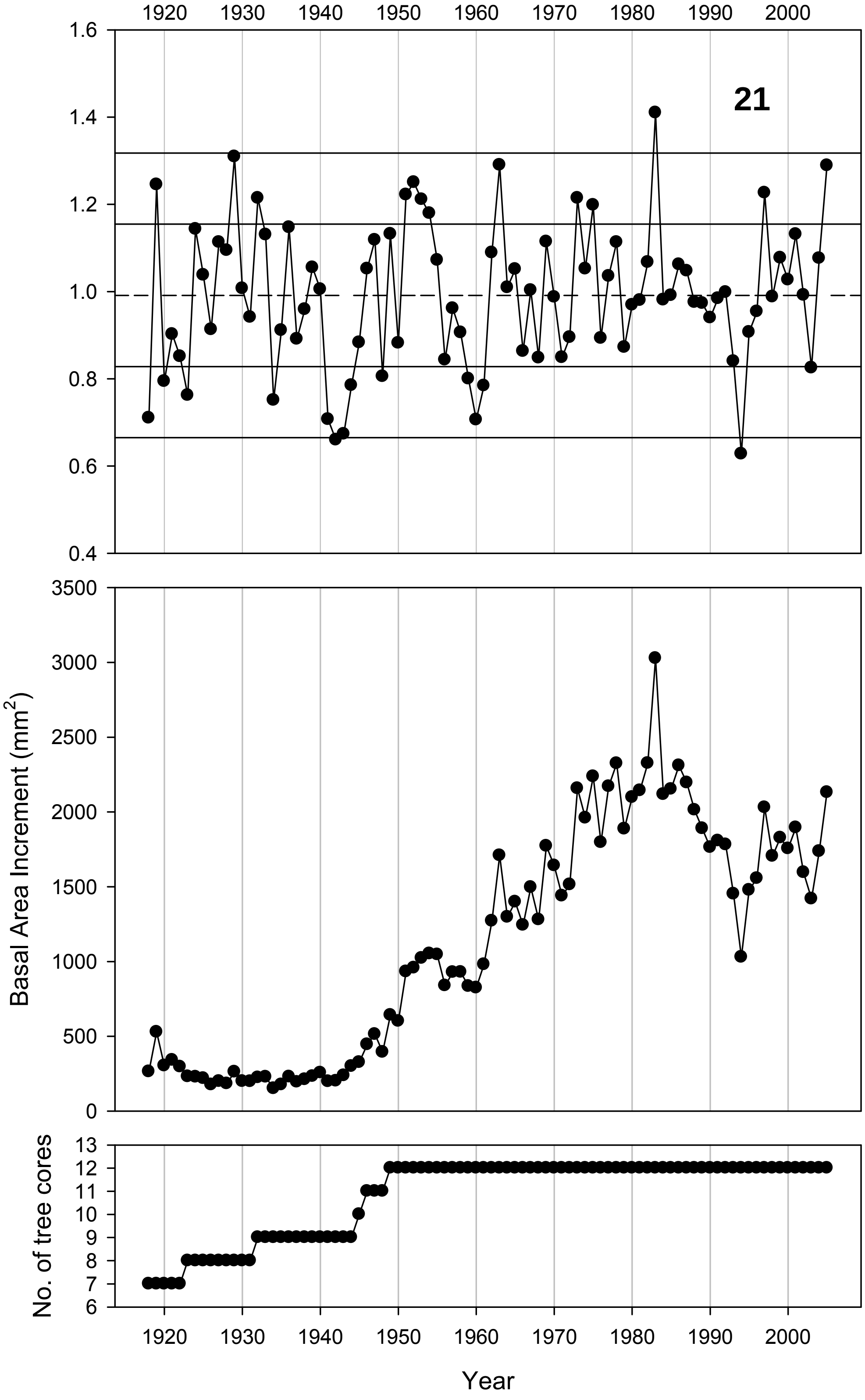

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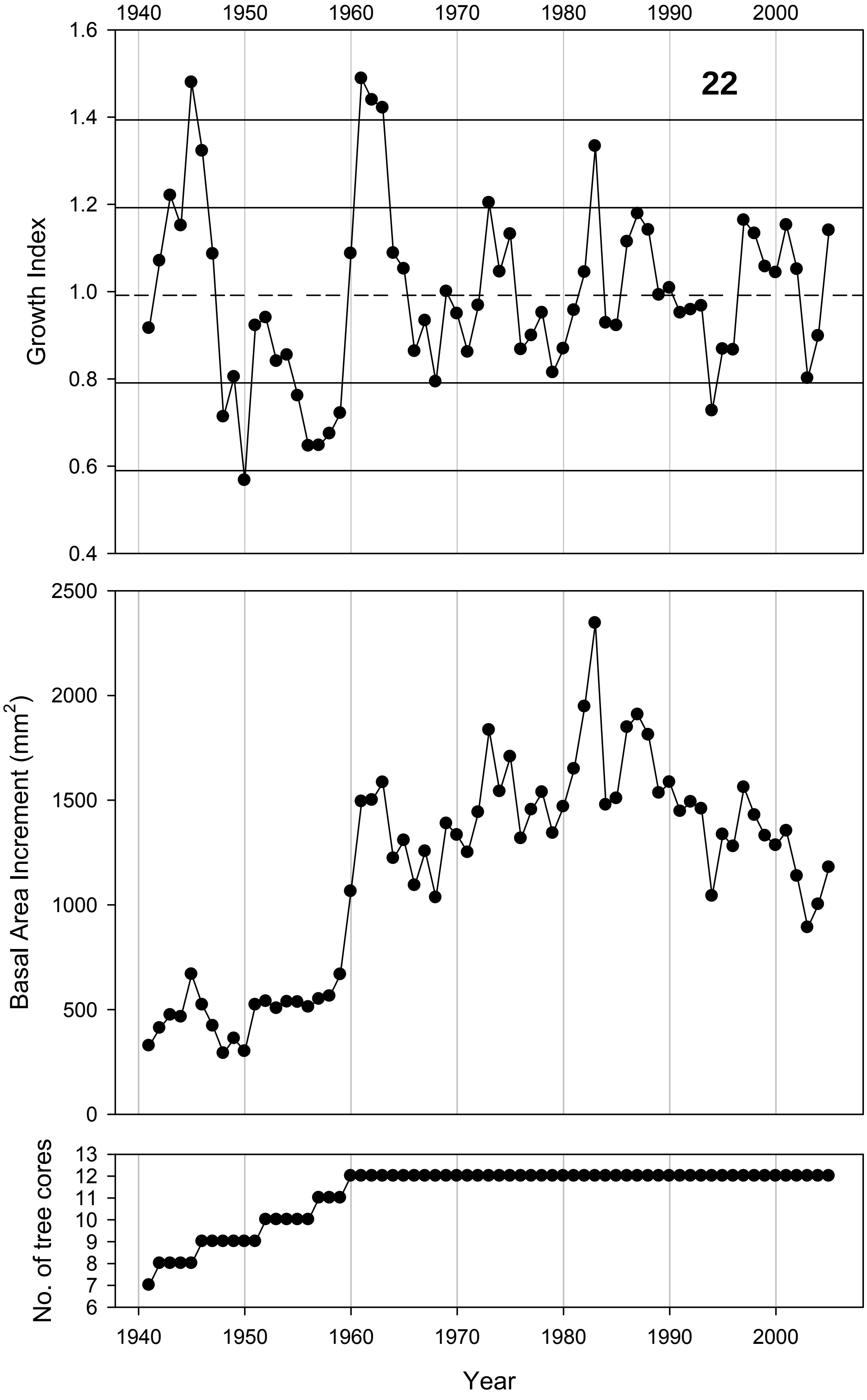

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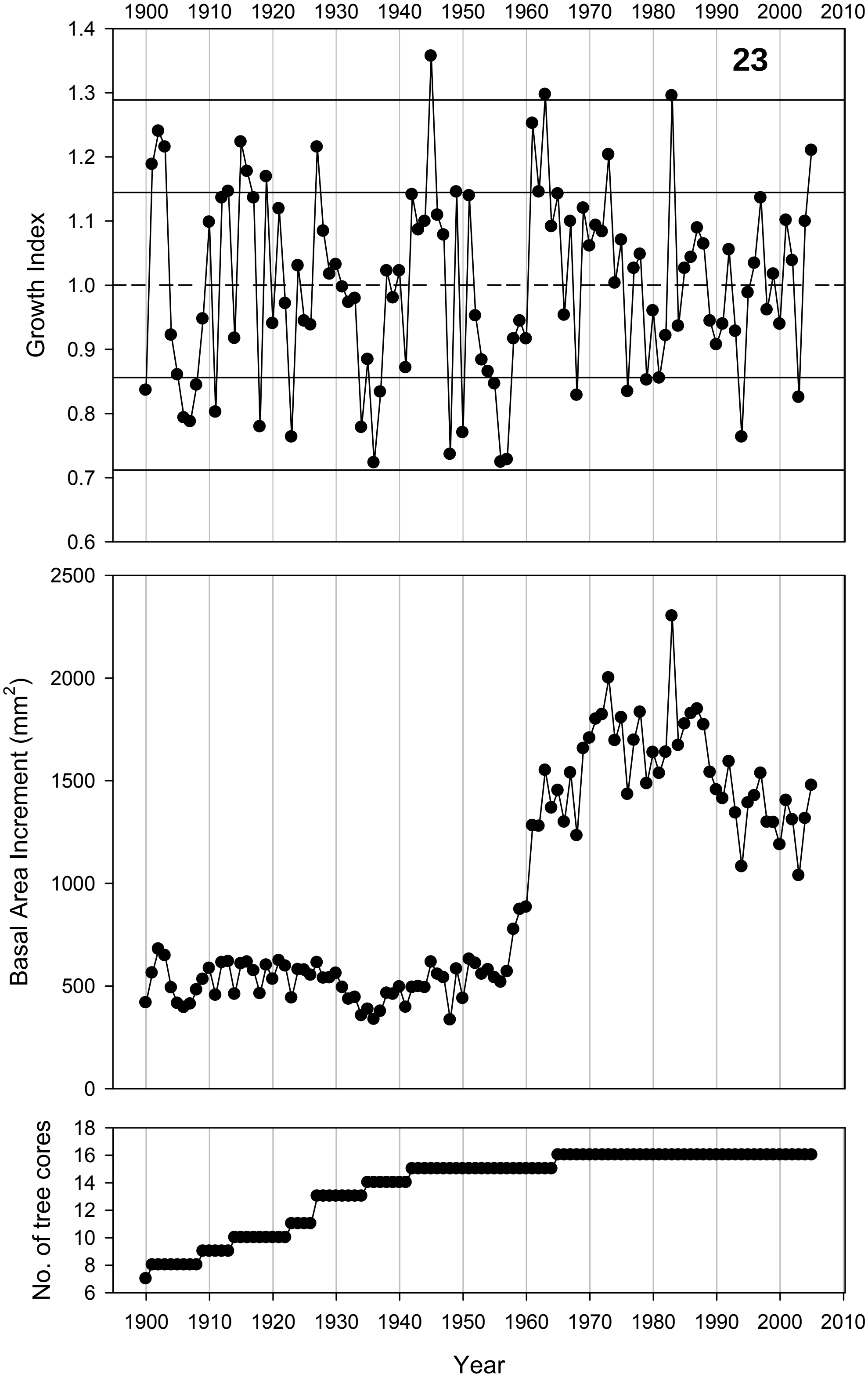

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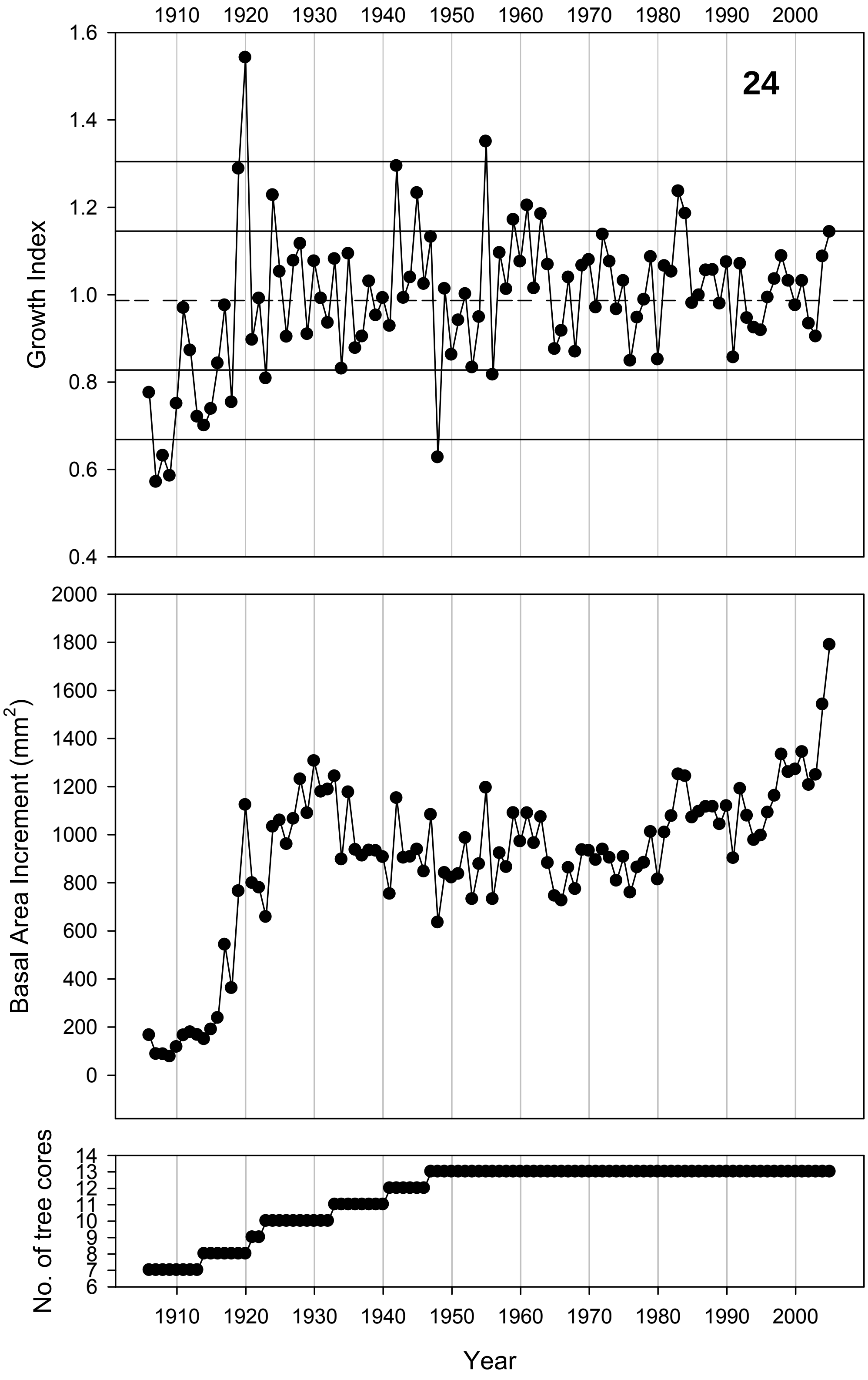

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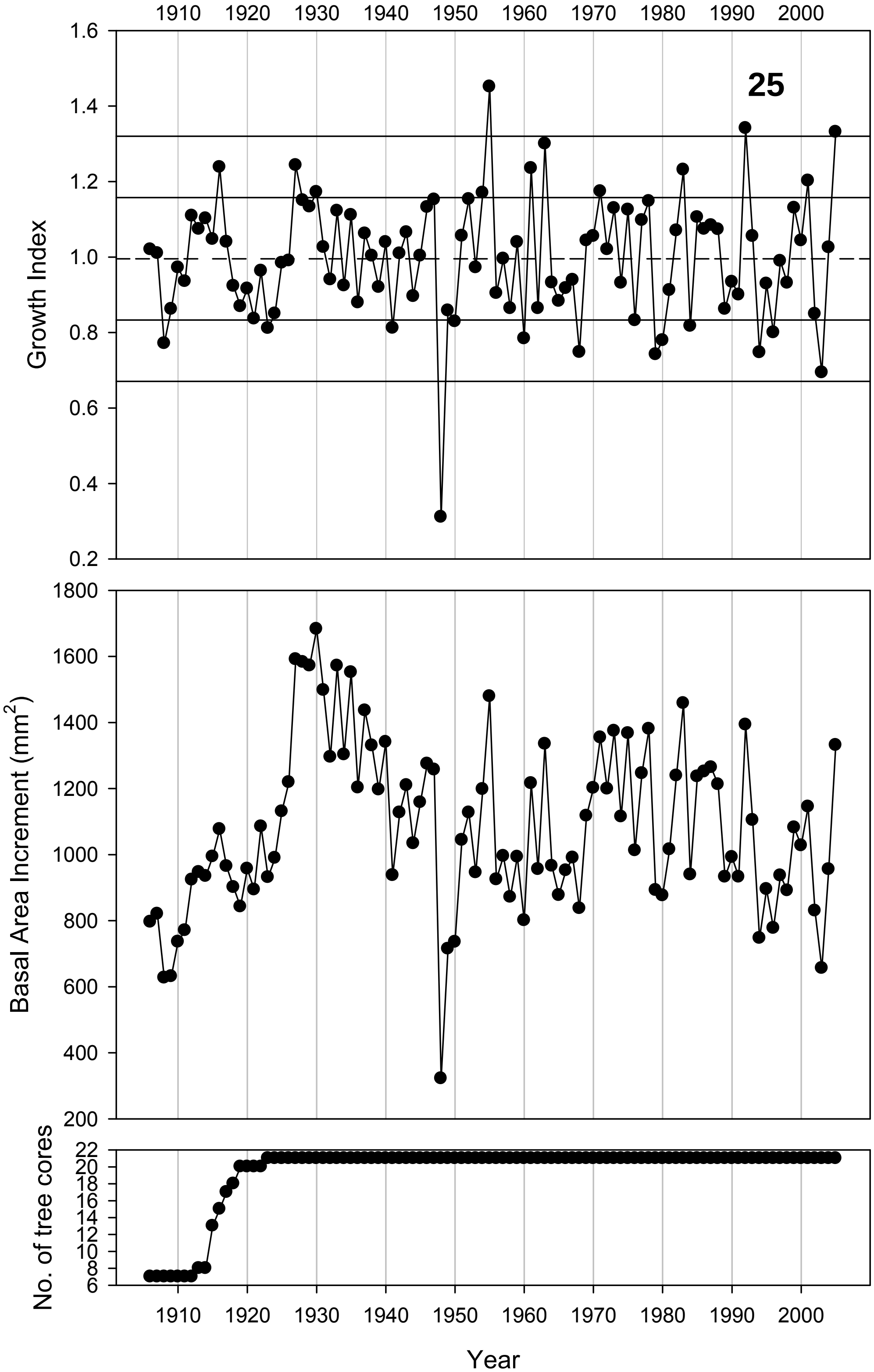

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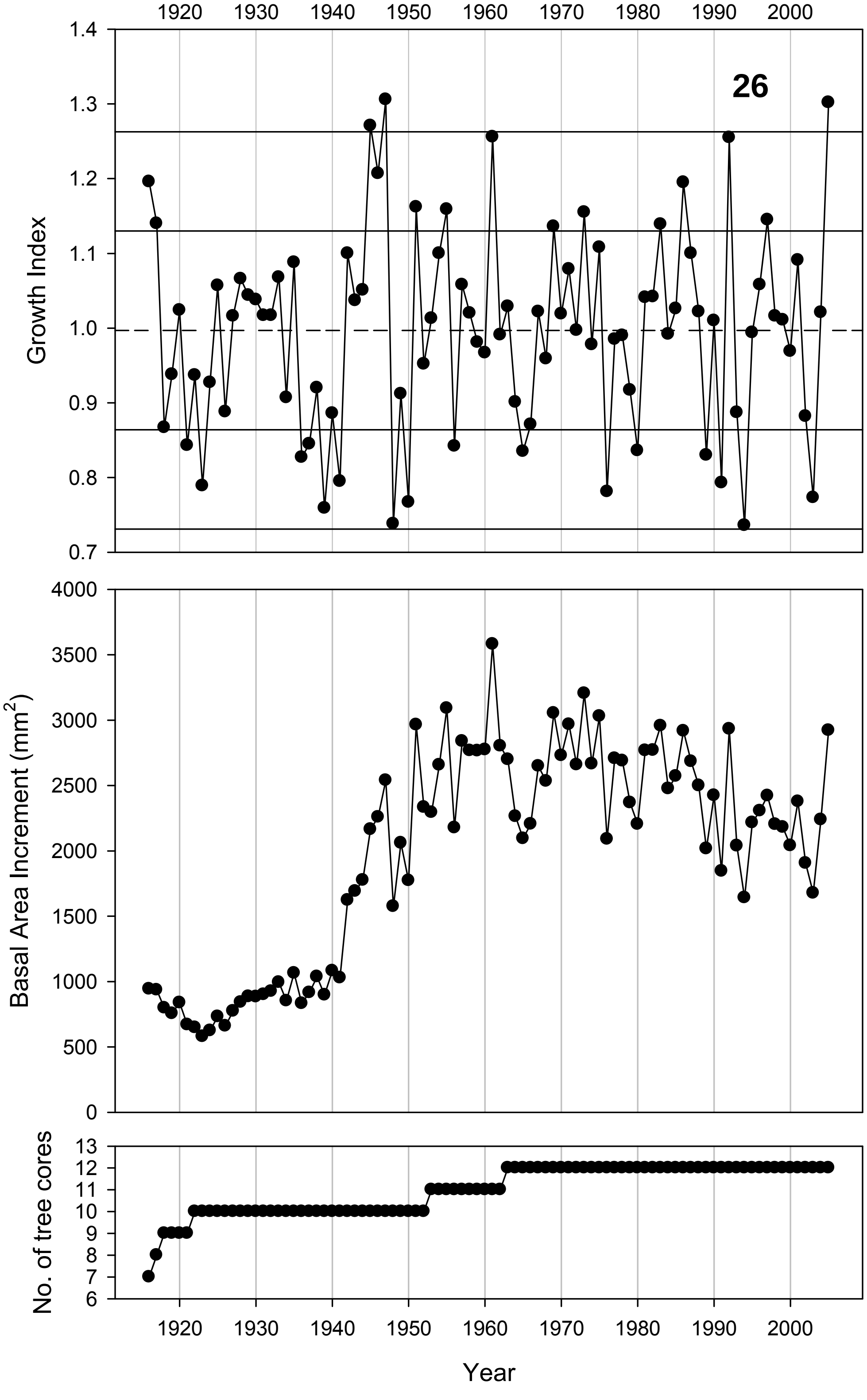

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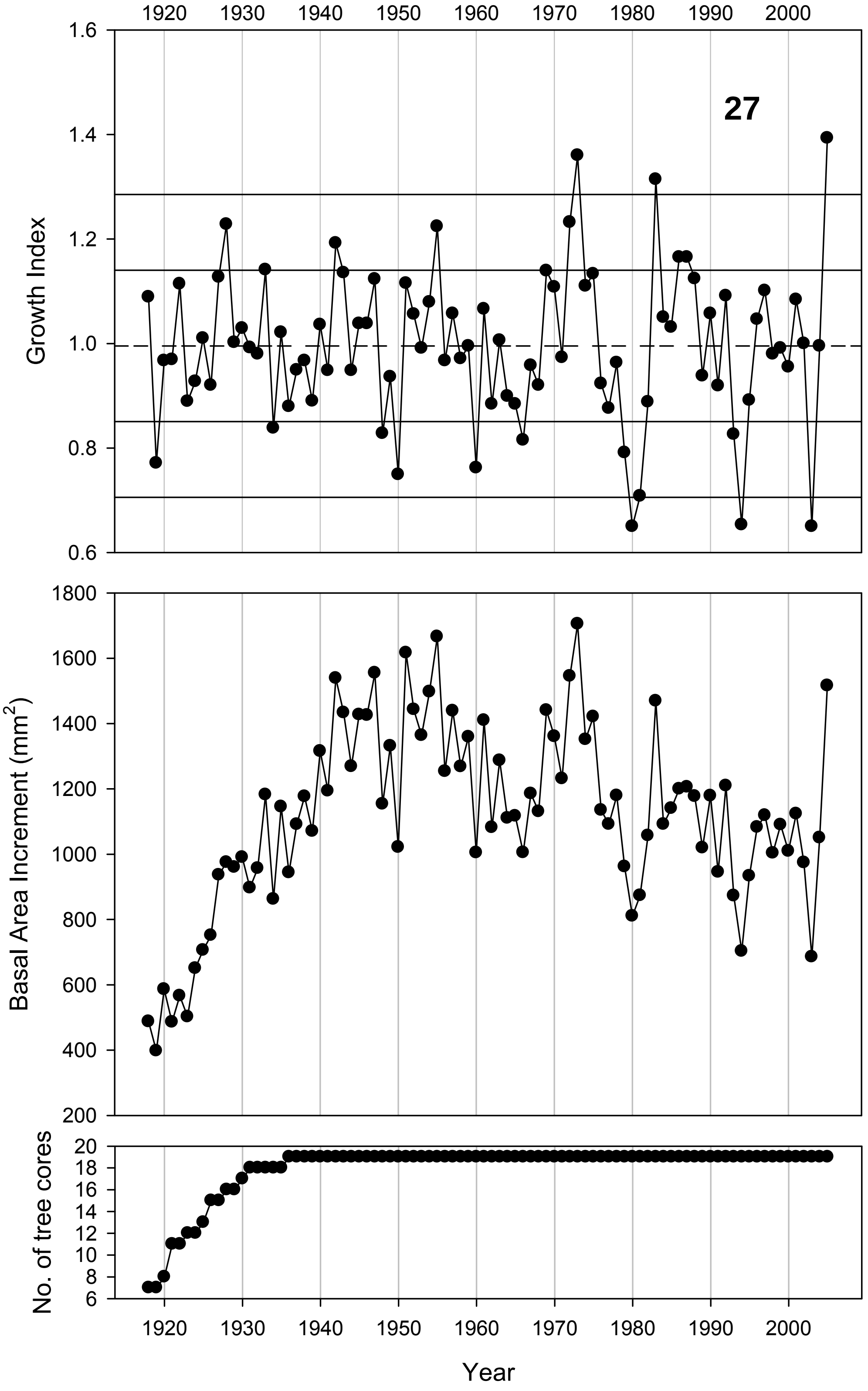

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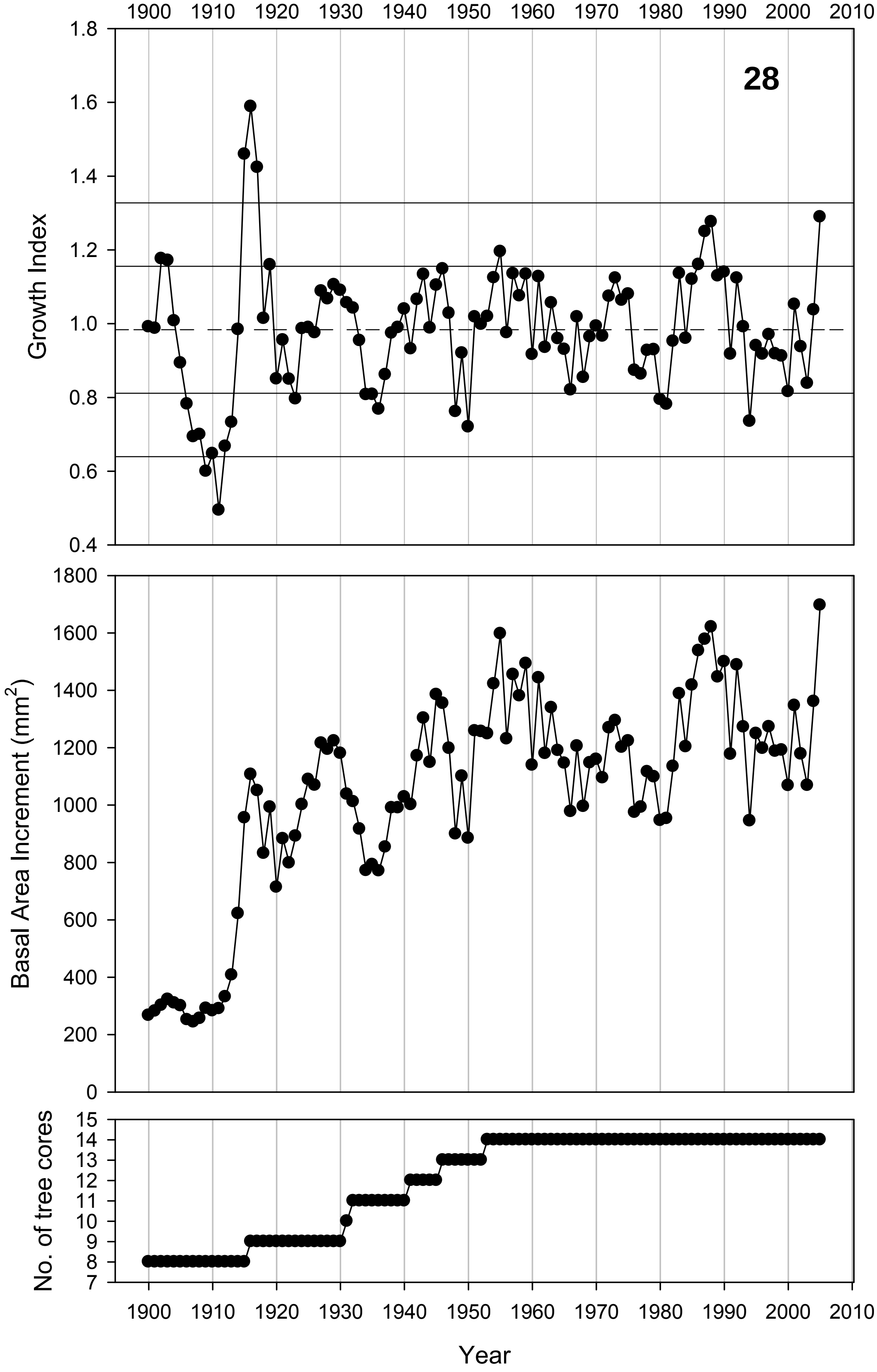

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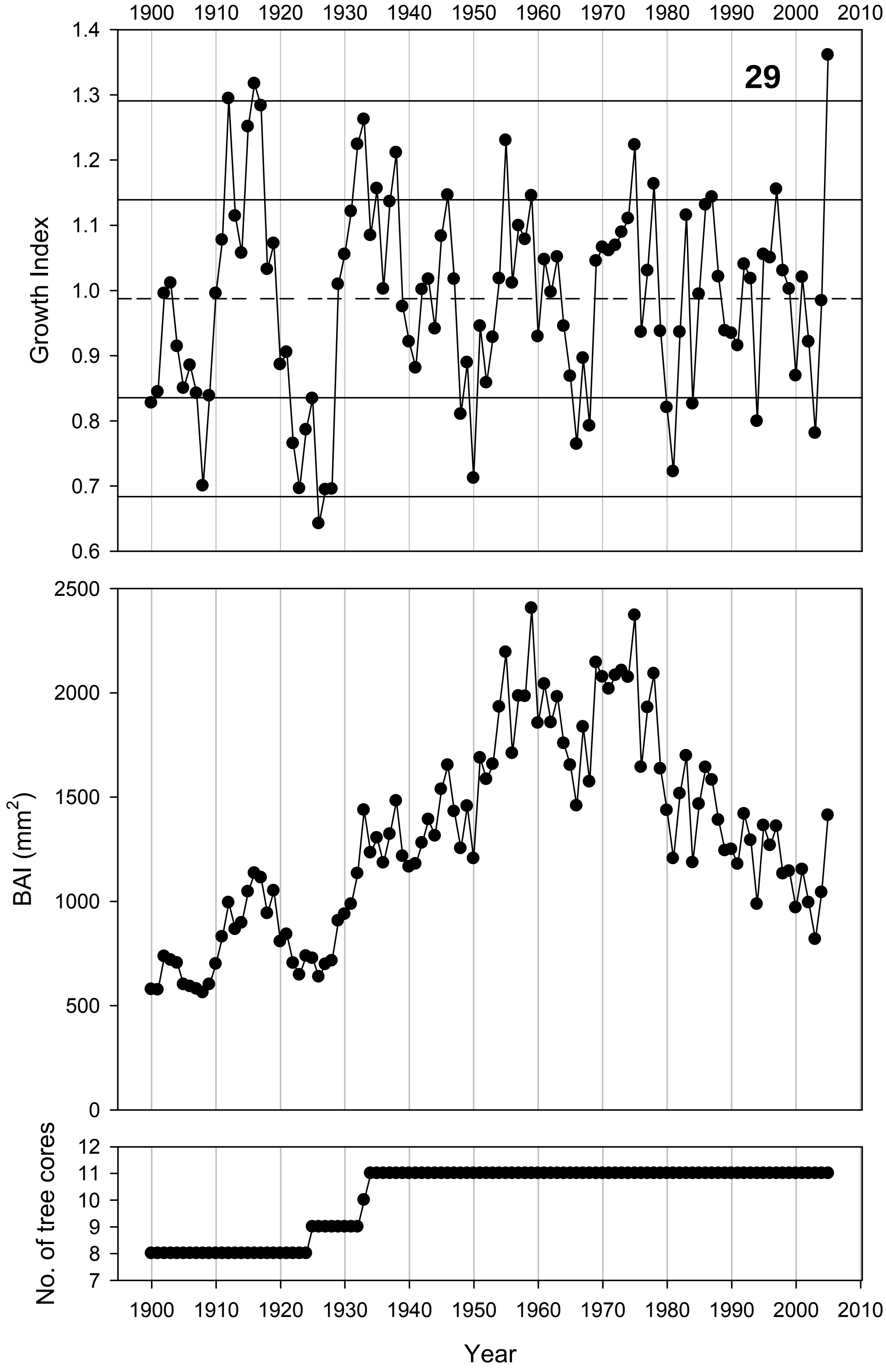
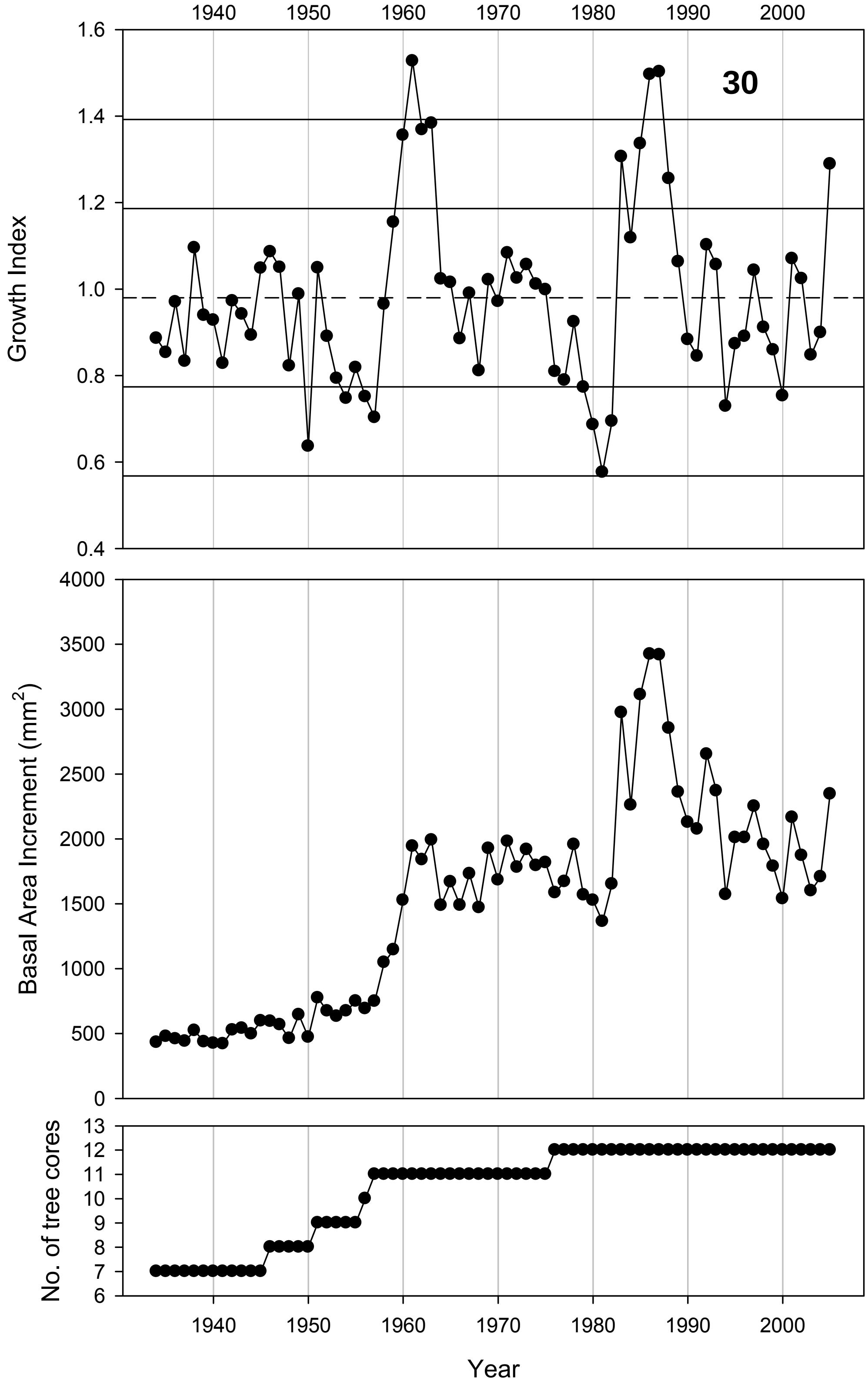


Figure A.1 continued.



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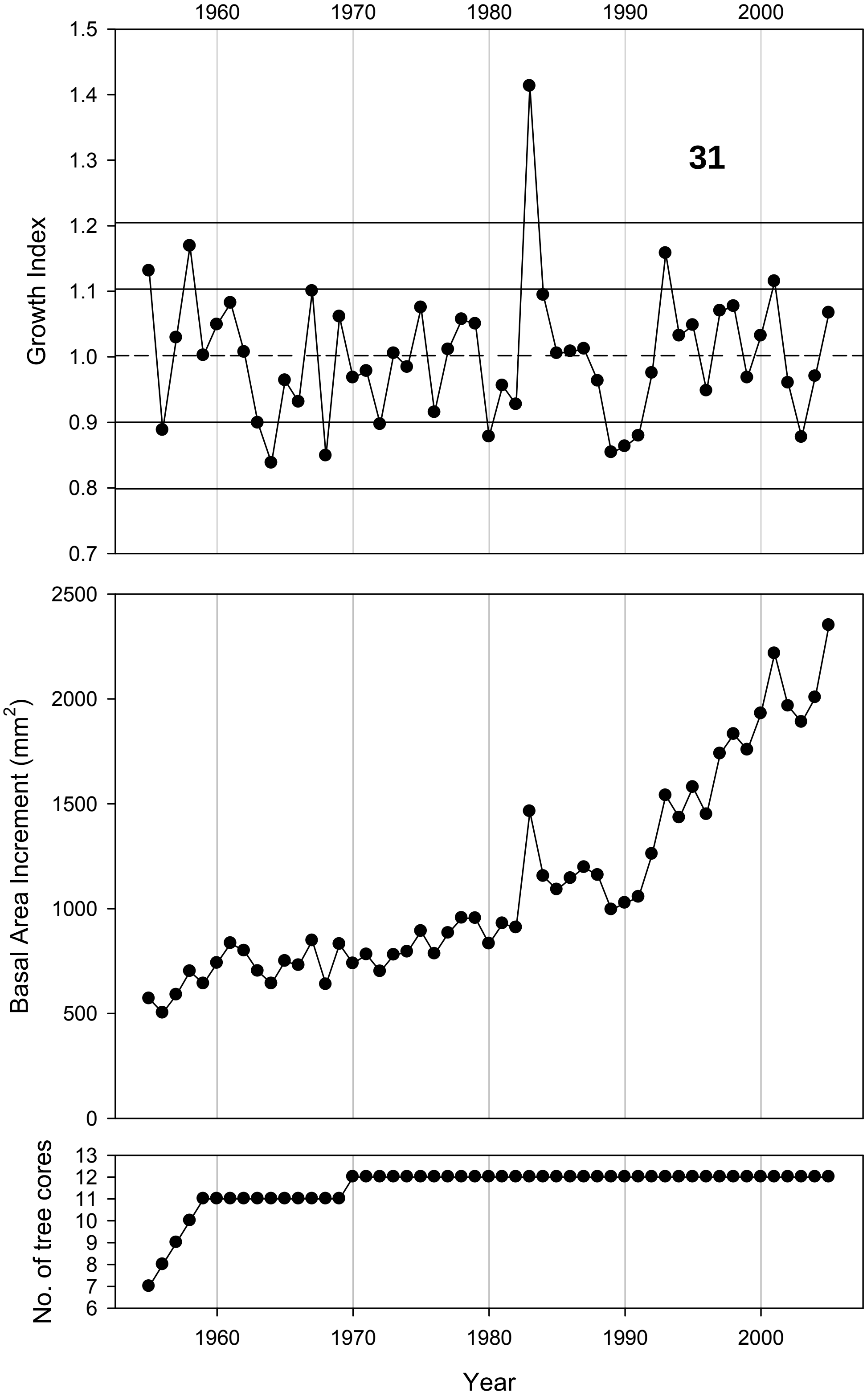

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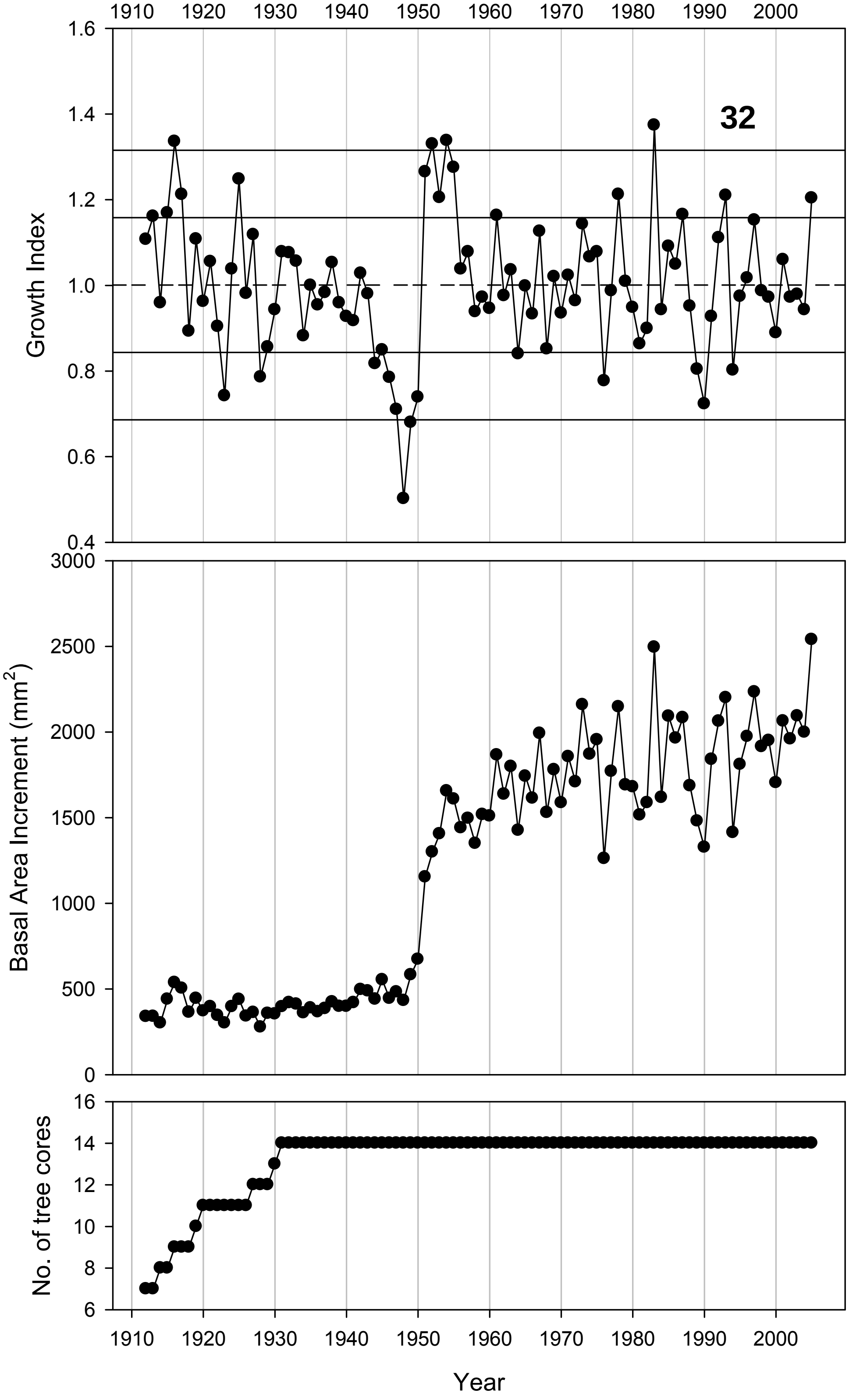

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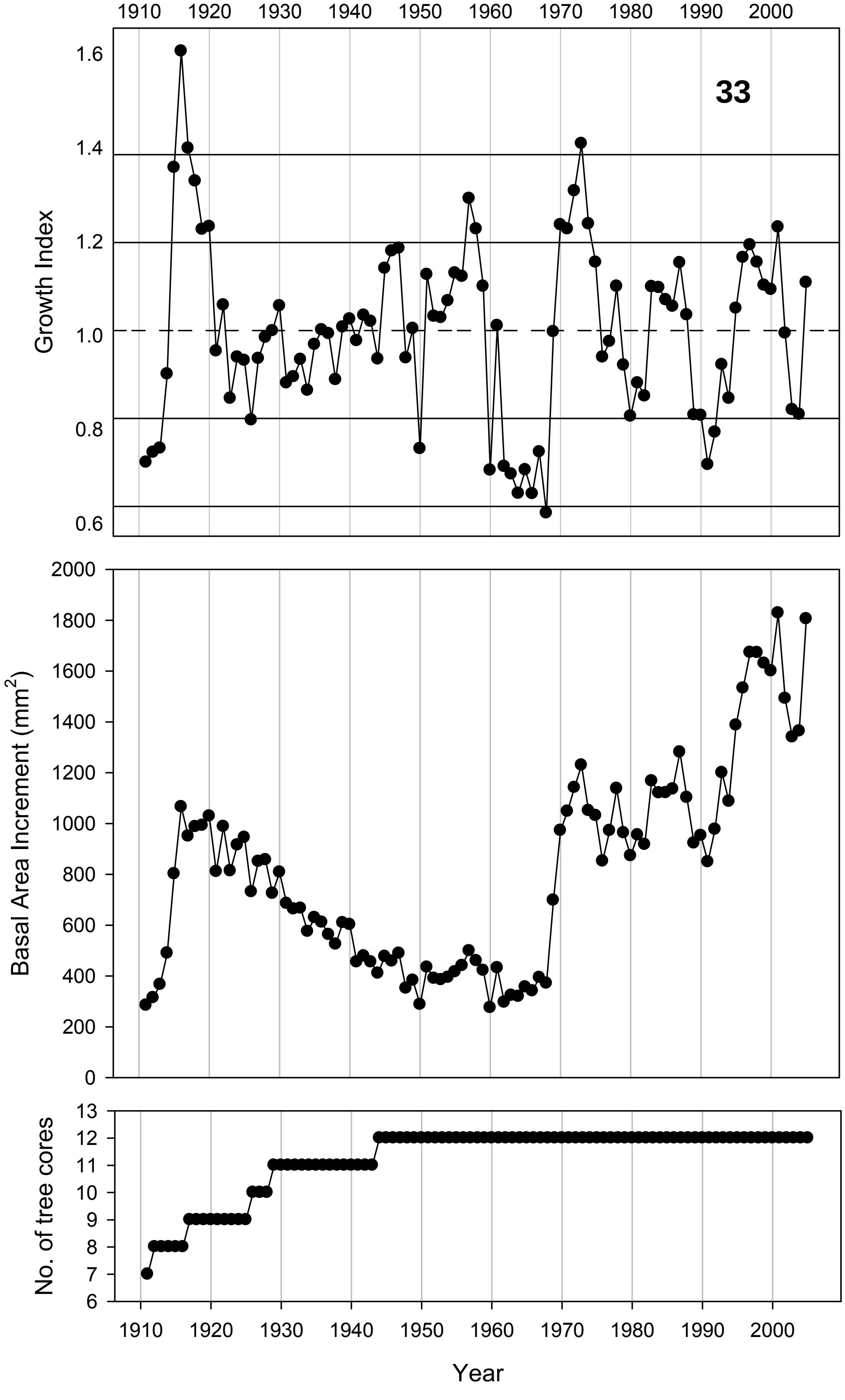

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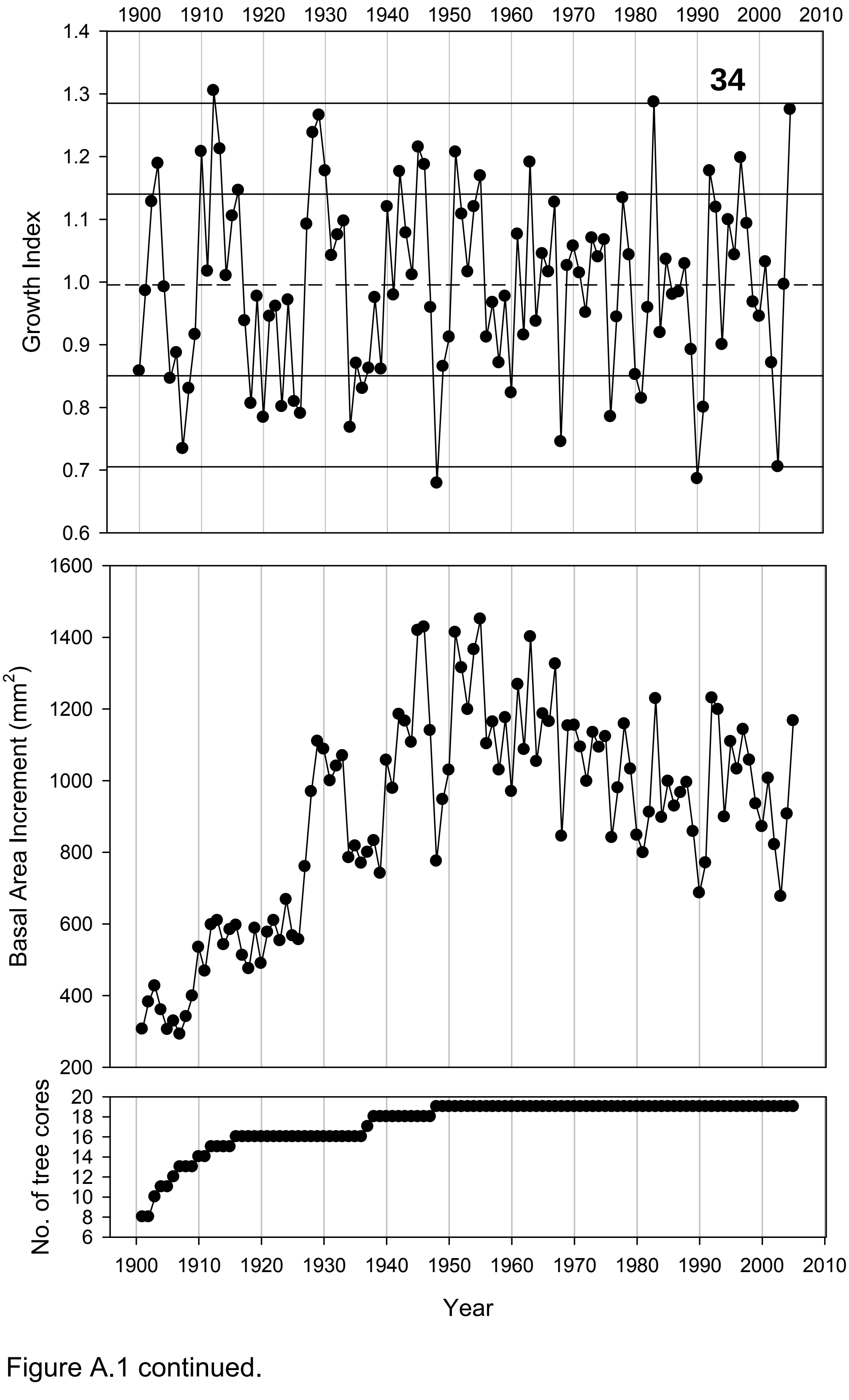

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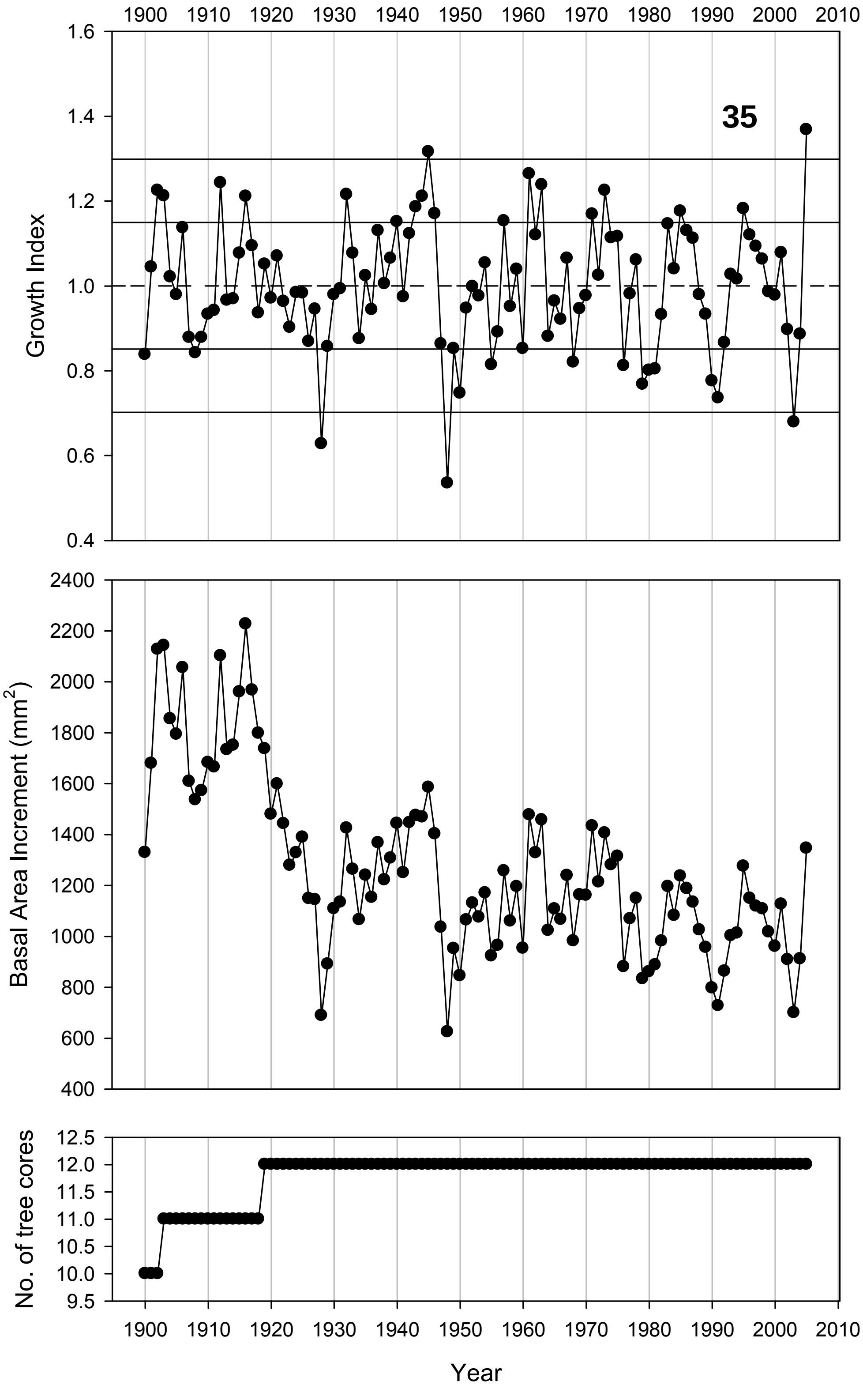

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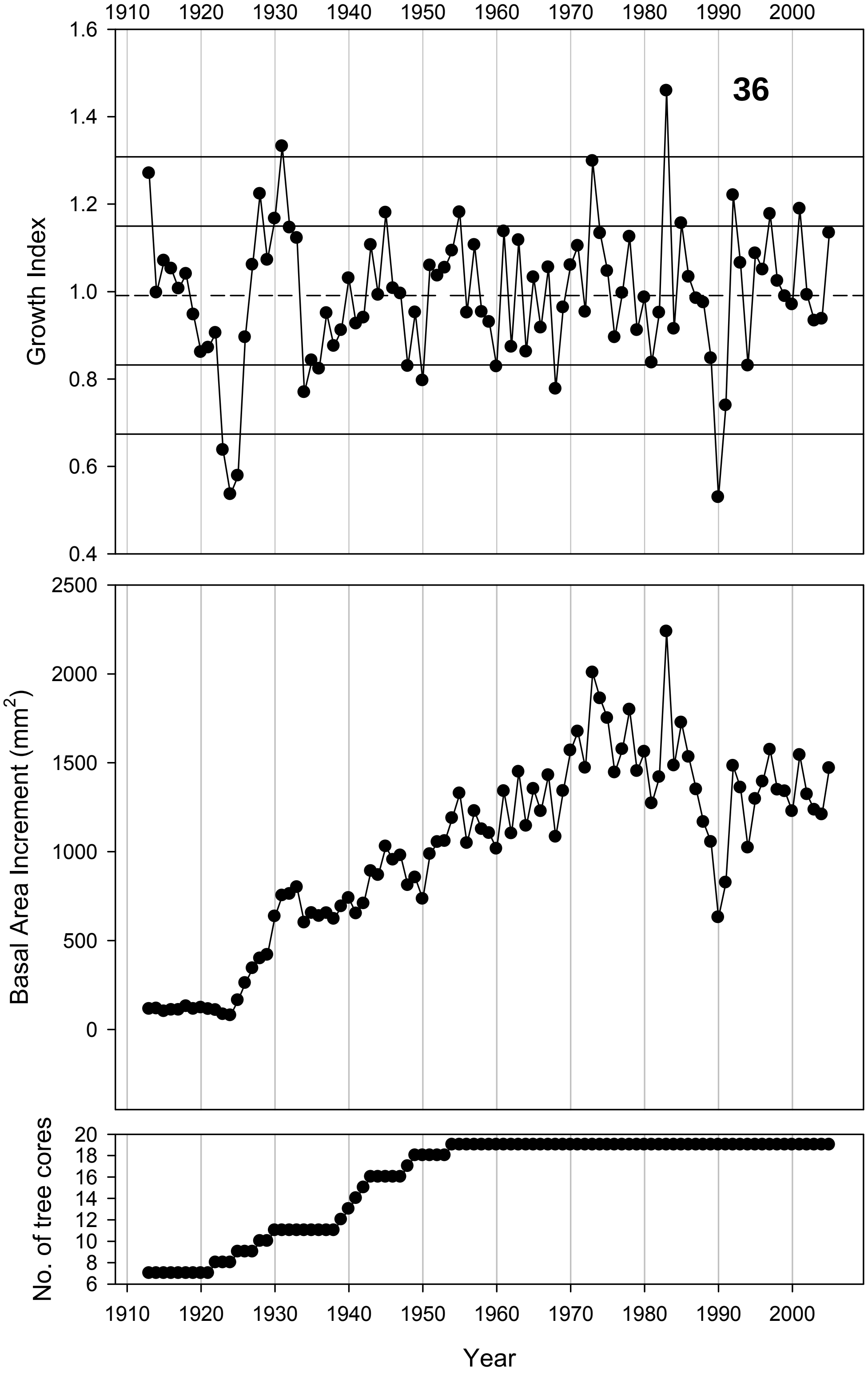

Figure A.1 continued.

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**Table A.1. Significant climate response coefficients by plot.** Capital letters indicate temperature (T) and precipitation (P) for monthly climate variables from the previous year. Lowercase letters indicate current year climate variables.

| Plot | JUN T | JUL T | AUG T | NOV T | DEC T | feb t | mar t | may t | jun t | sept t | JUL P | AUG P | DEC P | mar p | jun p | jul p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 M | -0.14 | -0.15 | | | | 0.15 | | | | | 0.16 | | | | 0.17 | 0.18 |
| 1 m | | | | | | 0.17 | | | | 0.21 | 0.19 | | | | 0.27 | 0.19 |
| 2 m | -0.23 | -0.18 | | | | | | | | 0.19 | | | | | | 0.18 |
| 3 M | | | | | | 0.3 | | | | | | | | | | |
| 3 m | | | | | | 0.28 | | | | | | | | | | |
| 4 M | -0.2 | | | | | | | | | | | | | | 0.13 | |
| 4 m | | | | | | | | | | | | | | | 0.18 | 0.2 |
| 6 M | -0.16 | | | | | | | -0.17 | -0.18 | | | | | | | |
| 6 m | -0.19 | -0.14 | | | | | | -0.17 | -0.18 | | | 0.15 | | | | |
| 7 M | | -0.18 | | | | | | | | | | | | | | |
| 7 m | | -0.17 | | | | | | | | | | | 0.22 | | | |
| 8 M | | | | | | | | | | | | | | | | |
| 12 M | | | | | | | | | | | | | | -0.19 | | |
| 12 m | | | | | | | | | | | | | | -0.2 | | |
| 13 M | | -0.19 | | | | 0.22 | | | | | | | | | | |
| 13 m | | -0.22 | | | | 0.19 | | | | | | | | | | |
| 15 M | | | | 0.16 | | | 0.19 | | | | | 0.18 | | | | |
| 17 M | | | | | | 0.17 | | | | | | | | | | |
| 17 m | | | | | | 0.14 | | | | | | | | | | |
| 18 m | | | | | | 0.15 | | | | | | | | | 0.16 | |
| 19 M | | | | | | | | -0.21 | | | | | | | | |
| 19 m | | | | | | | | | | | 0.2 | | | | | |
| 20 M | | | | | | | -0.26 | | | | | | | | | |
| 21 M | -0.27 | -0.15 | | 0.16 | | 0.18 | | | | | | 0.17 | | | | |
| 21 m | -0.17 | | | | 0.15 | 0.17 | | | | | 0.17 | 0.18 | | | | |
| 22 M | -0.21 | | | | | | | | | | | | | | | |
| 23 M | | | | | | | 0.25 | | | | | | | | | |
| 23 m | | -0.17 | | | | | 0.24 | | | | | | | | | |
| 24 m | | | | | | | 0.14 | | | | | | | | | |

Table A.1 Continued

| Plot | JUN T | JUL T | AUG T | NOV T | DEC T | feb t | mar t | may t | jun t | sept t | JUL P | AUG P | DEC P | mar p | jun p | jul p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 25 M | | -0.2 | -0.21 | | | 0.17 | | | | | 0.22 | | | | | |
| 25 m | | -0.27 | | | | | | | | | 0.28 | | | | | |
| 26 M | -0.21 | | -0.21 | | | | | | | | | | | | | |
| 26 m | -0.19 | -0.14 | -0.22 | | | | | | | | | | | | 0.18 | |
| 27 M | | | | | | | | | | | | | | | 0.21 | 0.18 |
| 27 m | | | | | | | | | | | | | 0.18 | | 0.27 | 0.19 |
| 28 M | | -0.25 | | | | | | | | | | 0.16 | | | | |
| 28 m | | -0.19 | | | | 0.15 | | | | | | 0.17 | | | | 0.16 |
| 29 m | | | | | | | | | | | 0.2 | | | | | |
| 30 M | -0.27 | -0.21 | | | | | | | | | | | | | | |
| 31 m | | | | | 0.22 | | | | | | | | | | | |
| 32 M | -0.15 | | | | | | | | | | | | | 0.21 | | |
| 32 m | | -0.23 | | | 0.15 | 0.14 | | | | | | | | 0.16 | | |
| 33 M | | | | | | | | | | | | | 0.15 | | 0.3 | |
| 33 m | | | | | | 0.16 | | | | | 0.25 | | 0.16 | | 0.27 | |
| 34 M | | | | | | | | | | | | 0.15 | | | | |
| 34 m | | -0.17 | | | | | | | | | | 0.18 | | | | |
| 35 M | | | | | | | | | | | 0.21 | | | | | 0.19 |
| 35 m | | | | | | | | | | | 0.23 | | | | | 0.19 |
| Master M | -0.18 | -0.16 | | | | 0.19 | | | | | | | | | | 0.15 |
| Master m | | -0.23 | | | | 0.18 | | | | | 0.22 | 0.16 | | | | 0.17 |

# BIOGRAPHY OF THE AUTHOR

Sophia DeMaio grew up in Westfield, Maine where she came to appreciate trees along with her family, friends, pets, and neighbors. She attended Westfield Elementary School and graduated from Presque Isle High School. Sophie completed a B.S. in Environmental Studies at Bates College in Lewiston, Maine, where she took every opportunity to travel. After graduating from college, Sonia spent a year teaching English in Chita, Russia. She worked in Rockland and for Tanglewood 4H Camp and Learning Center in Lincolnville, Maine before returning to Siberia with the Tahoe-Baikal Institute in 2005.

She began her master’s degree in the department of Forest Ecosystem Sciences at the University of Maine in the fall of 2005. While in the program, Sophie worked as a teaching assistant for Forest Biology and as a technician, helping to establish a forest restoration study on the Penobscot Experimental Forest in Bradley, Maine. She also volunteered for the newly created Wade Natural Resources Committee. She is a member of the Forest Guild and Society of American Foresters and received the Helen Belyea Blumenstock award in 2006. She is a candidate for the Master of Science degree in Forestry from the University of Maine in May, 2008.