Chronological Change in

Old-Growth Forests of the Chicago Region

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Abstract

Despite strong evidence for canopy closure and successional replacement of oak by sugar maple in Chicago region forests, no studies have documented such changes using chronological data from tree rings, nor have they compared rates of change among different stand types. Central questions addressed in this study are whether forest canopies were more open in the 1800s, whether canopy processes have changed over time, and whether accession into canopy gaps has shifted from oaks in the 1800s to non-oak species, primarily maples, in the 1900s. To provide this information, we analyzed change in tree growth from tree rings cored in 1997 and 1998 from 24 forest stands thought to have either undisturbed or lightly disturbed canopies representing maple, red oak, and white oak stand types in the Chicago region. We also compared growth among these stand types with four savanna stands, testing the hypothesis that oak stands were more open and had growth rates similar to savannas in the 1800s.

There were 27 occurrences of pre-1810 trees among 11 sites. White oak had the greatest number, 17, and the oldest recorded tree, which originated in 1687. Sugar maple was the second most abundant pre-settlement tree, with four individuals. There were two pre-1810 bur oaks and shagbark hickories, and a single swamp white oak. The greatest concentrations of these trees occurred at Lloyd Woods, which had 4 maples and 2 white oaks, and at St. Francis Woods, which had five white oaks. None of the stands may represent completely undisturbed forests. However, stands developed under canopy gap processes that may represent either old growth or lightly disturbed conditions included 89 % of the maple stands, 71 % of the white oak stands, and only 50 % of the red oak stands. The remaining stands (about 30 %) appear to have completely regenerated following disturbance in the early to mid 1800s.

Growth in more than half of the stands was significantly correlated with the Palmer Drought Severity Index during the 1895-1998 period, and growth among many stands was also highly correlated, indicating a landscape-scale climatic effect on tree growth. However < 30 % of the variation was accounted for by drought severity, indicating that other factors had strong effects on tree growth. Variability in growth among stand types, as indicated by the Coefficient of Variation, was low in savannas and in oak forests during the 1800s, but high and more stable in maple forests. This suggests more uniform growth under open canopies occurred in oak forests in the 1800s. Mean growth rates were also higher in savannas, but did not strongly differ between oak and maple forests, which partially supports a canopy closure hypothesis. Responses to canopy gap process differed among white oak, red oak, and maple species groups, with oaks having greater direct accession into canopy gaps, and maples having greater releases into gaps from suppressed understory conditions. Among all stand types, the greatest number of canopy accessions occurred between 1850-1899, with more responses by oaks than maples. However, maple dominated stands also had substantial maple regeneration during that period. Over time, there was a shift from direct establishment of trees into canopy gaps toward more gap releases of trees that had been suppressed in forest understories. These results support a hypothesis that oak forest canopies have gradually become more closed. Nevertheless, canopy gap processes were operating in oak forests in the 1800s, and also allowed oaks to access canopies of maple stands during that period.

An important implication for management and restoration drawn from this study is that although oak and maple stands had more open canopies in the 1800s, presumably due to landscape fire, they also operated under canopy gap processes. However, oak regeneration into canopy gaps was far more common than that of maple. Forests of today appear to have greater canopy cover, with gap access almost restricted to non-oak species. Research is needed to understand whether restored fire processes that reduce non-oak species, primarily maple, will allow oak regeneration into canopy gaps in these forests.

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INTRODUCTION

Oak (*Quercus*) forests are well known for their dependence upon fire (Abrams 1992). A critical problem for Chicago region oak forests is that elimination of fire following European settlement appears to be causing canopy closure, sugar maple (*Acer saccharum*) invasion, loss of oak regeneration and decline in biodiversity (Bowles et al. 2000). It is also thought to be leading to more mesic conditions though reduction of evapotranspiration as canopy cover succeeds to maple dominance, a process termed "mesophication" (Nowacki & Abrams 2008). Based on compositional studies of remaining old-growth forests in the CW region, as well as pre-settlement forests (http://www.greenmapping.org), there is ample evidence of former oak dominance, maple invasion and lack of oak generation (Bowles et al. 2003, 1994, 2005). These changes also appear to be occurring at different rates among stand types, with a slower rate in white oak (*Quercus alba*) dominated stands, an intermediate rate in red oak stands, and earlier or more rapid change in maple dominated stands (Bowles et al. 1994, 2005). Because of these ongoing changes, management of Chicago region forests and woodlands has focused on restoring fire processes and vegetation structure (e.g. Chicago Region Biodiversity Council. 1999). However, no studies have provided specific information about progressive changes in the canopy characteristics of Chicago region forests, nor have chronologies of stand structural and compositional change been established and compared among stand types.

Because this information is lacking, there are unanswered questions and unresolved issues about oak forests. For example: Have tree canopies become closed over time? What types and rates of tree recruitment occurred in the 1800s as compared to the 1900s? Has tree recruitment become restricted to canopy gap releases of shade tolerant advance regeneration that persists in forest understories? Have such changes differed among forest stand types? Answers to these questions are needed to help resolve issues about forest management, such as whether oak forests should be managed for more open canopy conditions, and whether maple dominated stands should be managed for oak regeneration.

A standard approach used to gain information about chronological change in forest stand structure and composition is tree-ring analysis of growth rates of dominant or invading tree species, and linkage of this information with timing of events of tree recruitment and stand disturbance, (e.g., Abrams et al. 1995, Abrams & Orwig 1996), as well as climatic variation (e.g., Abrams et al. 2000, Rubino & McCarthy 2000). Tree cores, which allow non-destructive measurement of growth-rings, provide the means for tree ageing and analysis of their growth rates (Sheppard & Cook 1988). In this study, we analyze tree cores from almost 600 trees growing in 24 old-growth or lightly disturbed forest stands in the Chicago region of northeastern Illinois. These cores were collected during a forest re-inventory funded in 1996 by the Chicago Wilderness. As described above, that project documented lack of oak reproduction and provided evidence for different rates of change across stand types dominated by white oak, red oak (*Quercus rubra*), and maple (*Acer saccharum*) (Bowles et al. 2000, 2005). This project is an extension of that work, and is designed to further elucidate historic information about these forests.

Project Goals and Objectives:

Our goal was to use tree-ring analysis to understand historic development of the Chicago region high quality or old growth forests and to compare this information with expected changes caused by loss of historic fire processes and other impacts. We also sought to determine stand level histories of development, and to assess the degree to which stands represent old-growth conditions and how their growth rates have responded to past climatic effects (primarily drought severity).

The basic questions guiding this research were whether old-growth forest trees developed under formerly open tree canopies in the early 1800s, how their canopies have changed over time due to post-settlement fire exclusion, and whether the rates of such changes differ across different forest types. Given this canopy closure hypothesis, expected change can be quantified and tested in several ways. First, average tree growth would be greater in open savanna conditions than in forested conditions because of the reduced amount of light available for tree growth under a forest canopy (McEwan & Mcarthy 2008). As a result, we would expect growth rates in sites that are now forests to be have been similar to those of savannas in the 1800s, and greater rates of growth in modern savannas than in modern forests. Second, variance in tree growth would be expected to be lower in savanna than in forest because of differences between exogenous (external) and endogenous (internal) canopy processes (Guyette et al. 2006). For example, savannas undergoing exogenous stand-scale fire processes would be expected to have uniform levels of synchronized tree growth with low variation among trees. In contrast, forest stands undergoing endogenous canopy processes would be expected to have more variable rates of tree growth as trees respond individualistically to randomly formed canopy gaps. We would expect variance in tree growth in sites that are now forests to have been similar to that of savannas in the 1800s, and greater variance in tree growth in modern forests than in modern savannas. Finally, if these changes have taken place, they also may vary among stand types. For example, most research indicates that rates of maple invasion and loss of oak regeneration have been slowest in white oak stands, and intermediate in red oak stands (Bowles et al. 2005), suggesting the lowest rate of canopy closure in white oak stands.

Analysis of tree growth rates as shown by variation in their tree-ring widths over time can be a guide to these changes. For example, because oaks are known to respond quickly to increased light from canopy gap openings, their average ten-year growth rates (radial growth averages) have been shown to be sensitive to changes in canopy conditions (Nowacki & Abrams 1997). Moreover, growth increases of 100% for at least 15 years usually indicate a major canopy disturbance in forests (Lorimer & Frelich 1989), which may be linked with pulses of tree establishment or canopy recruitment (Abrams et al. 1995). Likewise, a significant decline in growth would indicate canopy closure. In addition, ages and growth rates of fire-sensitive sugar maple can be used to document the timing of change in fire processes for these stands. In comparison, we would expect more uniform growth rates among canopy trees of old growth savannas where canopy gap processes have not developed. Finally, climatic variation is a well-known factor controlling tree growth, and both precipitation and drought can affect growth of white oak (Rubino & McCarthy 2000). As a result, climatic variation may affect tree growth rates in Chicago region forests and interact with canopy processe.

Our project goals were 1) to use tree-ring analysis to help understand historic development of Chicago region forests that appear to have been essentially undisturbed after settlement, 2) to compare this information with expected changes caused by loss of historic fire processes, and 3) to apply this information to management of forest vegetation. Project objectives included:

1) Prepare and maintain an archival tree-ring collection for research use. Represent old growth forest stand types, as well as replicate old growth savannas.

2) Develop a digital database of individual tree growth measured from the tree-ring collection.

3) Determine whether tree growth rates have changed over time in relation to hypotheses that predict

a) decreasing tree growth rates with closing canopy cover.

b) increasing variance in tree growth as stands shift toward canopy gap processes.

4) Characterize stand-level chronologies of structural and compositional change by

a) linking canopy processes, as shown by change in tree growth rates, with periods of tree recruitment and historic human events and

b) correlating tree growth rates with climatic variation.

5) Compare results among stand types, testing a hypothesis of earlier or more rapid rates of change in canopy cover, composition, and stand structure in maple stands; intermediate rates in red oak stands; and slower change in white oak stands.

Study area

The Chicago region occupies the most recently glaciated portion of Illinois, and comprises three natural divisions (Figure 1). The Lake Plain Natural Division represents the former glacial lake bed of Lake Michigan, and was primarily grassland, but also contained sand dunes and sand savanna along Lake Michigan. The Morainal Natural Division occurs on a series of concentric moraines and outwash plains left by Woodfordian glaciation, and extends west from the lake plain. Most of the region's savannas and forests occurred in this natural division. The Grand Prairie Natural Division occupies older and more level glacial drift extending beyond the Morainal Natural Division, and was primarily grassland. Forests in the Chicago region were originally restricted to fire protected habitats, usually on the east sides of water courses or along rugged morainal topography (Bowles et al. 1994). These forests were dominated by oaks, with fire intolerant maple present but sub-dominant in habitats receiving the greatest degree of fire protection. Entry of European settlers into the region occurred in the first decade of the 19^{th} Century, following an 1804 Indian treaty. However, settlement was restricted due to interactions with American Indians. Settlement began to escalate in 1832, after the Black Hawk War, and disruption of natural fire processes, as well as disturbance of forest stands, probably began to increase after 1840. In 1976, the Illinois Natural Areas Inventory (INAI) identified 28 high quality forest stands in this region and classified them based on canopy structure, age and size class distribution (White 1978). Grade A forests represented essentially undisturbed old growth conditions, with trees exceeding 120 years old. Grade B forests represented former old growth conditions that had been altered, such as by selective logging or by natural disturbance such as wind. By this definition, grade A stands would contain all older size classes, while Grade B stands would be missing one or more size classes in which some older size classes are missing due to human disturbance such as selective logging (White 1978). By this process, Grade B stands would have canopy and sub-canopy trees that had developed under the influence of former old growth canopy structure.

METHODS

Data collection and processing

Core Collection

Approximately 600 tree cores used in this study were collected in 1997-98 from 24 of the high quality forests identified by the INAI (Figure 1, Table 1). These cores were collected from trees occurring in 0.025 ha plots located along transects established by the INAI, and therefore represent a sample of the size class distribution present for species present within stands (Bowles et al. 2000). All cores were aged by counting (but not measuring) rings, and then stored for later use. The forest stands are dominated either by sugar maple, red oak, or white oak, which represent about 65 % of the sample cores (Table 2). Over 40 % of these cores were taken from trees greater than 50 cm dbh, most of which originated before 1900 (Bowles et al. 2005, Jones et al. 2006). Compositional and structural data were collected from these stands in 1976 and in 1996 (Bowles et al. 2000, 2005), which allowed determination of tree species recruitment at different time periods based on their age-dbh relationships. We also collect additional tree cores from four replicate old growth savannas, in which we assume that lack of canopy closure would result in more uniform rates of tree growth than in forest stands. These stands included a maple dominated savanna at McDowell Grove, DuPage Co., Ill. (N = 4 cores, 1854-1919), a white oak-dominated savanna at Silver Springs State Park , Kendall Co., Ill. (N = 4 cores, 1841-59), and bur oak dominated savannas at Spring Creek Forest Preserve, Cook Co., Ill. (N = 5 cores, 1856-1915), and at Bluff Springs Fen Nature Preserve, Cook Co., Ill. (N = 4 cores, 1833-69) No old growth red oak savannas were available for sampling.

Core processing, measuring and ageing

All tree cores were sanded with progressively finger grades of sand paper ranging from 80-400 grit to reveal tree-ring cell structure (at 40 x magnification), and glued to poplar mounting stocks following specifications in Stokes & Smiley (1968). All cores are maintained at The Morton Arboretum.

Standard procedure for analyzing tree cores is first to establish the age of the cored tree and to assign an exact year to each tree-ring (Sheppard & Cook 1988). Consecutive ring widths were measured to 0.01mm for each tree core using a 10-20 x stereo microscope mounted on a VELMEX unislide stage, ACU-RITE linear encoder and Quick-check digital readout (http://www.velmex.com) developed for measuring tree-ring widths. All measurement data were digitally processed using MeasureJ2X tree-ring measuring software (http://www.voortech.com/projectj2x). This allowed assignment of exact years to each measured tree ring.

Data processing

To compare stand level changes in growth over time, raw and standardized growth chronologies were developed for each stand. Ring widths for trees > 100 years old (dating to <1896) were first averaged into a single raw stand chronology representing average tree growth per year. To overcome temporal variability in tree growth, the raw tree-ring chronologies were detrended through conversion to a standardized index of relative growth (Fritts 1976). This was accomplished by computing a straight-line trend equation through Ln-transformed data using a standard least squares technique in which the dependent variable is the time series. The detrended series consisted of the ratios of each residual to the predicted value and adjusted to a mean of 1.0. These standardized metrics may be advantageous for correlations with long-term climatic data because they reduce the effect of local disturbances on tree growth (Sheppard & Cook 1988).

Data analysis

Stand-level data analysis

To assess climatic effects on tree growth, the raw ring width chronologies and standardized indices of each stand were correlated with the Chicago region Palmer Drought Severity Indices (PDSI) that represented monthly means for each year between the years 1895-1996 (http://www.drought.noaa.gov). The PDSI ranges from < - 4 to 4, with negative values representing increasingly severe drought, and positive numbers reflecting increasing levels of precipitation. Indices had similar correlations to those of raw chronologies and were used for further analysis. We used Analysis of Variance in a General Linear Model to test whether the relationship between PDSI and tree growth indices differed along the maple-red oak-white oak habitat gradient, and whether it had might have changed over time. In this test, the performance variable was the r-sq values between PDSI and each stand growth index, and factors were stand types and the 1896-1949 and 1949-1998 time intervals.

The developmental history of each stand was analyzed in several ways. Ages of cored trees were used to establish stand antiquity, as well as dates for stand initiation or invasion. We used 1810 as a conservative date for ages of trees that pre-date settlement because settlers were present in the first decade of the 19th Century. Growth rates of individual trees were then examined for responses to major canopy disturbances evidenced by 100 % changes in growth lasting for 15 years, following Lorimer & Frelich (1989). Responses are based on published data from white, red, and black oak, which grow at < 1.0 mm/year under canopy shade and respond to canopy openings with growth exceeding 1.0 mm/year (Rentch et al. 2003). These responses were placed into three canopy accession categories following Rentch et al. (2003): 1) origin and persistence in a gap is indicated by continuous average tree growth exceeding 1.0 mm/year; 2) gap origin followed by gap closure is indicated by initial growth exceeding 1.0 mm/year, which is followed by a decline in growth, usually to < 1.0 mm/year; this may be followed by a release indicated by an abrupt 100 % increase for 15 years; 3) canopy gap release indicated by continuous growth at 1.0 mm/year followed by an abrupt 100 % 15-year increase in growth. Maple has similar responses to gap processes, and can be sustained at lower light levels, with growth exceeding 0.5 mm/year thought to represent a release (Canham 1985). This species also develops missing rings when suppressed, which may make accurate aging problematic (Lorimer et al 1999). Although less information is known for other species, we also applied these response criteria to other oak species, as well as elm, hickory, ash, basswood, hickory, maple and walnut. Synchronized responses among trees were used to indicate dates for stand-level disturbances. We placed stands in three categories. We considered stands with multiple pre-1810 trees that underwent both canopy gap origin and gap release processes as Category I (old growth), which would be similar to the INAI Grade A category but would require presence of older age classes, as the INAI used 120 years (originating before 1856) as a threshold for old growth. Category II stands lacked pre-1810 trees but still underwent both canopy gap origin and gap release processes, indicating development under a forest canopy that may have been disturbed by tree removal after settlement. They were assumed to not represent presettlement conditions, and are most similar to the INAI grade B category. Category III stands lacked pre-1810 trees, underwent primarily gap origin processes, and were established following European settlement. The immediate establishment of trees into gaps in these stands, and a lack of early gap release events, would indicate that they originated after large scale human- or naturall-caused disturbances.

We used the Coefficient of Variation to detect change in variation in tree growth that would be associated with changes in canopy condition closure (Guyette et al 2006). At the stand level, the Coefficient of Variation was calculated for each year [CV = (St. Dev/Mean growth)*100], with average values compared at 15-or 25-year intervals. We assumed that periods of comparatively high CV values would be associated with random canopy gap processes, while low CV values would be associated with periods of synchronized canopy access and growth associated with open canopy conditions. This suggests that if meaningful, CV values should be significantly negatively correlated with tree growth at the stand level.

Temporal comparisons among stand types

A repeated measures Analysis of Variance (ANOVA) was used to test whether mean stand CV values differed among white oak, red oak, maple and savannas over time. For this analysis, stand values were averaged at both 15- and 25-year intervals. We used multiple time intervals to insure that statistical significance was not a product of an arbitrary choice of time interval. We expected that savanna stands would have lower CV values than forest stands, and that white and red oak stands would have lower CV than maple stands during the 1800s if they had more open canopies during that period. A significant interaction would indicate a shift in CV values over time. A repeated ANOVA was also used to test whether mean stand growth rates differed among white oak, red oak, maple and savanna stand types over time, with growth rates averaged at 15- and 25-year intervals. We also expected that savanna stands would have greater growth rates that forest stands, and that white and red oak stands would have greater growth rates than maple stands during the 1800s if they had more open canopies during that period. For both tests, we restricted the range of data to > 1824 because sample sizes from the 1700s did not represent all stands.

Species- and stand-level interactions with gap processes

We used the canopy accession framework of Rentch et al. (2003) to examine three separate but related questions concerning a canopy closure hypothesis. First, we asked whether the three dominant species groups (white oak group, red oak group, and maple group) had different canopy accession strategies. The white oak group included white oak (74 % of all cores), bur oak (*Q. macrocarpa*), and swamp white oak (*Q. bicolor*). The red oak group included red oak (85 % of all cores), black oak (*Q. velutina*), pin oak (*Q. palustris*), and Hills oak (*Q. coccinea/ellipsoidalis*). The maple group was primarily sugar maple (95 % of all cores), but included red maple (*Acer rubrum*) Second, we asked whether there had been a temporal shift in initial canopy gap accession events among the white oak, red oak and maple groups. Third, we asked whether there had been a temporal shift in the type of canopy accessions that could be identified by species responses.

To address the first question, whether species group accession strategies differed, we recorded the number of canopy gap accessions by each species group signaled by a 100 % increase or decrease in growth sustained over a 15-year period, placing them within one of three categories: 1) gap origin and gap persistence, 2) gap origin followed by canopy closure, which may be followed by a gap release, or 3) gap release from the understory. Stands were replicates for this test. Because of the presence of zeros, the number of each species canopy accession events was square root transformed after adding 3/8 to all values (Zar 1974) and tested with a nested ANOVA using a General Linear Model

(GLM) in which species, categories and stands were factors. Because of their greater shade tolerance, we expected that the mean number of accession events for maples would be greater for understory gap release events. Because of their greater shade intolerance, we expected that the mean number of accession events for oaks would be greater for gap origin events. A significant interaction between species group and gap and categories in the GLM would indicate these differences.

To address the second question, whether there had been a temporal shift in initial gap accession events among species groups, we recorded their responses to gap events within four time intervals: 1750- 1850, 2) 1850-1899, 3) 1900-1949, and 4) 1950-98. A 100-year interval was used for the first interval because fewer trees were available for analysis for that period. We used 1850 to initiate the second interval because we presume that disruption of fire processes, as well as logging disturbances, became more frequent after this time period. As above, the number of gap release events was identified by a 100% increase in growth sustained for 15 years, and stands served as replicates. The number of species accession events was square root transformed after adding 3/8 (Zar 1974) and tested with repeated measures ANOVA in which species, time and stand types were factors. With a canopy closure hypothesis, we expected that the number of release events by oaks would be greater in the 1800's, with a shift toward greater releases by maples in the 1900s. This would be indicated by a significant interaction among species groups, gap categories and stand types.

To address question three, whether there had been a temporal shift in the type of gap disturbance occurring among stands, we recorded the timing of gap release events by the three previously described gap categories, and placed them within the 1750- 1850, 1850-1899, 1900-1949, and 1950-98 time intervals. As above, stands served as replicates, and the total number of release events was square root transformed after adding 3/8 to all values, and tested with repeated measures ANOVA in which gap release category, time and stand types were factors. With a canopy closure hypothesis, we expected a temporal shift toward a greater average number of understory release events, and fewer canopy accessions through direct gap releases. A significant interaction between species and categories in the GLM would indicate these differences.

RESULTS AND DISCUSSION

Antiquity of trees and stands

Using 1810 or earlier as a basis for pre-settlement trees, we found 26 such occurrences of five species among 11 sites (Table 3). White oak had the greatest number, 17, and the oldest recorded tree, which originated in 1687 in Messenger Woods. However, a bur oak at Pilcher Park may have been older. This tree dated to 1707, but half the distance to the center of the tree was rotted, preventing a measure of its actual age. Surprisingly, sugar maple was the second most abundant pre-settlement tree, with four individuals at Lloyd Woods. A second bur oak occurred at Johnsons's Mound, while a swamp white oak occurred at Messenger Woods. Two presettlement hickories occurred at Thorn Creek Woods. Among sites, Lloyd Woods had the greatest number of presettlement trees, with four maples and two white oaks. St. Francis Woods had four presettlement white oaks, while Messenger Woods, McCormick Ravine and Thorn Creek Woods each had 3 individual trees. The remaining six sites had 2 or fewer presettlement trees. There was no relationship between age and size in these trees (Figure 2).

Stand characteristics

White oak stands

Elburn Forest Preserve contained trees only of post-settlement origin, with the oldest dating to 1847. Most oaks originating in the mid 1800s exhibited immediate canopy accession, with subsequent canopy closure occurring for some. Non-oaks began to appear after 1900, with many exhibiting canopy gap releases. The first maple was recorded in 1934. Average growth rates exceeded 2 mm/yr until about 1870, and then dropped to about 1.5 mm/yr. CV values were significantly negatively correlated with growth ($P < 0.0001$, $r = 0.6191$). CV values were low in the early 1800s, which would correspond with open canopies at that time. After about 1875 they exceeded 50, and remained high through the 1900s, indicating that canopies may have closed by the early 1900s. Among white oak stands, Elburn had its highest growth chronology with Johnson's Mound (Table 6). Stand characteristics are provided in the Appendices.

Helm's woods support one presettlement aged tree, a white oak. This tree originated in a gap in 1802, which closed by about 1810, with a release in about 1845. A white oak established in 1811 had low but variable growth until 1833, when it appears to have been released into a gap. Among 11 oaks established between 1840 and 1900, only three appear to have been released into gaps, while the remainder immediately accessed gaps, suggesting open canopy conditions during that period. Ash, elm and cherry began to appear after 1930, and no maples were aged. Average tree growth was highly variable until about 1885, and then averaged 1.5 mm/yr. CV values were significantly positively correlated with growth ($P = 0.0002$, $r = 0.2757$). CV values were below 50 until 1950, suggesting that closed canopy conditions developed at that time. Helm's woods had the highest correlation with the PDSI for any stand. In contrast, it had low growth correlations with other white oak stands; its highest correlation was $r = 0.326$, with Elburn Forest Preserve (Table 6).

Johnson's Mound contained two trees that were established before settlement. A white oak established in 1771 had immediate canopy access, which it maintained. However, a bur oak established in 1803 was released in about 1830, which would suggest that canopy gap processes were operating at that time. All other oaks were established after 1850. These individuals exhibited both canopy gap release and direct canopy access and subsequent canopy closure, indicating forest canopy processes were operating. The first non-oak, an ash, established after 1880 and was released after 1900. The first maple was established after 1900. Average tree growth was variable but > 1.5 mm/yr until about 1940, and then declined. CV values were significantly negatively correlated with growth ($P < 0.0001$, $r = 0.3909$). CV values suggest that canopy closure took place about 1900, which corresponds to the influx of most non oak species including sugar maple. This stand had a high landscape correlation with the Elburn Forest Preserve.

MacArthur woods appears to be primarily post settlement in origin, although it had a single white oak that originated in 1753. This individual averaged 0.50 mm/year growth until it was released in about 1840, which suggests that it originated in forest conditions. All other oaks were also established after that time, indicating a large scale disturbance. However, these species had variable release methods, including both immediate gap accession as well as canopy gap release. Hickory was recorded in 1860, and the earliest maple aged was in 1900. Tree growth averaged 2 mm/yr until about 1900 and then dropped to 1.5 mm/yr. CV values were not correlated with growth ($P = 0.587$, $r = 0.045$). They also remained well under 50 throughout the history of the stand. Raw tree ring chronology was moderately correlated with the McCormick Ravine and Thorn Creek woods white oak stands

McCormick Ravine appears to represent old growth conditions. It supported two white oaks established in 1775. These trees had different chronologies. One sustained an understory growth rate throughout the stand history, while the other had initial accession into a canopy gap, followed by canopy closure and a second release in about 1850. Two oaks established in the early 1800s were released into the canopy in about 1860. Two maples entered the stand in about 1860, possibly from adjacent mesic habitat, and both were released into canopy gaps in about 1900. Tree growth averaged < 1.0 mm/yr until about 1860, then increased to 2.0 mm/year until about 1900, and then dropped to < 1.5 mm/yr. CV values were not correlated with growth ($P = 0.067$, $r = 0.1175$). CV values were cyclic, suggesting forested conditions until about 1825, followed by a sequential periods of low and high variability, with a return to closed canopy conditions in about 1900. This stand had growth highly correlated with stands at Thorn Creek Woods, MacArthur Woods and Mooseheart Ravine.

Mooseheart Ravine contained no trees of post settlement origin. However, four white oaks established before 1850 underwent dynamic canopy gap processes. The oldest tree, a white oak, was established in 1839 in a gap that closed in 1850, with a second release in 1881. A white oak established in 1840 was suppressed until released in 1875. In 1848, a white oak established directly into a gap that closed by 1900. A white oak established in 1849 remained suppressed until released in 1900. After 1850, most trees established immediately into gaps, many of which closed during the early 1900s. Non-oaks, including elm, as and cherry, began to establish after 1920, but the first maple that was aged was not established until 1975. The last oak was established in 1941. Tree growth was variable, but averaged about 2mm/yr until about 1900, and then declined to < 1.5 mm/yr by the late 1900s. CV values were nor correlated with growth ($P = 0.821$, $r = 0.0173$). CV values were > 50 until 1900, suggesting forested conditions, and then dropped but returned to > 50 after 1925 and remained so through the late 1900s. This suggests that older canopy trees were removed in about 1900, or earlier, and that canopy conditions became more closed in about 1925. Growth was highly correlated with the McCormick Ravine white oak forest.

Thorn Creek Woods appears to represent old growth conditions. It contained three pre-1800 trees. The oldest, a white oak, established in 1740 and remained in the understory until released in 1850. A hickory underwent immediate gap accession 1761, followed by several gap closure and releases events. A second hickory established in 1773 apparently remained suppressed until released in about 1830. Fourteen oaks and hickories established in the early to mid 1800s had similar variability in establishment, indicating dynamic canopy conditions. An ash was established in about 1870, and the first maple in about 1960. Average growth was variable but extremely low (< 0.4 mm/yr) until about 1840, and then increased to about 8.0 mm/yr through the 1900s. There was also an abrupt increase in growth about 1900 that may indicate a large-scale canopy disturbance. CV values were significantly positively correlated with growth ($P < 0.0001$, $r = 0.3787$). They were also low until about 1850, and then increased to > 60 by 1900. They abruptly dropped, indicating a disturbance, and then returned to >60 by 1950, possibly indicating a return to more closed canopy conditions. Growth was highly correlated with growth rates at MacArthur Woods and Mooseheart Ravine.

Red oak stands

Busse Woods supported no presettlement trees, and is probably post-settlement. The oldest established in 1845. It appears to have been suppressed for about 50 years, with a canopy release in about 1900. At least four trees established in the 1800s had immediate canopy accession, while others underwent canopy release after suppression, as well as gap closure-release cycles. The first maple occurred in the stand in 1900, with oaks continuing to be established through the 1920s. Average growth was about 2mm/yr throughout the life of the stand, while CV values dropped below 50 only in 1945. CV values were also not significantly correlated ($P = 0.084$, $r = 0.149$) with growth. These conditions suggest that most of the stand originated from a post settlement canopy disturbance, and that older presettlement trees may have been removed in about 1945, reducing variance in growth until the canopy closed after about 1960. Growth was highly correlated with Norris, Crabreee and St. Francis Woods.

Crabtree Woods had a single presettlement-aged tree, a white oak established in 1752. This individual had highly variable initial growth, with multiple gap closure release cycles. The rest of the stand appears to have originated in about 1840. Although most trees immediately established in gaps, at least one underwent a gap release from suppressed growth. This suggests that most of the stand regenerated after a large scale disturbance before 1850. Non oaks, cherry and maple, entered the stand in about 1940. Stand growth averaged about 1.5mm/yr until about 1875, then dropped to < 1mm/yr by 1900, only to rapidly peak at 2mm/y by 1900 and then from back to 1.5 mm/yr. CV values were significantly positively correlated ($P = 0.005$, $r = 0.224$) with growth. They reached 50 only in about 1875-99, then gradually declined to a low of about 40 by the 1930s and then gradually increased. Growth was most highly correlated with growth at Messenger Woods, St. Francis Woods, and Busse Woods.

Messenger Woods (dry-mesic) appears to represent old growth conditions. It contained three pre-1800 trees that appear to have developed in forested conditions. The oldest, a white oak, averaged < 1.5mm/yr from 1687-1825, with multiple gap accession, closure, release cycles. A second white oak gained immediate canopy access in 1710, and then declined, averaging 1.25mm/yr over time through the 1900s. A swamp white oak established in 1758 had a similar growth pattern, but averaged 1.5mm. Additional oaks, as well as maples entered the stand during the 1800s, and displayed gap and gap release canopy accessions. Cherry and basswood entered the stand in the early 1900s, while the last oak generated in about 1930. Stand growth rates were cyclic and variable; they averaged < 1mm/yr until about

1850, and then increased to 2mm/yr by 1870, dropped to 0.50 mm/y by the 1930s, and then increased to 1.5mm/yr. CV values were also cyclic, peaking in the early 1700s, 1800s and 1900s. They were also negatively correlated ($P = 0.004$, $r = 0.1673$) with growth rates, suggesting that higher growth rates corresponded to canopy disturbance in the mid 1700s and early 1800s and 1900s. Growth was most highly correlated with the Messenger mesic stand, as well as Paw Paw Woods.

Messenger Woods (mesic) contained no presettlement-aged trees and appears to be of post-settlement origin. The oldest tree, a red oak, established by directly accessing a canopy gap in 1847. Five other trees, including oak, ash and maple, established also accessioned directly into gaps in the 1800s. This suggests the stand originated after a large scale disturbance. Elm and cherry entered the stand in the 1930s, and the last oak originated in 1945. Tree growth averaged 2mm/yr until 1900, then dropped to about 1.25mm/yr by the 1930s and then increased back to 2mm/yr. CV values were significantly negatively correlated with growth ($P < 0.0001$, $r = 0.436$), with low values in the 1800s and higher values in the mid to late 1900s. This suggests the stand reached closed canopy conditions in the 1930s. Growth was most highly correlated with the Messenger dry-mesic and Paw Paw Woods stands.

Norris Woods had no presettlement trees, with canopy trees established in the mid 1800s. The oldest tree, a red oak, was established in 1844. Among 12 trees established between before 1900, only one, a red oak, appears to have been gap released. Most trees, including white oak, walnut and hickory, appear to have directly accessed canopy gaps, but had highly variable growth. The timing of this cohort suggests that the stand originated after a large scale disturbance. Elm and cherry were established in 1920, and the first maple was established in 1970. The last oak was established in about 1945. Tree growth was relatively stable, averaging 1.5mm/yr, with an increase to 2.5 mm/yr between 1912-17. CV values were significantly positively correlated with growth ($P = 0.0379$, $r = 0.1703$), but were cyclic. They were low in the 1800s, suggesting open canopy conditions, but exceeded 50 between about 1855-1915, only to drop by 1930 and return to > 50 by 1960. This suggests a second disturbance event in the early 1900s, which may have removed older canopy trees, and would correspond to invasion by elm and cherry. The stand apparently returned to closed canopy conditions by 1960. Tree growth was highly correlated only with growth at Busse Woods.

Paw Paw Woods supported no presettlement trees, and appears to have undergone multiple post settlement disturbances with most canopy trees established in the late 1800s. However, the oldest tree, a maple, established in 1860 and was released into a gap about ten years later, suggesting forest canopy processes. Between 1860-74, nine additional trees, including maple, red and white oak and ash established through gap accession as well as gap release processes. Basswood, elm and cherry appeared in the 1920s. Tree growth was cyclic. It exceeded 3.0 mm/yr until about 1880, and then declined to 1.25 mm/yr. It abruptly increased to 2.5 mm/yr by 1900, and then dropped back to 1.25 mm/y through 1950, after which it stabilized at slightly under 2.0 mm/yr. CV values were negatively correlated ($r = 0.2676$, $P = 0.0017$) with growth and somewhat cyclic. They were lowest in the late 1800s, which suggests open canopy conditions, and then increased to about 70 by 1875. They dropped back to 50 by 1900, followed by cyclic increases and decreases through the 1900s. This suggests several periods of large scale canopy disturbance after the stand was initiated in the late 1800s, which probably removed any presettlement trees. Growth was most highly correlated with growth in both Messenger Woods stands.

Raccoon Grove supported no presettlement trees, but appears to have developed under forested conditions. The oldest tree, an ash, established by gap release in 1841. This was followed by multiple canopy gap accessions and gap closure for red oak and white oak through the 1800s. A single maple established through gap release in about 1870, and the oldest basswood was established in the 1940s. The youngest red oak established in about 1920. Tree growth was comparatively stable, averaging about 1.5 mm/yr after about 1850. CV values were not correlated with growth (Pearson's r = 0.01606, P = 0.117). They exceeded 50 from 1855-1915, dropped to < 50 between 1915-44, and then increased to about 50. The drop in CV in the early 1900s may indicate a logging or disturbance event that removed older canopy trees, allowing synchronous growth during that period. This would explain canopy gap processes during the 1800s. Tree growth was highly correlated only with St. Francis Woods.

St. Francis Woods appears to represent old growth conditions. This stand contained five white oaks established between 1737 and 1801. These trees displayed canopy release and suppression, indicating they developed under forested conditions. This process continued through the 1800s, during which ash, hickory and basswood entered the stand. Single red and white oaks underwent immediate and permanent canopy accession in the 1850s, as well as a red oak in 1885. Elm and cherry entered in the 1930s, and the first maple was recorded from 1954. Tree growth averaged about 1.0 mm/yr through the mid 1800s, and then increased to 1.5 mm/y through the 1900s. CV values were moderately cyclic, and significantly positively correlated with tree growth (P < 0.0001, r = 0.3964). They were low in the late 1700s, increased to about 50 through the mid 1800s, increased to 70 by 1900 and then remained above 50, suggesting forested conditions through the 1900s. Growth was most highly correlated with Busse woods.

Maple stands

Busse Woods appears to have supported no presettlement trees. The oldest tree, however, was a white oak established before 1828, but cored only to that age. This tree has occupied a canopy gap since 1928, but it is unknown whether it directly occupied the gap or was released into it. Four maples established between 1846-64 were released into gaps, and most of the remaining trees established before 1900 were either released or entered gaps that eventually closed, indicating forest gap processes. The youngest oak was established in 1883. Tree growth averaged about 1.5 mm/yr after 1843, with little variation except for a minor spike in about 1900. CV values were not correlated with growth (P = 0.6126, r = 0.0412) and were cyclic but averaged over 50 for the life of the stand. Lower values suggest more open canopy conditions between 1855-84 and between 1930-60, which may correspond to tree removal or large scale canopy disturbances. Tree growth in Busse woods had low correlations with other maple stands.

Johnson's Mound supported no presettlement trees, but appears to have developed under forested conditions. The oldest tree, a red oak established in a canopy gap in 1844, which closed in about 1860. Among six trees established between 1860-70, a maple, ash and red oak were released from suppressed conditions, while a white oak, red elm and maple were originally established in canopy gaps. This process continued through the 1900s. The youngest oak was established in 1909. Tree growth was cyclic, but tended to average 1.0 mm/yr in the mid 1800s, about 2.0 mm/yr in the late mid to late1900, and almost 2.5 mm/yr in the late 1900s. CV values were marginally negatively correlated (P = 0.0549, r – 0.1587) and also cyclic but consistently over 50. They tended to be high in the mid 1800s, which would correspond to lower growth rates in that period, and forested conditions. They were lowest in

1930-44, and high in the mid to late 1900s, which would correspond to closing canopy conditions. Growth was not highly correlated with other maple stands.

Maple Grove appears to have developed under forest canopy processes. The oldest tree, a white ash, was established in 1818 and released into a canopy gap in about 1840. Among ten trees established between 1840 and 1860, only a sugar maple and a white oak appear to have immediately accessed gaps and maintained canopy dominance. One maple and three white oaks were gap released, and the remainder entered gaps that eventually closed. These processes continued in the 1900s, with the last oak established in 1882. Tree growth was extremely low until 1840, and then increased to 2.0 mm/yr between 1840 and 1900; it then dropped to 1.5 mm/yr by 1925 and continued at that rate. CV values not correlated with growth ($P = 0.1382$, $r = 0.12$). They were low until 1855 and then increased to > 50 through the 1900s. This combination of low initial growth rate and continued high CV values suggests that forested conditions occurred throughout the stand history. The high growth rates between 1840 and 1900 could represent released growth caused by selective cutting, which would have removed presettlement trees from the stand. Tree growth was most highly correlated with Meacham Grove.

Lloyd Woods probably represents old growth conditions. This stand contained four maples and two white oaks that appear to have been established under a forest canopy in the 1700s and subsequently released into canopy gaps. Gap release and canopy accession and closure processes continued through the 1900s, with only a single white oak and red oak apparently accessing and maintaining dominance in a canopy gap. Tree growth averaged < 1.0 mm/yr until 1850, and increased to 1.5 mm/yr by 1870 before returning to 1.0 mm/yr until 1900. It then spiked to 2.5 mm/yr by 1910, and then dropped and stabilized at about 1.5 mm/yr. CV values were highly negatively correlated with tree growth ($P < 0.0001$, $r = 0.4736$). They were variable but consistently above 50 through 1900, with a minor drop that corresponded to the increased growth in 1850. This probably represents a release from a moderate scale canopy disturbance. The much greater increase in tree growth in 1900 corresponded to a greater drop in CV values, indicating a larger scale canopy disturbance at that time. Growth was moderately correlated with growth at Meacham Grove, and negatively correlated with growth at Maple Grove and the Moron Arboretum.

Meacham Grove contained no pre-settlement tees but appears to have developed under forest canopy conditions. The oldest tree, a bur oak, was established in1833, and was released into a canopy gap in 1880. Among 11 additional trees established before 1900, a maple, red oak and bur oak also were released into canopy gaps. Two white oaks and a red oak appear to have accessed and maintained dominance in gaps, while the remainder entered gaps that eventually closed. These processes continued into the 1900s, with the most recent oak established in 1918. Tree growth was highly variable and cyclic. It averaged 1.5 mm/yr until 1880, increased to 2.5 mm/yr for ten years and then dropped back to 1.5 mm/yr. After ten years, it again increased to 2.5 mm/yr for another ten years before dropping back to about 1.5 mm/yr. CV values were highly negatively correlated with growth ($P < 0.0001$, $r = 0.32062$). They were also variable but usually > 50, with their greatest decline between 1900-1915. This period underwent a rapid increase in growth that probably corresponds to a large scale canopy disturbance. Tree growth was most highly correlated with growth at Maple Grove and Pilcher Park.

The Morton Arboretum mesic forest stand contained no trees established prior to 1842, and appears to have developed after a large-scale canopy disturbance. Four of the five trees established before 1850 directly entered gaps.

The oldest, a red oak, did not receive gap closure until 1970, while two white oaks had suppressed growth within 20 years. One maple persisted in an open gap for about 30 years, while a second maple appears to have persisted in a gap into the 1900s. Similar processes continued through the late 1800s, with the first gap releases occurring for maples established in 1888 and 1908. These dynamics, and the absence of early gap releases, suggest that the canopy had been relatively open in the mid 1800s and did not close until about 1900. Growth rates were between 2.0 – 3.0 mm/yr until bout 1890, and then dropped to about 1.5 mm/yr through the 1900s. CV values were significantly negatively correlated with growth (P = 0.0002, r = 0.29155). They were initially high, but dropped to < 50 in the late 1800s, and increased to > 50 by 1900 and continued above 50 through the 1900s. This also suggests an open canopy in the 1800s with canopy closure about 1900. Stand growth was most highly correlated with Maple Grove.

Pilcher Park probably represents old growth conditions. This stand contained one of the oldest trees cored in the Chicago region. The core terminated at 1707, but the inner half of the tree was rotted and could not be aged. This tree encountered gap closure in about 1715, after which it averaged 0.50 mm/yr until about 1830, when it under went a series of gap releases. Of nine trees, including three maples, established before 1900, eight were released into gaps from a suppressed condition, while the ninth directly accessed a gap, which it maintained through the 1900s. These dynamics indicate that forested conditions persisted at Pilcher Park through the 1800s. Between 1900 and 1917, seven trees, including oak, ash, walnut and maple, appear to have directly accessed canopy gaps, indicating a large scale canopy disturbance. Canopy gap release and closure processes continued after 1920, with the last oak established in 1927. Tree growth averaged about 1.0 mm/yr until 1870, but rose sharply to 3.5 mm/yr by 1884, and then dropped to 1.5 mm/yr by about 1950. CV values were not correlated with tree growth (P = 0.1092, r = 0.1196) and were > 50 for most of the stand chronology. They dropped below 50 between 1915-44, which corresponds to a period of higher growth rates and canopy disturbance. Growth was most highly correlated with Meacham Grove and Maple Grove.

River Road Woods may represent old growth conditions. It had two white oaks established in 1803 and in 1805, and white and red oaks established in 1818, 1825 and 1843. All of these trees were initially suppressed and released into gaps between 1850-60. During the same period a cohort of seven trees, including white oak, red oak, maple and elm, was established into gaps, while four additional trees were established in understory conditions. This suggests that a large scale canopy disturbance occurred in the 1950s which could have removed older trees. Gap release, as well as canopy accession and closure, dynamics continued through the 1800s and early 1900s. The first maple was established in 1863, and the last oak, a red oak, was established in about 1885. Tree growth was < 1.5 mm/yr until about 1860, and than increased to 2.5 mm/yr by 1885, probably in response to canopy disturbance. It then declined to back to 1.5 mm/yr by 1930, which may indicate canopy closure, and then returned to 2.5 mm/yr by the late 1900s. CV values were positively correlated with growth (P = 0.0186, r = 0.1691). They were highest between 1825-1875, and after 1975. These higher CV values would be expected to correspond with periods of reduced growth in forested conditions. However, they correspond to periods of rapidly increasing growth at River Rd., which most likely would have occurred following canopy disturbance. Stand growth was most highly correlated with mesic forest at the Ryerson Forest Preserve.

Ryerson Forest Preserve did not support trees established before 1800. However, a walnut established in 1812, a bur oak in 1815, and a maple in 1828 may predate settlement in that region. Each of these trees were established in understory conditions and released into canopy gaps in the mid to late 1800s. Among 13 additional oak, ash and walnut established through the 1850s, only five were directly established into gaps, with the remainder established in understory conditions. This indicates that canopy gap processes prevailed during the development of the modern stand. Direct gap establishment became more frequent in the late 1800s and early 1900s, probably in relation to post settlement logging, followed by tree poaching and death of American elm in the 1960s. The last oak, a red oak, was established directly into a gap in 1943. Three maples established in the 1950s were released by canopy gaps in about 1970, which may have been caused by death of American elm. Tree growth was cyclic but usually comparatively high. It was between 1.0-1.5 mm/yr until 1840, and then increased to 2.0 mm/yr by 1850. Except for reduced growth between 1885-1903 and 1932-1941, growth continued to average 1.5 mm/yr or more through the late 1900s. CV values were significantly positively correlated with growth ($P = 0.0007$, $r = 0.2468$). They were also cyclic, with rates below 50 in the early 1800s and between 1885-1930. Stand growth was most highly correlated with mesic forest at River Road Woods.

Savannas

The open grown trees in the savannas we studied originated between the years 1833-1859, or later. Although we consider this period to reflect presettlement, or very early settlement, conditions, the absence of older open grown trees is worrisome, as large bur oaks often post-date settlement (Szafoni et al. 1994). One explanation might be that open grown savanna trees were susceptible to fire and did not live as long as slower growing trees developed in forests. An alternative explanation might be that fires were being suppressed during this period, and that many of these trees developed from grubs that were maintained by more frequent fires during earlier years. With the exception of maples at McDowell Grove, these trees appear to have been established and maintained in very large canopy gaps – suggesting savanna conditions in the early 1800s. The two oldest maples at McDowell Grove had initial growth rates of about 1.0 mm/year, and appear to have been released into canopies from forest understories in the late 1870. This suggests that McDowell Grove was originally forested, and may have been partially cleared for pasture after settlement. A similar chronology was identified for oak savannas found in Kentucky, which were apparently forested when initial trees were established and then cleared after European settlement (McEwan & McArthy 2008). However, we do not apply this hypothesis to the oak dominated stands. Two of the white oaks at Silver Springs appear to have had moderate releases in about 1880. Although this might reflect a canopy disturbance at that time, their initial growth rates were above 2.0 mm/year and suggest they had been established under open canopy conditions. All stands, including McDowell Grove, maintained growth rates of about 2.0 mm/year into the 1900s, and Coefficient of Variation values tended to be < 50, suggesting that tree growth was uniform and not indicative of forest canopy gap processes.

<u>Representation of old growth conditions</u>

Using two criteria for old growth, presence of trees established before settlement, and canopy gap processes representing gap accession, gap closure, and gap release, seven (~30 %) of the stands we studied represent old growth, or Category I, conditions (Table 4). These include two white oak stands (McCormick Ravine and Thorn Creek Woods), two red oak stands (Messenger Woods dry-mesic, and St. Francis Woods), and three maple stands (Lloyd

Woods, Pilcher Park, and River Road). The Illinois Natural Areas Inventory assigned grade A status to five of these stands. About 40 % of the stands had no, or few, trees that predated settlement, but had trees established in the early to mid 1800s that developed under canopy gap processes, and would represent Category II conditions. The INAI assigned grade B status to all but one of these stands. About 30 % of the stands were post settlement in age, with most trees established primarily by direct accession of canopy gaps, and would represent Category III conditions. These stands were represented by a single maple stand, two white oak stands, and four red oak stands. Two of the red oak stands were assigned grade A status by the INAI.

Climatic signals

Climate apparently had a strong effect on tree growth, as 75 % or more of the stands within each stand type had significant positive correlations of the standardized ring width, as well as raw ring width, with the PDSI before 1950 (Table 5). After 1950, < 30 % of these measures were significant, suggesting less sensitivity to drought. With pairwise correlations of raw ring width chronologies among stands, which would indicate landscape level responses among stands, many sites had Pearson's r values > 0.50 (Table 6), and significantly lower mean correlations occurred among maple stands than among oak stands (Figure 3). This suggests more correlated growth among sites with greater drainage, which would be expected to be more sensitive to climatic effects. There was also a significant difference among stand types and between time intervals in correlations between ring-width indices and PDSI, with greater mean correlations before 1950, and greater correlations among white oak stands (Figure 4). These results support hypotheses that drought stress and climatic sensitivity is greater in white oak stands, and that it has lessened over time, which could represent reduced loss through evapotranspiration due to increased canopy cover. Despite these significant differences, overall r-sq values for correlations with PDSI's averaged < 0.30. This indicates that > 70 % of the variation in tree growth is influenced by other factors, and expected result for stands with strong canopy gap processes (McCarthy & Rubino 2000).

Stand-type growth and variation over time

Mean Coefficient of Variation values differed significantly over time with either 15-or 25-year time intervals, and also differed among stand types, with lower values for white and red oak stands in the 1800s and lower values for savannas (Figure 5). Maple stand CV's tended to be higher and more stable over time. These results support a canopy closure hypothesis, suggesting more open canopies and less variation in growth in the 1800s for oak-dominated stands, open canopies for savannas over time, and more closed canopies for maple stands over time. Tree growth was also significantly higher for savannas than for forest stands with either time interval; however, oak stands did not have greater growth than maple stands in the 1800s (Figure 6). This partially supports a hypothesis that tree growth is greater due to open canopies, but does not suggest that oak forests had more open canopies that maple forests in the 1800s. Nevertheless, maple stand growth exceeded that of red oak, which in turn exceeded that of white oak. This may indicate a response to most favorable growing conditions in more mesic sites preferred by maple.

Species and stand-level interactions with gap processes

The average number of gap accession events differed significantly among species groups, with a significant interaction with gap release category (Figure 7). Oaks had more such events than maples because they were more common. However, white oaks had a greater average response to gaps followed by subsequent canopy closure, and this effect was most apparent in white oak dominated stands. Red oaks had their lowest average response to understory gap release events, which was most apparent in red oak dominated stands. In contrast, maples had their greatest response to understory gap release events, which was also most apparent in stands dominated by this species. These results suggest that white and red oak are more light dependent than maples, but differ in their responses. Red oaks appeared to be equally adapted to persisting in gaps that remain open, or in gaps that subsequently close. The greater response of white oaks to gaps that subsequently closed may indicate greater shade tolerance in this species. The greater response of maple to gap releases from understory conditions indicates greater shade tolerance, and probably the greater amount of canopy shade in maple dominated stands.

Among all stands, the greatest average number of initial gap accession events occurred in the period between 1850 and 1899 (Figure 8). This effect may have resulted from a combination of cessation from landscape fires, which allowed advance oak regeneration from fire-suppressed grubs, as well as a response to a greater number of large canopy openings that were present at that time, including those in Category III stands that completely regenerated due to stand clearing disturbances.. These release events also differed among species within stand types (Figure 8). Before 1850, white oak had the greater average number of gap accessions across all stand types. In white oak stands, white oak had a greater average number of gap releases than did red oak between 1850-1900; white oak, red oak and maple were similar between 1900-49, but maple exceeded red oak after 1950, and no gap responses were recorded for white oak. In red oak stands, white oak and red oak had similar average gap responses between 1850-1950. After 1950, white oak was not recorded and maple exceeded red oak in release events in red oak stands. In maple stands, average maple and white oak release events exceeded those of red oak between 1850-1900, and were similar to red oak between 1900-1949. After 1950, maple exceeded red oak, and white oak was not recorded. These results indicate that canopy gap release events have shifted toward maple in all stand types since 1950, and that red oak has exceeded white oak during this period.

Over time, there was a significant shift toward a greater average number of understory releases, with a decrease in trees originating directly in canopy gaps (Figure 9). Within 50-year time periods, there was also a shift among stand types. Before 1850, maple stands had greater releases from understory trees, while red oak stands had a greater response to gap-releases and white oak stands had greater responses to either gaps or gap-releases. During the 1850-99 time period, maple stands had a greater average response to either gap release or understory releases, while red oak stands had greater responses to gap releases and white oak stands had greater responses to gaps. During the 1900-49 period, gap processes had shifted to greater numbers of understory releases in maple and red oak stands, but not in white oak stands. By 1950-99, understory releases were predominant across all stand types.

CONCLUSIONS

Old growth conditions

Our assessment of old growth conditions, based on presence of trees established before settlement and canopy gap processes, differed somewhat from grade assignments made by the INAI. For example, our classification of old growth might include stands in which older trees were not always represented by larger size classes. Smaller trees in this category would have been mistaken for younger trees by the INAI. Nevertheless, the assignments were in agreement for the most part. Among the seven old growth, or Category I, stands, the Messenger Woods dry-mesic stand and the Thorn Creek stand were assigned grade B status. Both may have received post settlement canopy disturbance, but retained presettlement trees. Among the ten Category II stands, which we considered to lack presettlement trees but probably developed under canopy processes, only the Busse Woods stand was assigned grade A status by the INAI. Our post settlement Category III stands differed more from the INAI assignments, as two of the seven stands were assigned grade A status while the remainder were considered high enough quality to be assigned grade B status. Red oak stands appear to be most problematic in this category, as they accounted for half of the post settlement stands, and two, the Messenger Woods mesic stand and the Crabtree Woods stand, were assigned grade A status. Red oak typically establishes after large scale disturbance and, rapidly gains canopy status (Crow 1985). Given this strategy, young stands that have reached maturity and contain all size classes, including old-aged trees might be considered old growth even though they developed after recent large scale disturbances. Nevertheless, such stands will remain successional, as other species will replace red oaks without recurring large-scale disturbance (Abrams et al. 1998).

Climatic effects

Climate appears to affect growth in Chicago region forests, as 75 % or more of the stands had significant correlations with the Palmer Drought Severity Index before 1950, and because growth in many stands was correlated at the landscape scale. This relationship appears sensitive to drainage, as evidenced by higher mean correlations in growth among white oak and red oak stands in comparison to maple stands, and greater r-sq values before 1950. White oak and red oak typically occupy more well drained sites than maple, and white oak is known to be sensitive to climatic variation (Rubino & McCarthey 2000). Because of the climatic response of growth within and among stands, direct interpretation of stand growth and CV values may be confounded by climate, as apposed to either endogenous or exogenous disturbance processes. However the low r-sq values for correlation of growth with PDSI indicate that about 70% or more of the variation in growth is due to other factors, presumably canopy disturbance processes. Cause of the reduced sensitivity to climate after 1950 is not clear. Although it could represent reduced moisture loss through evapotranspiration due to canopy closure, most of the oaks we studied occupied canopy positions where they would not be subjected to shade from maple invasion in forest subcanopies. Thus an explanation for this change is not well understood; It could be related to the increased environmental factors associated with the greater urban development occurring in the Chicago region after 1950.

Effects of post-settlement change beginning in the 1800s

Analysis of tree ring data provide strong supportive evidence that forest canopies were open in the mid to late 1800s, which allowed recruitment of large numbers of oak and subsequent changes in forest structure after settlement began to reduced the frequencies of landscape fires after about 1850. This is evidenced by the great number of initial canopy accession events that occurred between 1850-1900, which would correspond to a large volume of canopy gaps, as well as greater regeneration available at that time. Analysis of types of gap accessions also indicates that direct accession into gaps that eventually closed was most frequent. A plausible explanation for these events is a situation in which canopy conditions were relatively open due to presettlement fires occurring before 1850. This is supported by the similar Coefficient of Variation values in savanna and oak stands at that time, as well as analysis of public land survey data (e.g. Bowles et al. 1994). As settlement reduced landscape fires, advance regeneration from post-fire sprouting oak grubs, as well as natural reproduction, would have been available to access the great number of comparatively large canopy gaps. Over time, these gaps then closed due to reduced fire frequencies, as well as growth of the large cohort of trees that had been established (Bowles et al. 2005). This process differed at the stand level. White oak had the greatest number of responses to canopy openings in white oaks stands, while it shared greatest abundance with maple in maple stands, and with red oak in red oak stands. This suggests that white oak had the greatest ecological amplitude among these species before settlement, and that post settlement processes have reduced its landscape abundance. During this period, gap processes differed among stand types, with fewer direct permanent gap accessions in maple stands, but more such events in white oak stands, and more gap access closure events in red oak stands. Our analysis of gap process preferences among species groups suggests that the white oak species group preferred gaps that eventually closed; however this may be circular if white oak was more abundant and gap closure was the most abundant process. Nevertheless, this analysis also indicated that maple preferred understory gap releases, a well known strategy for this species (Canham 1985), and that red oak preferred direct gap access over gap releases, also a well known strategy for that species (Crow 1988). A secondary effect on this process is that seven (25 %) of the stands actually originated in the mid 1800s following stand clearing disturbances. This would inflate the number of canopy gap accessions that occurred during the 1850-99 period strictly due to the loss of fire processes. Four of these were red oak stands, which makes this stand type most problematic for interpretation of a post-fire process as causing the canopy changes after 1850.

Cascading effects in the 1900s

Tree ring data also provide strong evidence for cascading effects after 1900, with ongoing canopy closure that varied among species and stand types. Canopy accession events during the 1900-1950 period dropped by 50 % from the previous fifty years, indicating more closed canopies. The pattern among species changed little; white oak predominated in white oak stands, and shared dominance with red oaks in red oak stands and maple in maple stands. However, direct accession and persistence in gaps dropped relative to gap accession followed by gap closure and gap release events, indicating less open canopies during this period. Gap processes also shifted toward gap releases in red oak stands, and fewer direct gap accessions in white oak stands. After 1950, canopy accession events dropped by < 30 %. However, as indicated by the increase in mean Coefficient of Variation among stand types, random gap release events predominated across all stands, and maple became the predominant tree accessing canopy gaps. These changes suggest that as canopies closed and fire frequencies dropped, selection shifted toward the shade tolerant maple, and against successful regeneration of oak species.

Management implications

An important implication for management and restoration drawn from this study is that although oak and maple stands had more open canopies in the 1800s, presumably due to landscape fire, they also operated under canopy gap processes. Although fewer data are available for the period before 1850, which best represent presettlement conditions, they suggest that gap release processes may have been as frequent as direct canopy access events and may have been more frequent in maple stands. However, oak regeneration into these canopy gaps was far more common that that of maple. Although Coefficient of Variation data suggest that oak stands were more open during this period, maple stands were less so. As a result, we can project that oak forests were different from maple stands, and they may require different management strategies. Forests of today also represent a legacy of cascading events that began with reduced fire frequencies in the mid 1800s, followed by rapid accession of canopy gaps, first by oaks and later by non-oaks. They now appear to have greater canopy cover, with gap access almost restricted to non-oak species. Given the long-term changes in these forests, it may be difficult to return to a presettlement structure without canopy management. Research is needed to understand whether restored fire processes that reduce invading non-oak species, primarily maple, will allow oak regeneration into canopy gaps in these forests and maintenance of viable populations of oaks. Management of maple-dominated stands represents the greatest challenge, as these stands shared dominance with white oak in the early 1800s, and their presettlement structure is poorly understood. The post settlement origins of red oak stands is also problematic, as little information is available on presettlement structure of such stands. The relatively short life span and lack of regeneration of red oak suggests that these stand types will undergo the most rapid changes in the near future, and may require disturbance management to maintain red oak abundance (Abrams et al. 1988).

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Table 1. Old growth forest study sites used for tree ring anlaysis. Site numbers refer to Figure 1. Excluded sites: Herrman's Woods, McCormick Ravine Maple (M). INAI quality grade: A = undisturbed and B = moderately disturbed. INAI drainage categories: (DM) = dry-mesic, (M) = mesic. Community classification (Bowles et al. 2000): Maple = maple dominated, Red oak = red oak dominated, White oak = white oak dominated.

			←--------Community Classification--------->		
Site No.	Site name	County	Maple	Red oak	White oak
1)	Bloomingdale (Meacham) Grove F. P.	DuPage Co.	B (DM)		
2)	Busse Woods F. P.	Cook Co.	A (DM)	B (DM)	
3)	Crabtree Farm Woods	Lake Co.		A (DM)	
4)	Elburn F. P.	Kane Co.			B (DM)
5)	Glen A. Lloyd Woods Nature Preserve	Lake Co.	A (M)		
6)	Helm's Woods F. P.	Kane Co.			B (DM)
7)	Herrman's Woods	Lake Co.			A (DM)
8)	Johnson's Mound F. P.	Kane Co.	B (M)		B (DM)
9)	Maple Grove F. P.	DuPage Co.	B (M)		
10)	MacArthur Woods F. P.	Lake Co.			B (DM)
11)	McCormick Ravine Preserve	Lake Co.	A (M)		A (DM)
12)	Messenger Woods F. P.	Will Co.		A (M), B (DM)	
13)	Mooseheart Ravine	Kane Co.			B (DM)
14)	Morton Arboretum	DuPage Co.	B (M)		
15)	Norris (Jones) Woods	Kane Co.		B (DM)	
16)	Paw Paw Woods F. P.	Cook		B (DM)	
17)	Pilcher Park	Will Co.	A (M)		
18)	Raccoon Grove F. P.	Will Co.		B (DM)	
19)	River Road Woods F. P.	Lake Co.	A (M)		
20)	Ryerson Conservation Area	Lake Co.	B (M)		
21)	St. Francis Boy's Camp F. P.	Lake Co.		A (DM)	
22)	Thorn Creek Woods N. P.	Will Co.			B (DM)

Table 2. Number of tree-ring cores sampled by species and stand from INAI high quality forests.

a) tree species 50 cm or more dbh, average date of origin is 1866 or earlier.

	Maple stands		**Red oak stands**		**White oak stands**		Total
	No. cores	No. stands	No. cores	No. stands	No. cores	No. stands	Cores
Quercus alba	20	8	22	7	27	8	69
Quercus rubra	19	8	28	8	18	7	65
Acer sacchrum	24	8	9	4	1	1	34
Quercus macrocarpa	6	4	3	2	7	3	16
Fraxinus americana	8	6	3	2	2	2	13
Juglans nigra	5	3	2	1	6	3	13
Quercus biccolor			2	2	5	1	7
Tilia americana	6	3	1	1			7
Quercus velutina					6	3	6
Ulmus rubra	3	2	1	1	1	1	5
Ulmus americana	2	2			2	2	4
Quercus palustris			2	1			2
Cara ovata			1	1			1
Prunus serotina					1	1	1
Quercus coccinea					1	1	1
	93		74		77		244

b) tree species less than 50 cm dbh, average date of origin is after 1866.

	Maple stands		**Red oak stands**		**White oak stands**		Total
	No. cores	No. stands	No. cores	No. stands	No. cores	No. stands	Cores
Acer sacchrum	39	8	18	8	15	7	72
Quercus alba	5	3	13	5	29	8	47
Quercus rubra	8	4	21	8	17	6	46
Tilia americana	16	6	9	5	9	3	34
Fraxinus americana	4	3	9	4	17	6	30
Prunus serotina	3	2	9	6	15	4	27
Ulmus rubra	4	2	5	3	8	3	17
Ulmus americana			3	2	13	4	16
Carya ovata			1	1	12	4	13
Juglnas nigra	5	3	1	1	2	2	8
Ostrya virginiana	4	1	1	1	3	2	8
Quercus palustris			4	1	4	1	8
Acer rubrum			4	1	2	1	6
Carya cordiformis			4	2	1	1	5
Quercus macrocarpa					4	3	4
Quercus bicolor					4	1	4
Fraxinus nigra					3	1	3
Quercus coccinea					2	2	2
Celtis occidentalis	1	1					1
Fraxinus quadrangulata	1	1					1
Quercus velutina					1	1	1
	90		102		161		353

Table 3. Ages of pre-1810 trees cored in 1997-98 from INAI high quality forests of the Chicago region.

Site	Co.	INAI Grade	*Acer saccharum*	*Quercus alba*	*Quercus bicolor*	*Quercus macrocarpa*	*Carya ovata*
Lloyd Wds	Lake Co.	A	1784	1730			
			1788	1762			
			1768				
			1794				
Messenger Wds dry-mesic	Will Co.	B		1687	1758		
				1710			
Pilcher Park	Will Co.	A				1707	
Crabtree Wds	Lake Co.	A		1752			
St.Francis Wds	Lake Co.	B		1777			
				1764			
				1758			
				1737			
				1801			
Johnson's Mound dry-mesic	Kane Co.	B		1771		1803	
River Road Wds	Lake Co.	A		1803			
				1805			
McCormick Ravine dry-mesic	Lake Co.	A		1755			
				1755			
Thorn Creek Wds	Will	B		1740			1761
							1773
MacArthur Wds	Lake	B		1753			
Helms Wds	Kane	B		1802			

Table 4. Age/Canopy classification of INAI high quality forest stands. Category I = presence of presettlement trees and canopy gap processes (gap accession, gap accession-closure, gap release), Category II = absence of presettlement trees, presence of canopy gap processes, Category III = absence of presettlement trees, presence of gap accession as primary process. INAI quality grade: A = old growth and B = old second growth or selectively logged. INAI drainage categories: DM = dry-mesic, M = mesic. Community classification: Maple = maple dominated, Red oak = red oak dominated, White oak = white oak dominated, following Bowles et al. 2000).

	←--------------------- Age/Canopy Classification -------------->		
Stand type / name	Category I	Category II	Category III
Maple stands			
Pilcher Park	A (M)		
River Road Woods F. P.	A (M)		
Glen A. Lloyd Woods Nature Preserve	A (M)		
Bloomingdale (Meacham) Grove F. P.		B (DM)	
Johnson's Mound F. P.		B (M)	
Maple Grove F. P.		B (M)	
Ryerson Conservation Area		B (M)	
Busse Woods F. P.		A (DM)	
Morton Arboretum			B (M)
Red oak stands			
St. Francis Boy's Camp F. P.	A (DM)		
Messenger Woods F. P.	B (DM)		
Paw Paw Woods F. P.		B (DM)	
Raccoon Grove F. P.		B (DM)	
Messenger Woods F. P.			A (M)
Norris (Jones) Woods			B (DM)
Busse Woods F. P.			B (DM)
Crabtree Farm Woods			A (DM)
White oak stands			
Thorn Creek Woods N. P.	B (DM)		
McCormick Ravine Preserve	A (DM)		
Mooseheart Ravine		B (DM)	
Helm's Woods F. P.		B (DM)	
Johnson's Mound F. P.		B (DM)	
Elburn F. P.			B (DM)
MacArthur Woods F. P.			B (DM)

Table 5. Temporal change in correlations between Palmer Drought Severity Indices and tree growth chronologies based on ring width indices and raw ring width. Significant probabilities (<0.05) are indicated in bold.

	1896-1949				1950-1998			
	Index		Ring-width		Index		Ring-width	
Maple stands	R-sq	Prob	R-sq	Prob	R-sq	Prob	R-sq	Prob
Busse	0.0171	0.3413	0.0421	0.1329	0.0130	0.4395	0.0001	0.9570
J'Mound	0.0790	**0.0376**	0.0594	0.0731	0.0051	0.6304	0.0081	0.5435
Lloyd	0.1442	**0.0042**	0.1484	**0.0037**	0.0640	0.0828	0.1343	**0.0104**
Maple Grv	0.0937	**0.0230**	0.0914	**0.0249**	0.0080	0.5467	0.0167	0.3807
Meacham Grv	0.1127	**0.0122**	0.0967	**0.0208**	0.0006	0.8734	0.0002	0.9261
Morton Arb	0.1192	**0.0098**	0.1666	**0.0020**	0.0360	0.1967	0.0609	0.0908
Pilcher Pk	0.0508	0.0979	0.1170	**0.0106**	0.0220	0.3144	0.0244	0.2895
River Rd	0.2239	**0.0003**	0.2501	**0.0001**	0.0276	0.2595	0.0437	0.1538
Ryerson	0.0967	**0.0209**	0.0963	**0.0211**	0.0799	0.0516	0.0852	**0.0441**
Red oak stands								
Busse	0.2333	**0.0002**	0.2228	**0.0003**	0.0029	0.7171	0.0019	0.7679
Crabtree	0.1375	**0.0053**	0.1218	**0.0090**	0.0004	0.8966	0.0002	0.9165
Messngr DM	0.1475	**0.0038**	0.1411	**0.0047**	0.0904	**0.0378**	0.1068	**0.0234**
Messngr M	0.1770	**0.0014**	0.1354	**0.0057**	0.0613	0.0897	0.0478	0.1353
Norris	0.0991	**0.0192**	0.0955	**0.0217**	0.0085	0.5335	0.0152	0.4036
PawPaw Wds	0.0960	**0.0213**	0.0865	**0.0293**	0.0007	0.8580	0.0077	0.5543
Raccoon Grv	0.0260	0.2398	0.2054	**0.0005**	0.1597	**0.0049**	0.1430	**0.0080**
St.Francis Wds	0.1691	**0.0018**	0.1547	**0.0030**	0.0377	0.1862	0.0676	0.0743
White oak stands								
Elburn	0.2440	**0.0001**	0.2391	**0.0002**	0.0134	0.4331	0.0021	0.7578
Helms	0.3222	**0.0000**	0.2984	**0.0000**	0.3483	**0.0000**	0.3566	**0.0000**
J'Mound	0.3253	**0.0000**	0.3012	**0.0000**	0.2336	**0.0005**	0.1784	**0.0028**
MacArthur	0.1418	**0.0046**	0.1603	**0.0025**	0.0003	0.9143	0.0210	0.3262
McCormick	0.1525	**0.0032**	0.2067	**0.0005**	0.0011	0.8250	0.0038	0.6768
Mooseheart	0.0696	0.0516	0.0667	0.0570	0.0512	0.1218	0.0243	0.2896
Thorn Crk	0.2392	**0.0002**	0.2419	**0.0001**	0.0150	0.4072	0.0387	0.1799

Table 6. Pairwise correlations (Pearson's r) of mean wraw ring width chronologies among stands within stand types

White oak stands

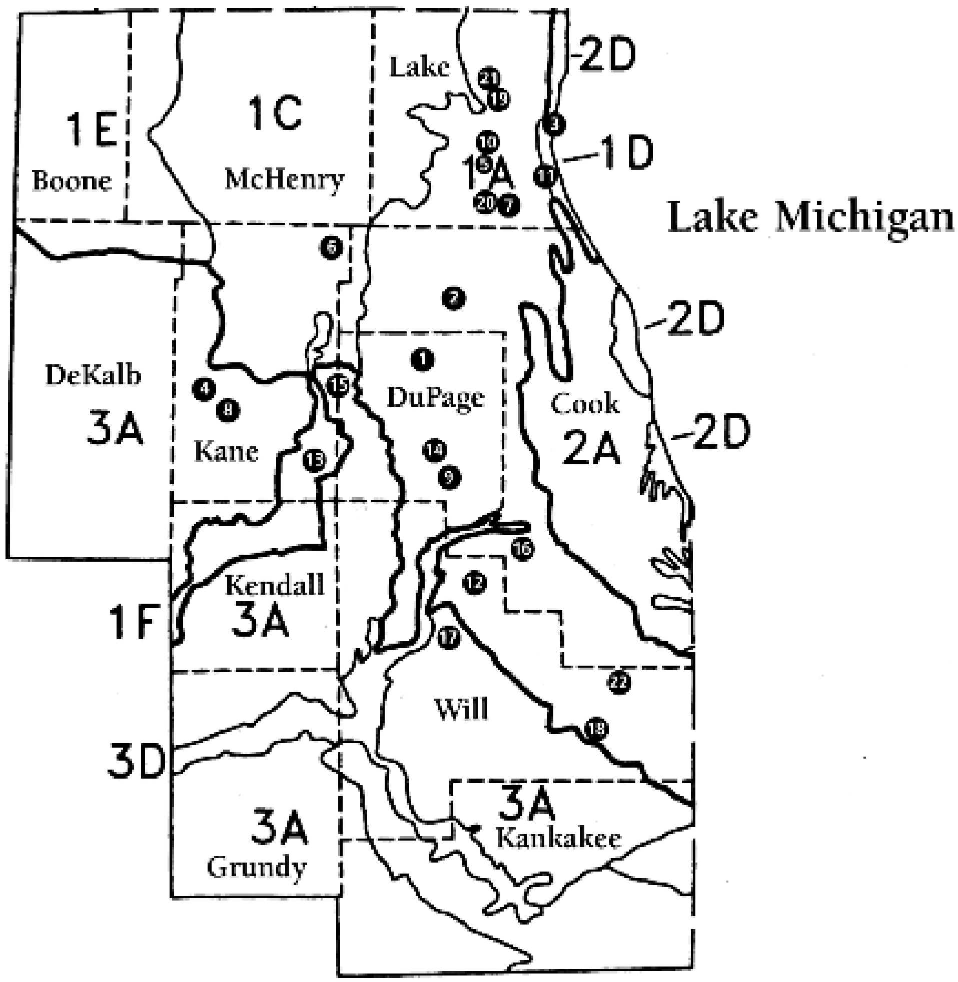
	Elburn	John's Mnd	McCorm dm	ThornCk	MacArth	Moose
Elburn	1					
John's Mnd	0.695477	1				
McCorm dm	-0.082332	0.093998	1			
ThornCk	0.139552	0.223463	0.689	1		
MacArth	0.298272	0.363568	0.556749	0.510084	1	
Moose	0.284458	0.409157	0.535039	0.489018	0.420782	1
Helms	0.326427	0.141442	-0.082609	0.215694	0.200397	-0.093433

Red oak stands

	Raccoon	Messngr dm	Norris	Crabtree	Mess M	St. Francis	Busse
Raccoon	1						
Messngr dm	0.168439	1					
Norris	0.096682	-0.17755	1				
Crabtree	0.235533	0.304836	0.066753	1			
Mess m	0.125667	0.658156	0.042545	0.586165	1		
St. Francis	0.479963	0.228779	0.282106	0.557639	0.304522	1	
Busse	0.190159	-0.044484	0.520749	0.527923	0.15657	0.566516	1
PawPaw	0.075845	0.610467	-0.104129	0.64113	0.593898	0.386766	0.240516

Maple stands

	Maple Grove	Pilcher Pk	Lloyd Wds	Ryerson	John's Mnd	Meacham Grv	Morton Arb	Busse Wds
Maple Grove	1							
Pilcher Pk	0.466716	1						
Lloyd Wds	-0.252034	0.218763	1					
Ryerson	0.053573	-0.223797	0.092672	1				
John's Mnd	-0.220202	0.004563	0.270931	-0.038502	1			
Meacham Grv	0.526815	0.573347	0.347332	0.191537	-0.028851	1		
Morton Arb	0.65645	0.040105	-0.328149	0.15058	-0.20335	0.302432	1	
Busse Wds	0.087054	-0.113389	0.217863	0.002304	0.282224	0.136324	0.245469	1
River Rd	0.25269	0.280337	0.181137	0.516715	0.035373	0.38246	0.137384	-0.126598



MORAINAL NATURAL DIVISION
1A - Western Morainal Section
1B - Eastern Morainal Section
1C - Kettle Moraine Section
1D - Racine Till Plain Section
1E - Winnebago Drift Section
1F - Fox River Bluff Section

LAKE PLAIN NATURAL DIVISION
2A - Chicago Lake Plain Section
2D - Illinois Dunes Section

GRAND PRAIRIE NATURAL DIVISION
3A - Grand Prairie Section
3D - Bedrock Valley Section

Figure 1. Locations of Chicago region high quality forests identified by the Illinois Natural Areas Inventory. Locations in relation to counties and Natural Divisions of the Chicago Region (Swink & Wilhelm 1994). Map numbers refer to Table 1

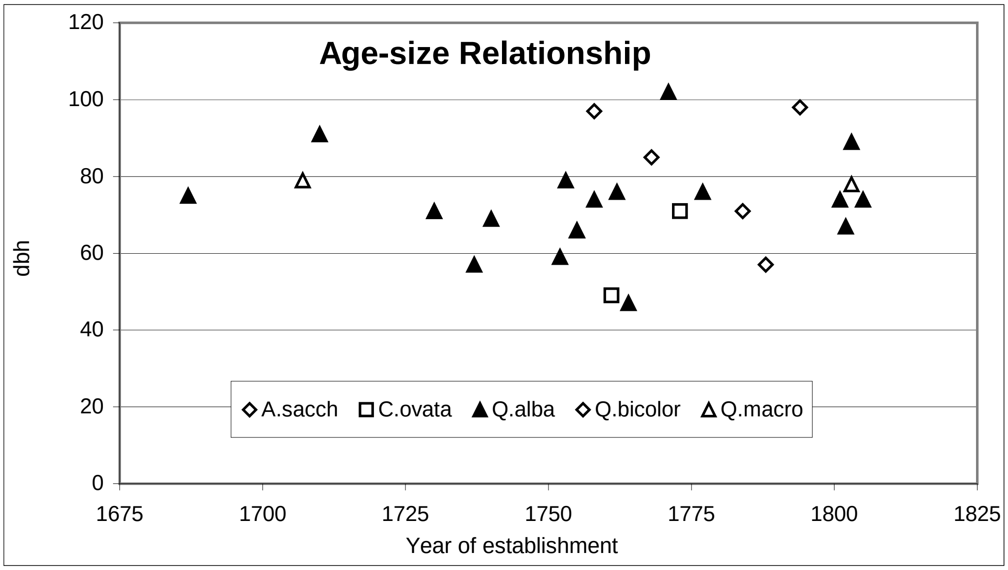


Figure 2. Age-size relationship (P = 0.8001, r = 0.051) of presettlement (pre-1810) trees cored in high quality forests of the Chicago region.

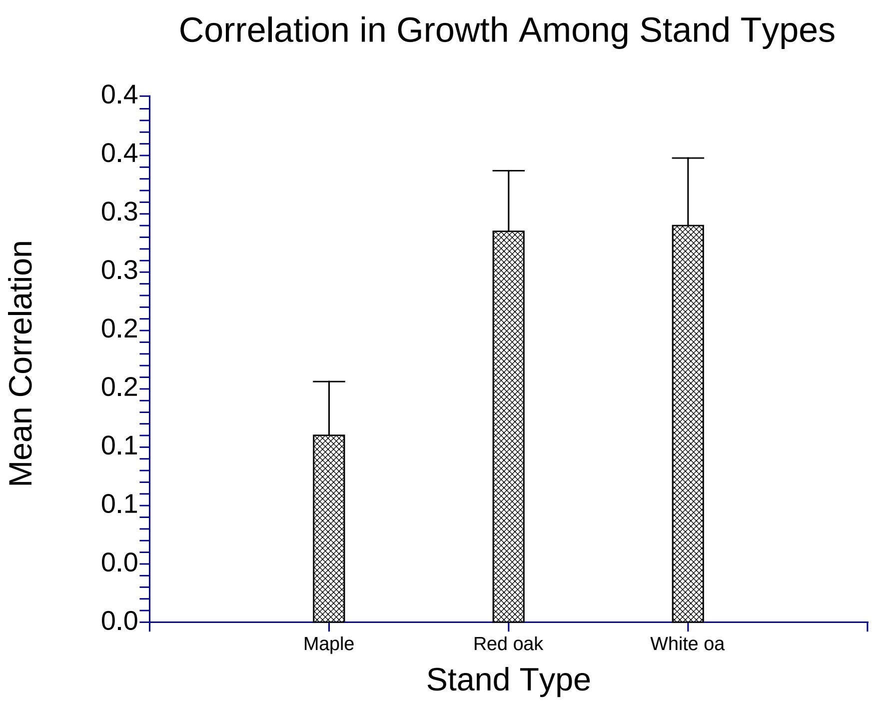


Figure 3. Growth correlation among stand types, as shown by the mean pair-wise correlations (Pearson's r) of raw ring-widths. One-way ANOVA of stand type: F = 0.0158, P = 0.74057.

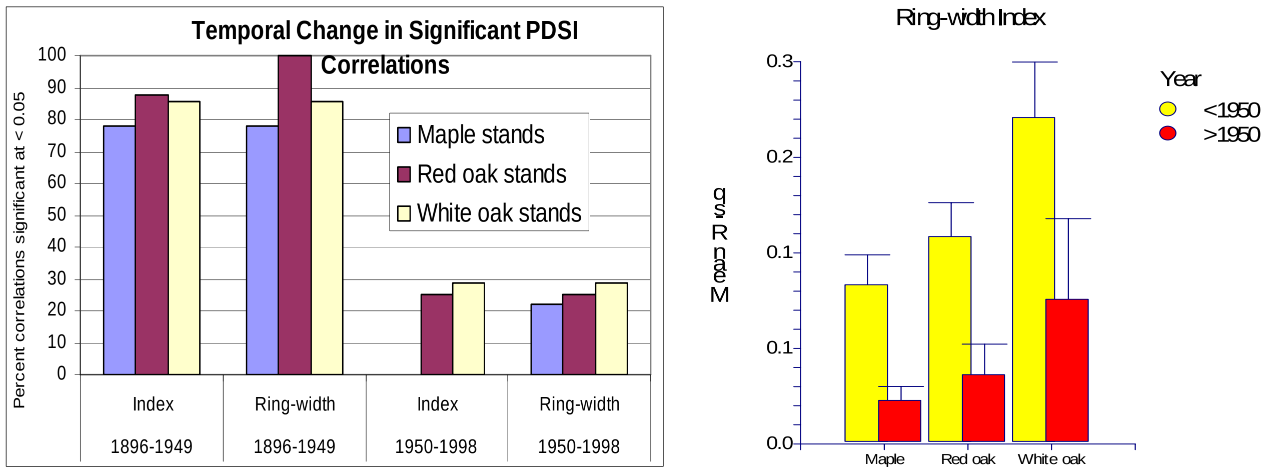


Figure 4. Temporal differences among stand types in correlations between PDSI and tree growth index. Left: percentage of correlations significant at $P < 0.05$. Right: mean index values: stand type ($F = 32.02$, $P < 0.0001$), Year ($F = 9.4$, $P = 0.0018$). No significant interactions. Tukey MR test: White oak different from Red oak & Maple. Ring-width (not shown): stand type ($F = 46.2$, $P < 0.0001$), year ($F = 8.51$, $P = 0.0028$). No significant interactions. Tukey MR test: White oak different from Red oak & Maple.

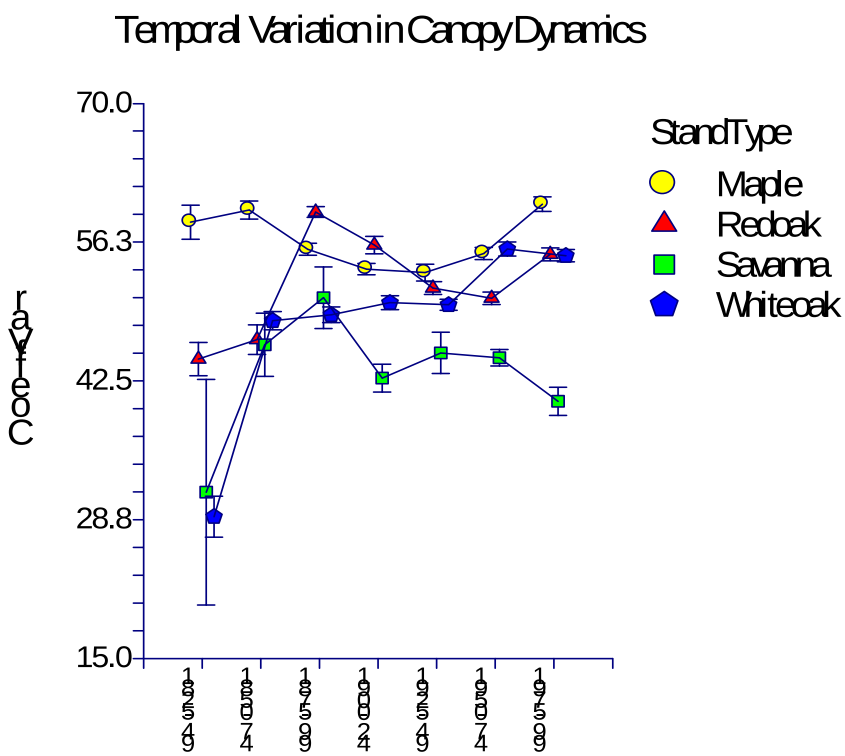


Figure 5. Temporal variation in canopy dynamics as shown by the mean coefficient of variation compared among stand types. Repeated ANOVA: time interval ($F = 25.91$, $P < 0.00001$), stand type ($F = 98.3$, $P < 0.00001$), time x stand type ($F = 13.55$, $P < 0.0001$); 15-year time interval ($F = 13.08$, $P < 0.00001$), stand type ($F = 65.11$, $P < 0.00001$), time x stand type ($F = 8.07$, $P < 0.0001$).

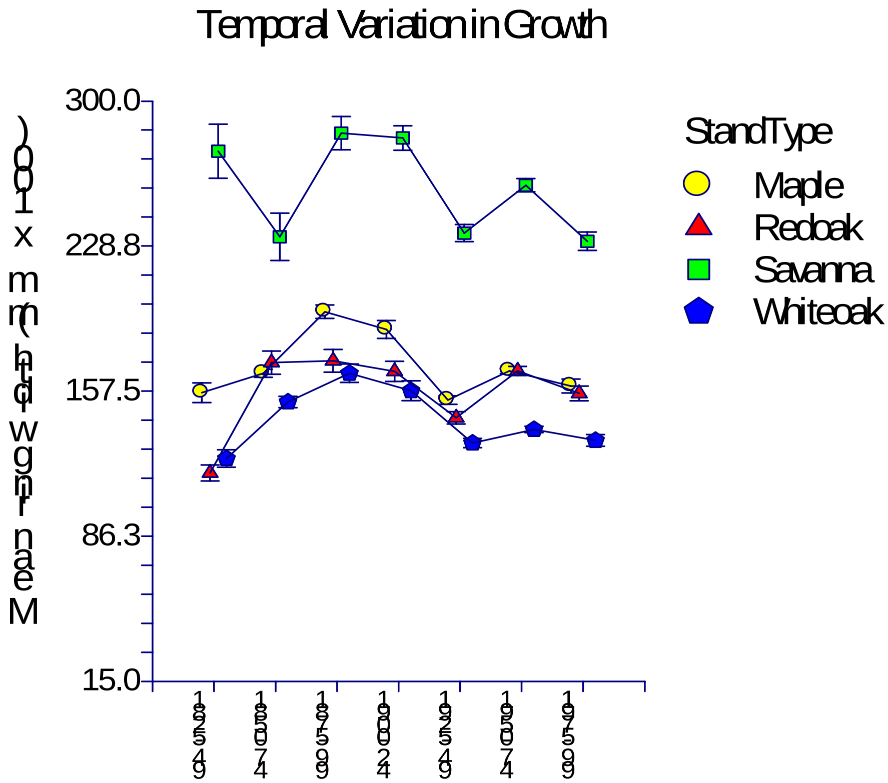


Figure 6. Temporal variation in tree growth compared among stand types. Repeated ANOVA: 25-year time interval (F = 16.65, P < 0.00001), stand type (F = 1254.19, P < 0.00001), time x stand type (F = 11.86, P < 0.0001). ; 15-year time interval (F = 10.26, P < 0.00001), stand type (F = 1515.55, P < 0.00001), time x stand type (F = 13.87, P < 0.0001).

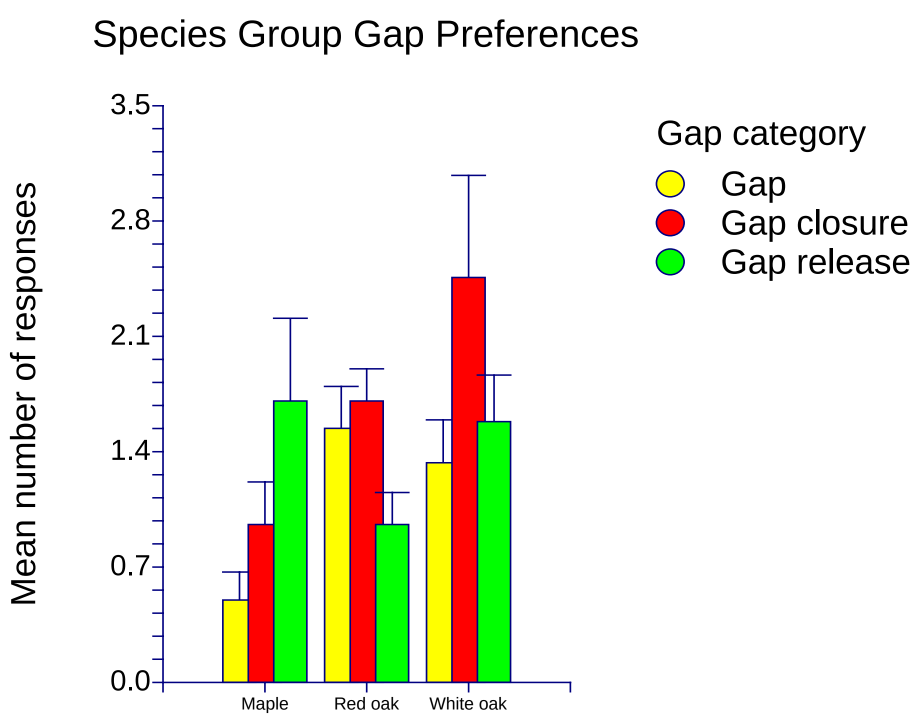


Figure 7. Gap accession preferences by species groups. Stand type (F 0 0.98, F = 0.3765), species group (F 9.35, P = 0.0001), gap category (F = 3.24, P = 0.041265), all interactions significant at P ≤ 0.01). Vertical axis = mean number of gap responses. Gap category: Gap = establishment by immediate and permanent gap access, Gap closure = establishment by gap access followed by gap closure, and possible release, Gap release = establishment by gap release from suppressed condition.

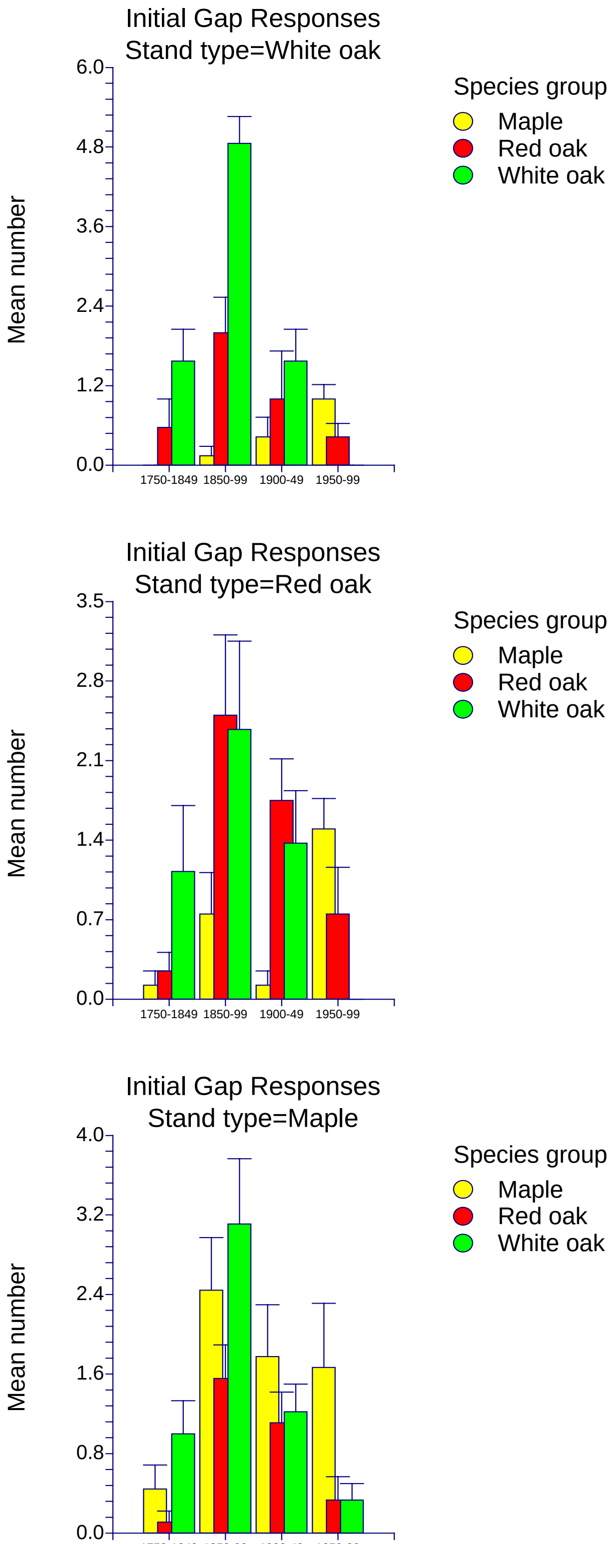


Figure 8. Temporal variation in number of initial gap accessions among stand types and species groups. Repeated ANOVA: stand type ($F = 1.31$, $P = 0.29055$), Years ($F = 27.91$, $P < 0.00001$), stand type x year ($F = 0.74$, $P = 0.6168$), species ($F = 9.54$, $P = 0.001129$), species x year ($F = 199.71$, $P =< 0.0\text{-}0001$).

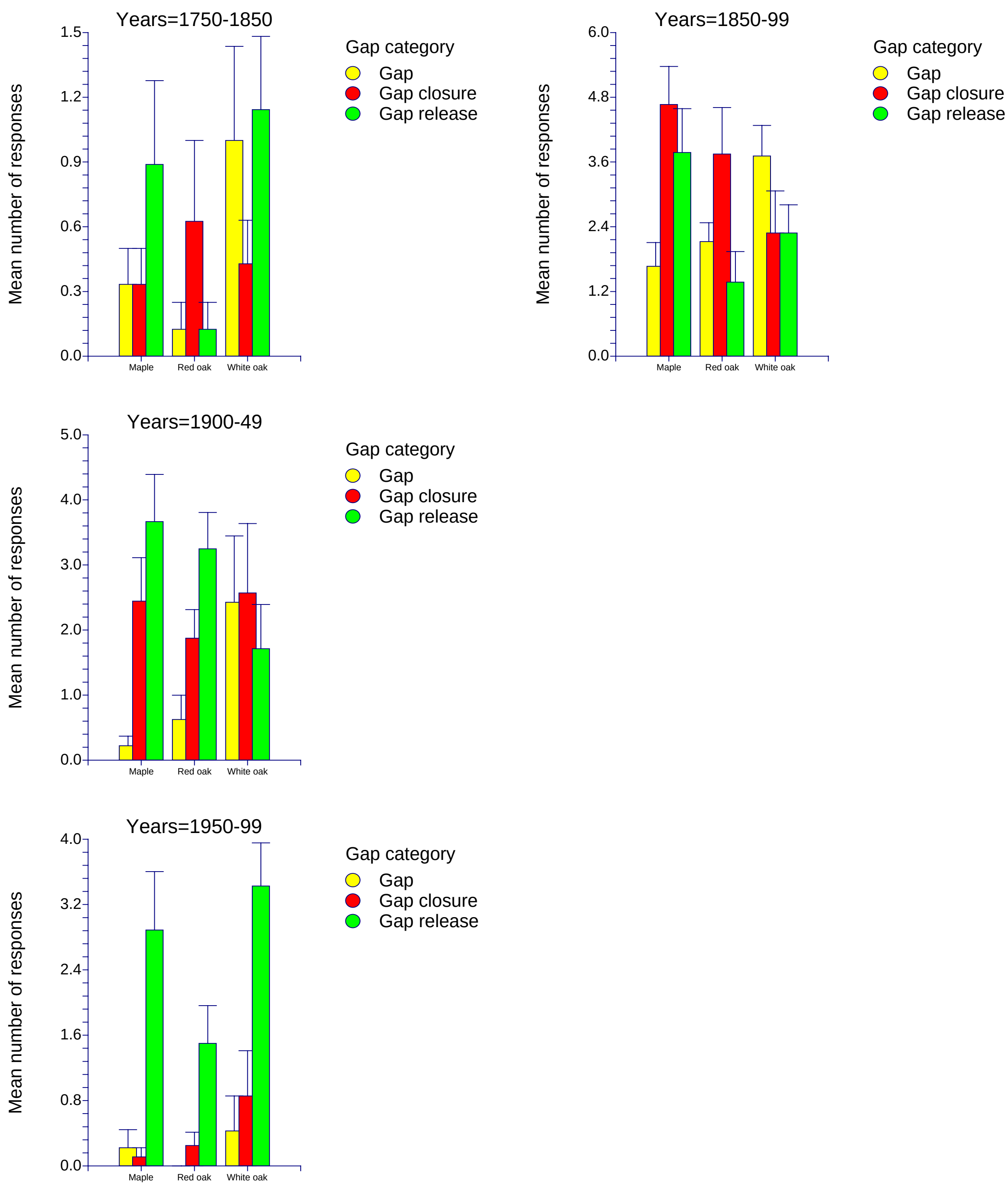
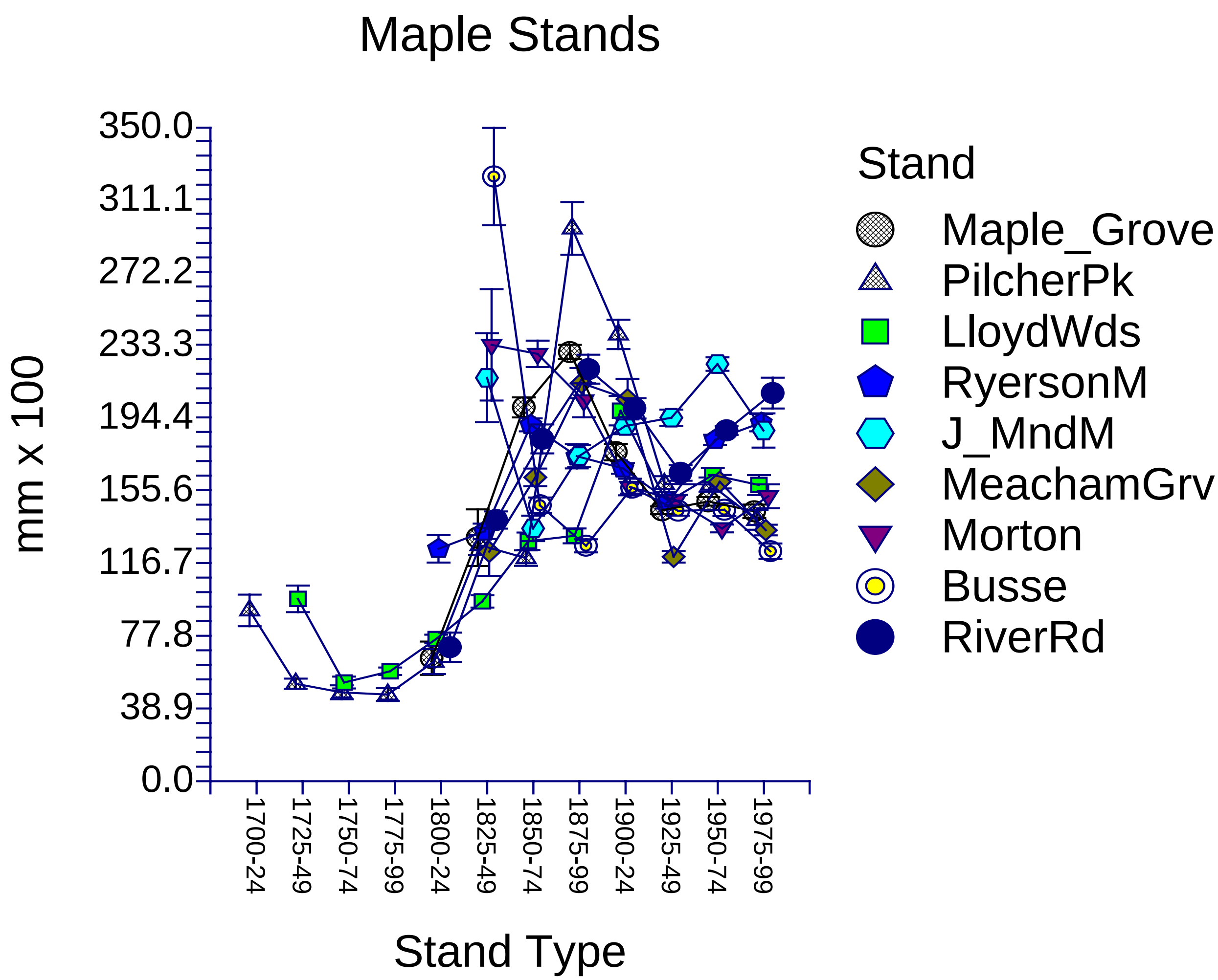


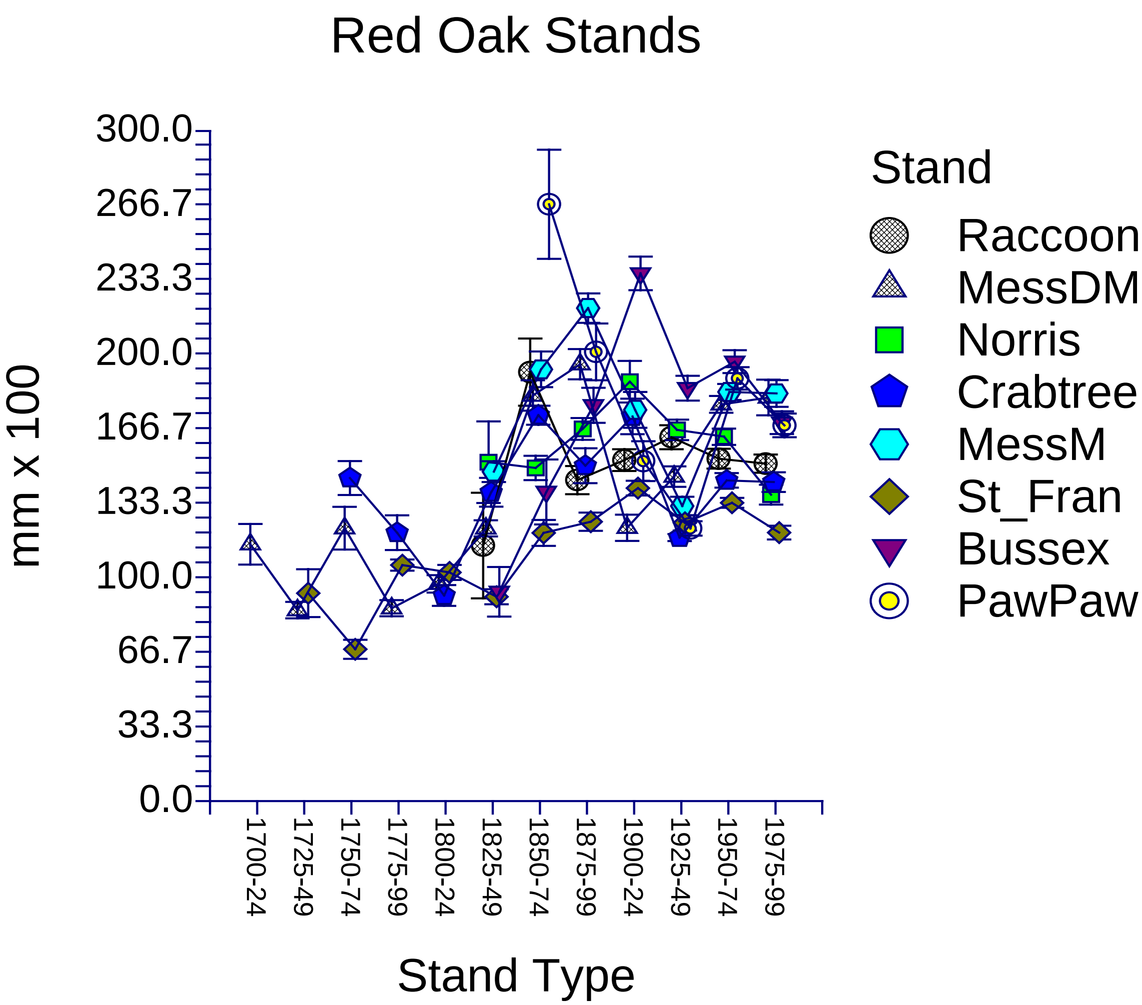
Figure 9. Temporal change in gap accession by stand type and gap category. Repeated ANOVA: Stand type ($F = 4.54$, $P = 0.02372$), years ($F = 36.36$, $P < 0.00001$), stand type x year ($F = 0.79$, $P = 0.582029$), gap category ($F = 14.15$, $P < 0.0001$), stand type x year x category ($F = 2.65$, $P = 0.00355$). Vertical axis = mean number of gap responses. Gap category: Gap = establishment by immediate and permanent gap access, Gap closure = establishment by gap access followed by gap closure, and possible release, Gap release = establishment by gap release from suppressed condition.

Appendix I. Variation among stand type chronologies

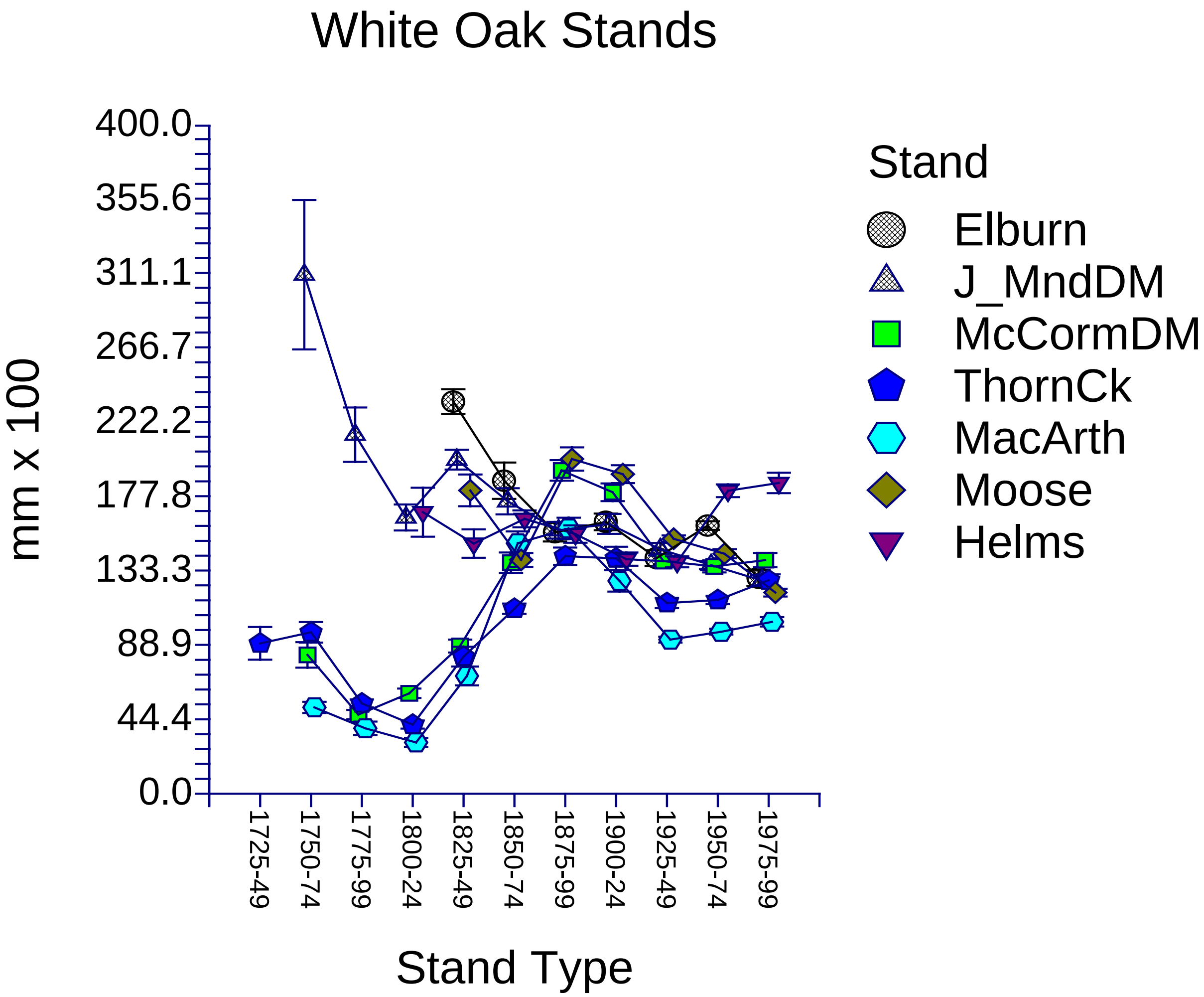
1) Maple stand type mean ring width chronologies averaged by 25-year time interval.
2) Red oak stand type mean ring width chronologies averaged by 25-year time interval.
3) White oak stand type mean ring width chronologies averaged by 25-year time interval.
4) Savanna stand mean ring width chronologies averaged by 15-year time interval.
5) Average standardized ring width indices for maple (SM), red oak (RO) and white oak (WO) stand types.



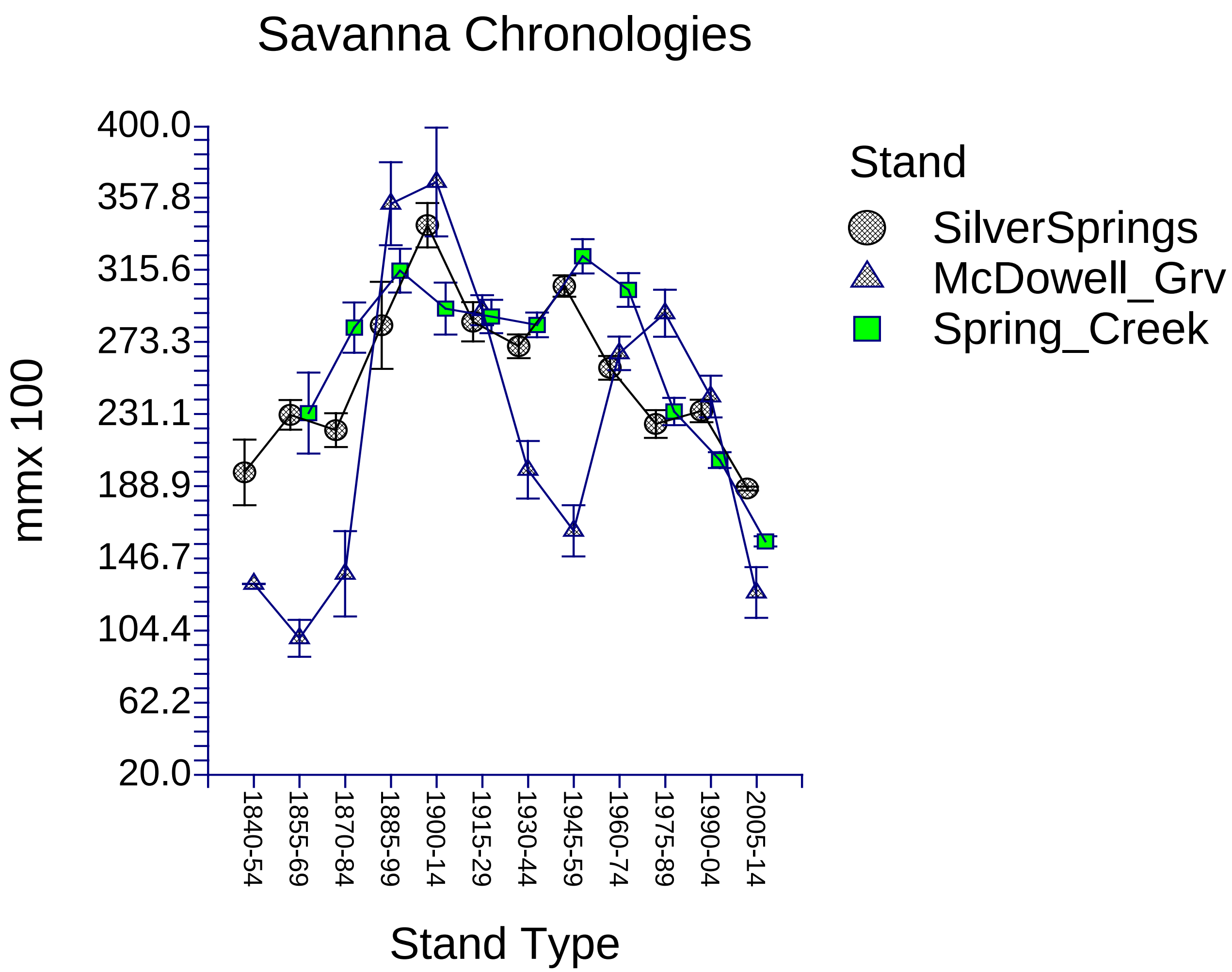
1) Maple stand type mean ring width chronologies averaged by 25-year time interval.



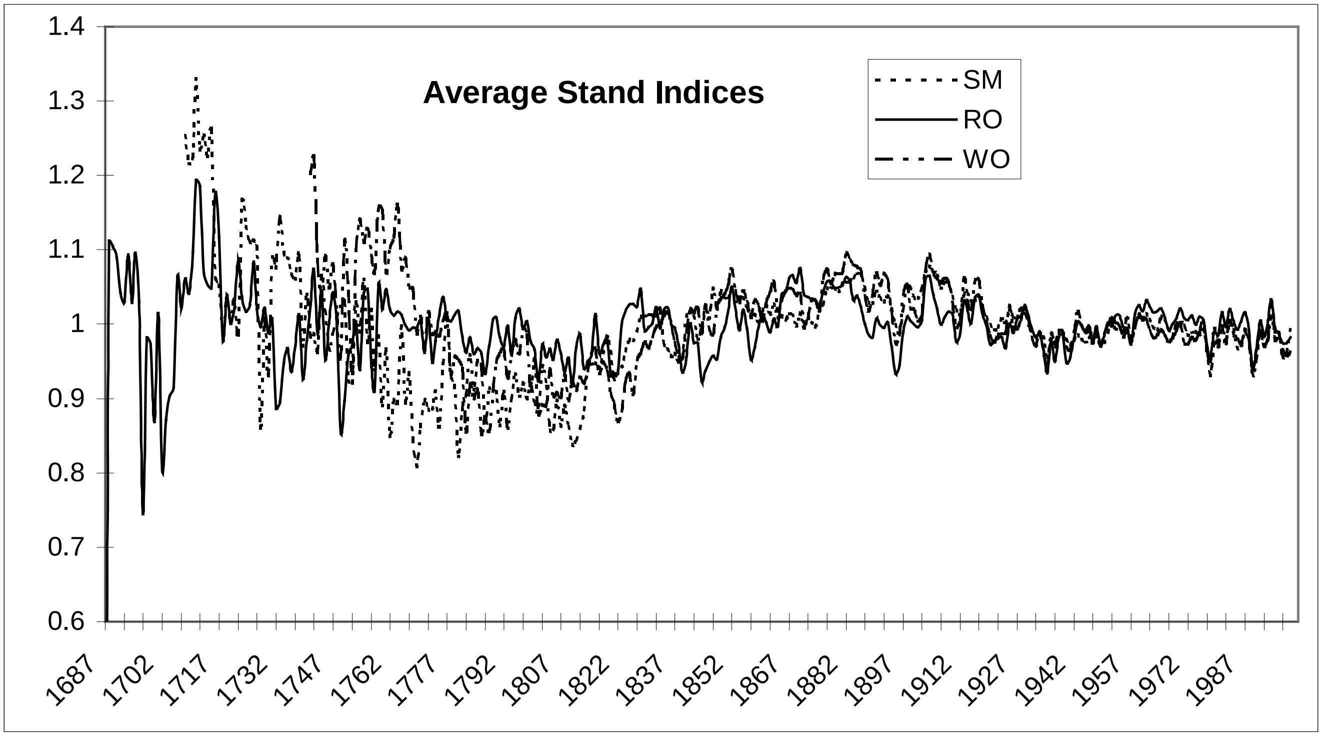
2) Red oak stand type mean ring width chronologies averaged by 25-year time interval.



3) White oak stand type mean ring width chronologies averaged by 25-year time interval.



4) Savanna stand mean ring width chronologies averaged by 15-year time interval.



5) Average standardized ring width indices for maple (SM), red oak (RO) and white oak (WO) stand types.

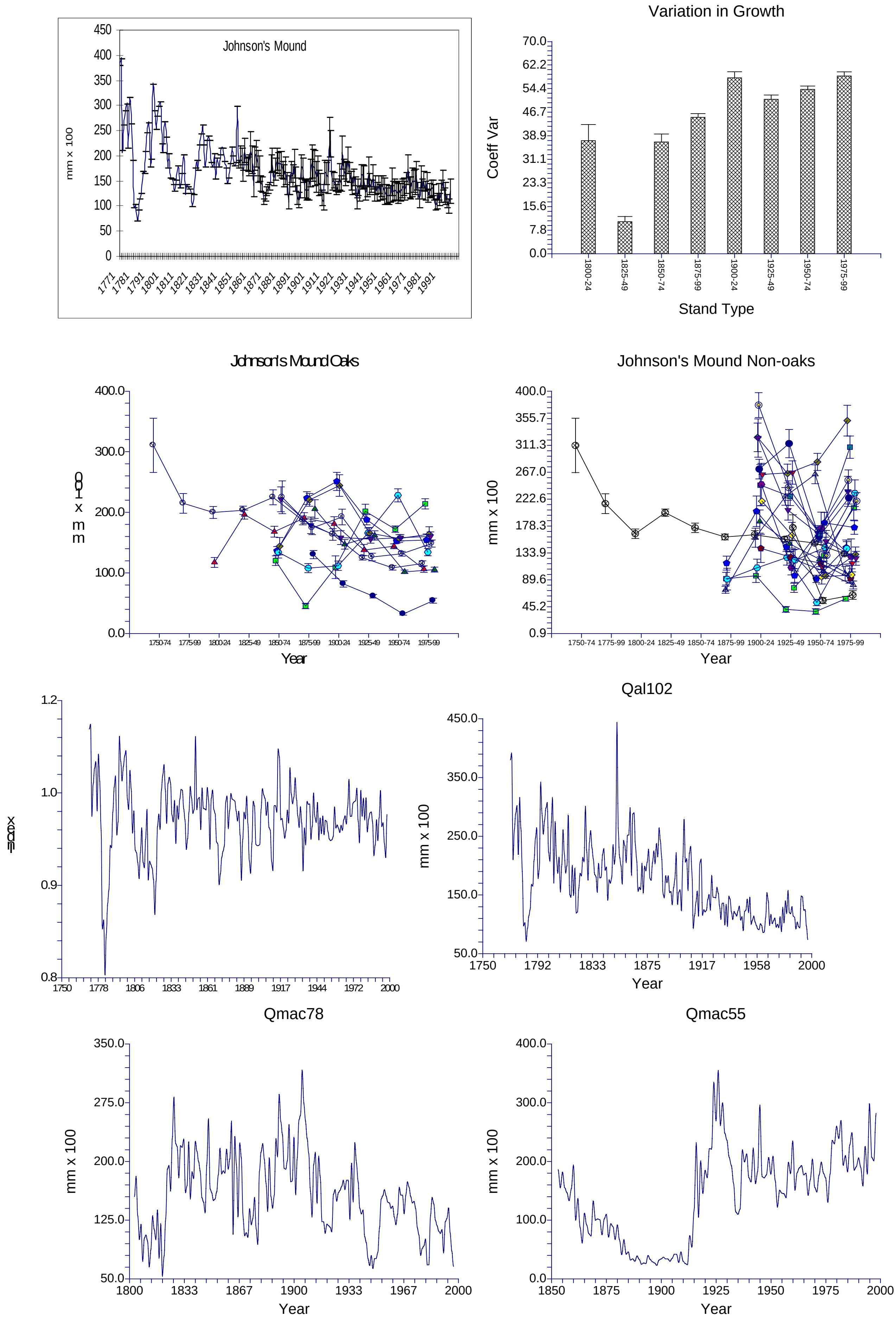
Appendix II. Within stand variation in 1) raw ring width chronology; 2) growth as shown by the Coefficient of Variation, 3) growth of oaks at 15-year intervals, 4) growth of non-oak (compared to mean of all oaks) at 15-year intervals, 5) standardized index of growth, 6) annual growth of three oldest trees (tree dbh follows tree abbreviation).

White oak stands
- Johnson’s Mound
- McCormick Ravine
- Thorn Creek Woods
- Elburn Forest Preserve
- Helm’s Woods
- McArthur Woods
- Mooseheart Ravine

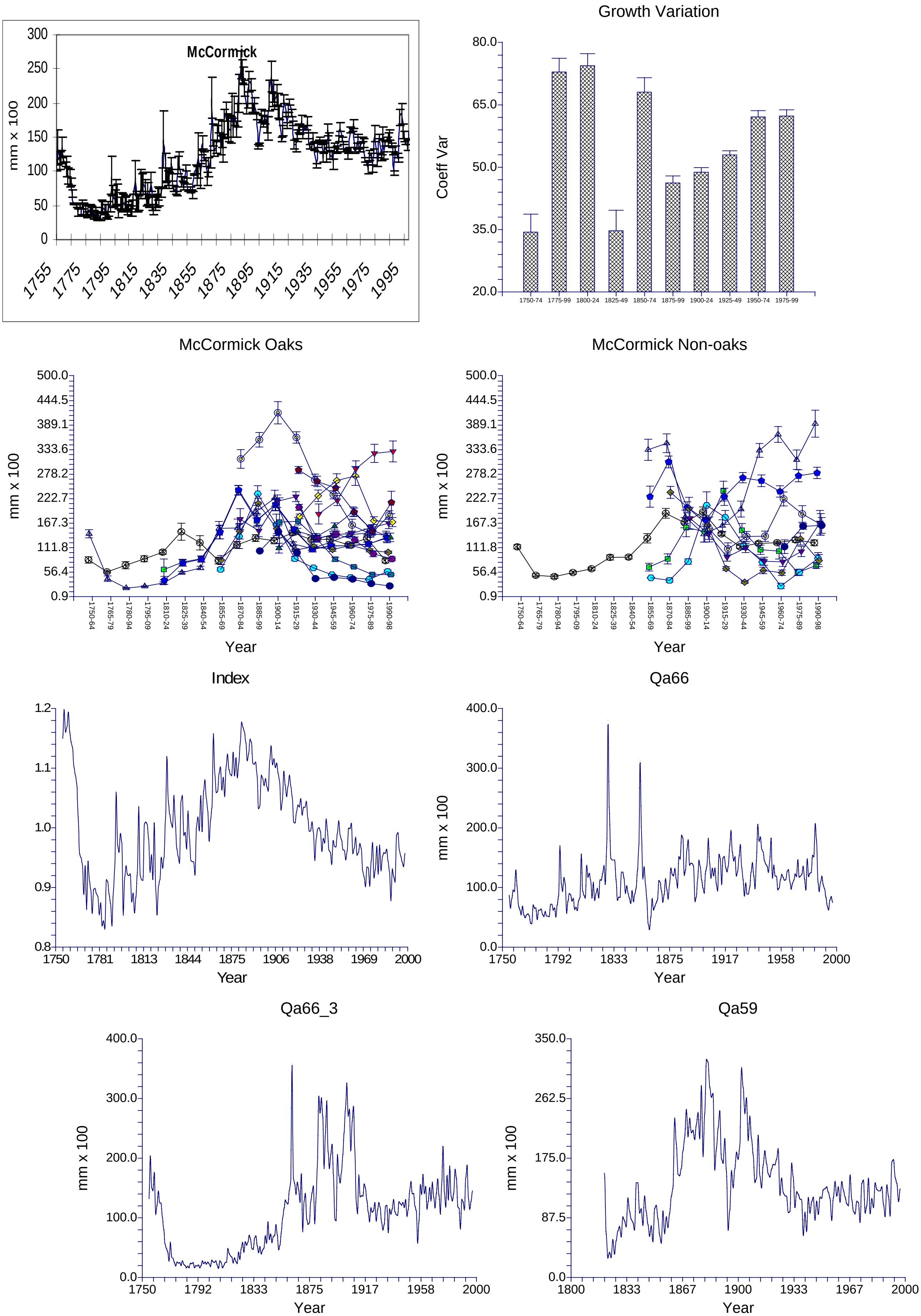
Red Oak Stands
- Crabtree Woods
- Messenger Dry-meisc
- Messenger Mesic
- Norris Woods
- Busse Woods
- Paw Paw Woods
- Raccoon Grove
- St. Francis Woods

Maple Stands
- Busee Woods
- Johnson’s Mound
- Lloyd Woods
- Maple Grove
- Meacham Grove
- Morton Arboretum
- Pilcher Park
- Ryerson Forest Preserve
- River Road Woods

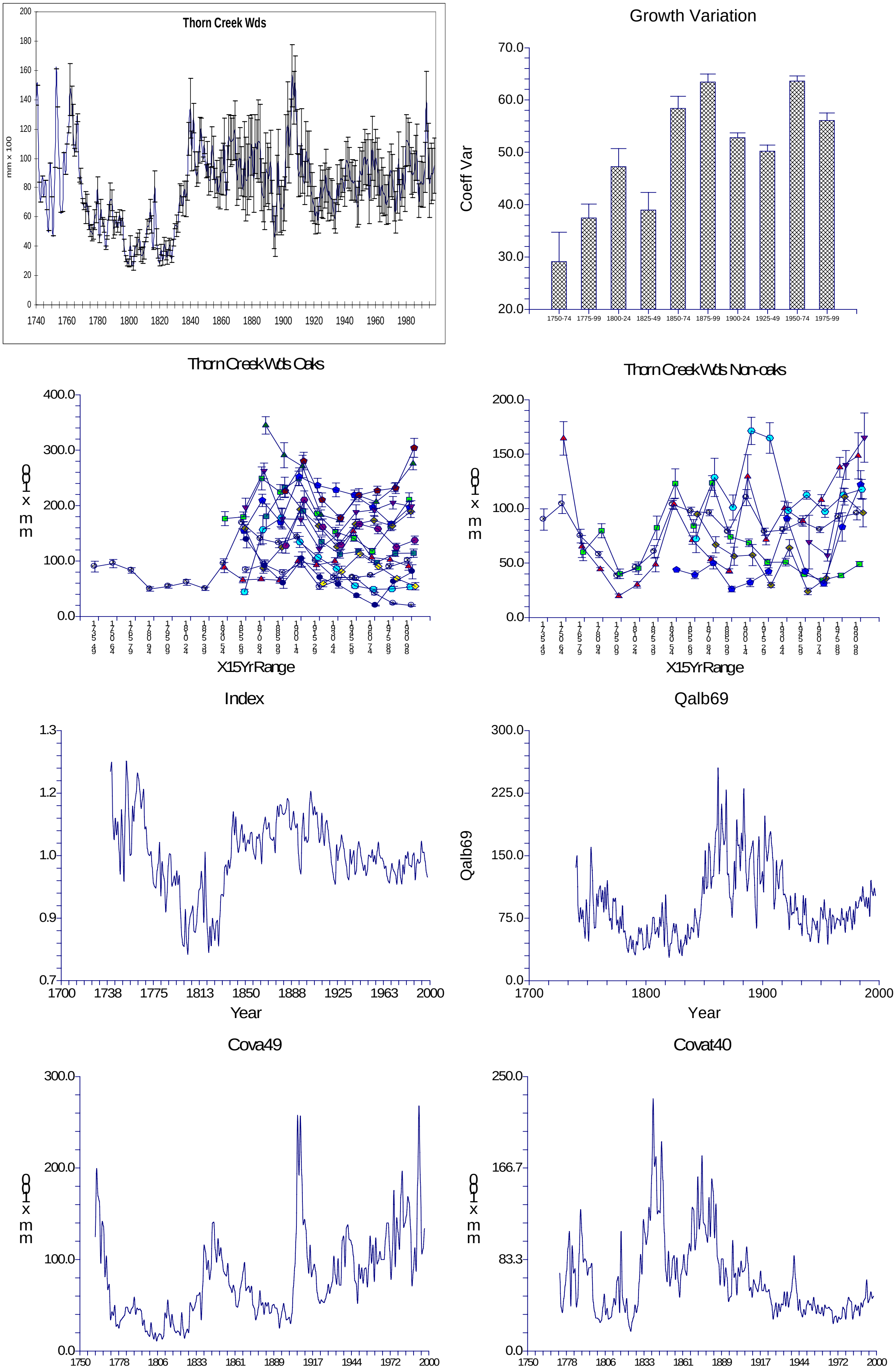
Savannas
- Bluff Springs Fen Savanna
- Silver Springs Savanna
- Spring Creek Savanna
- McDowell Grove Savanna



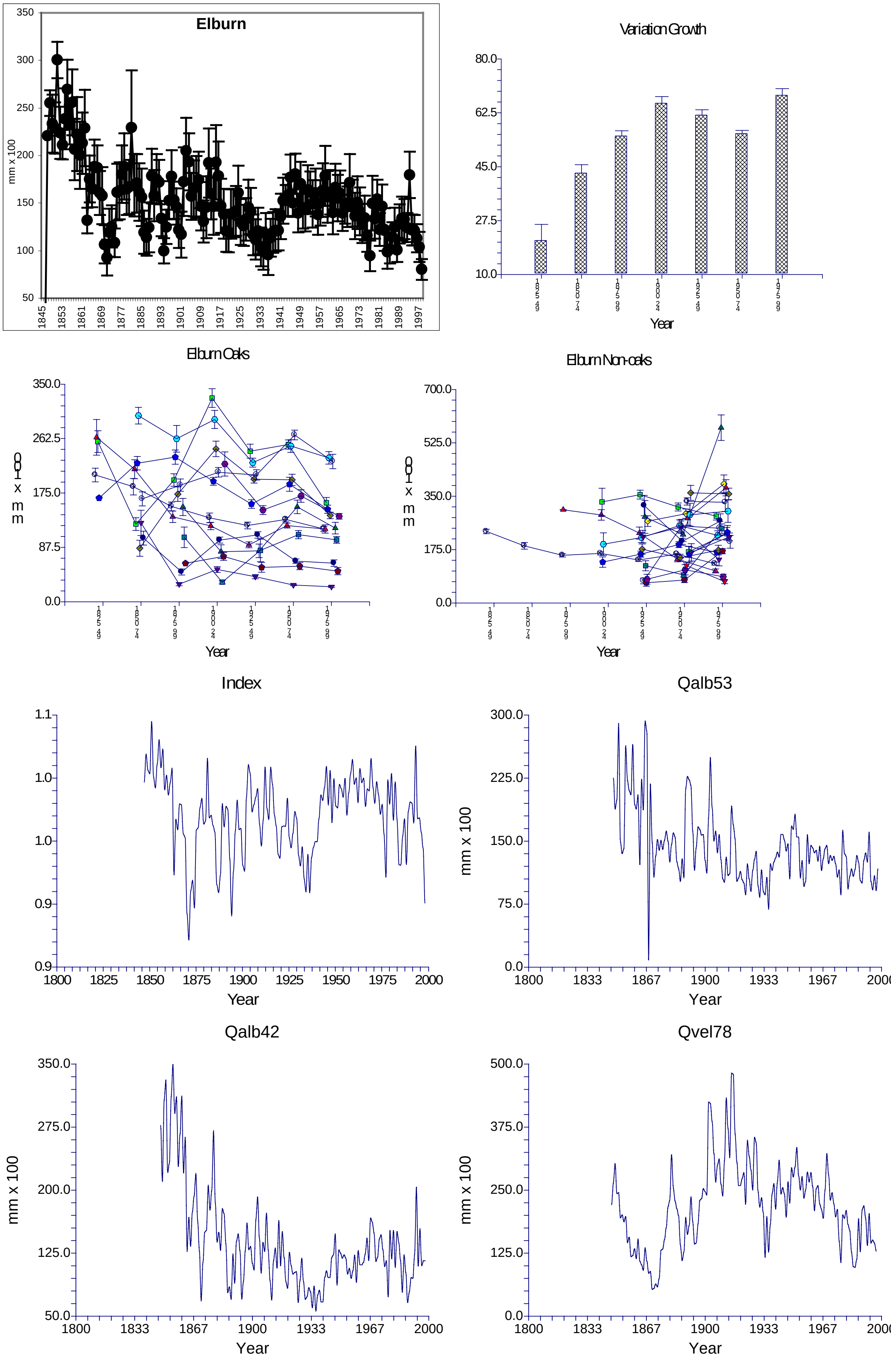
Appendix II. Johnson's mound dry-mesic stand chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



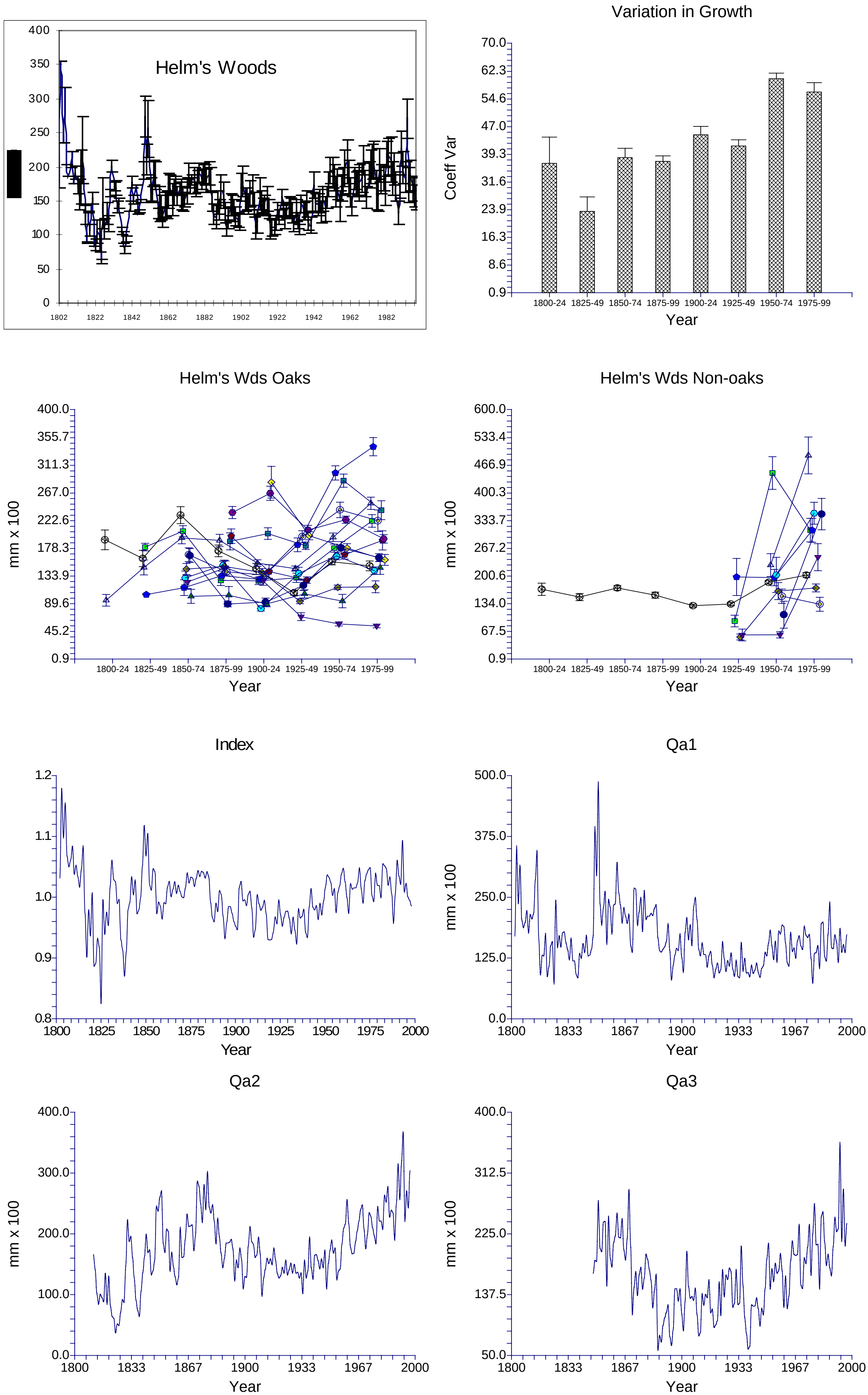
Appendix II. McCormick Ravine dry-mesic stand chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



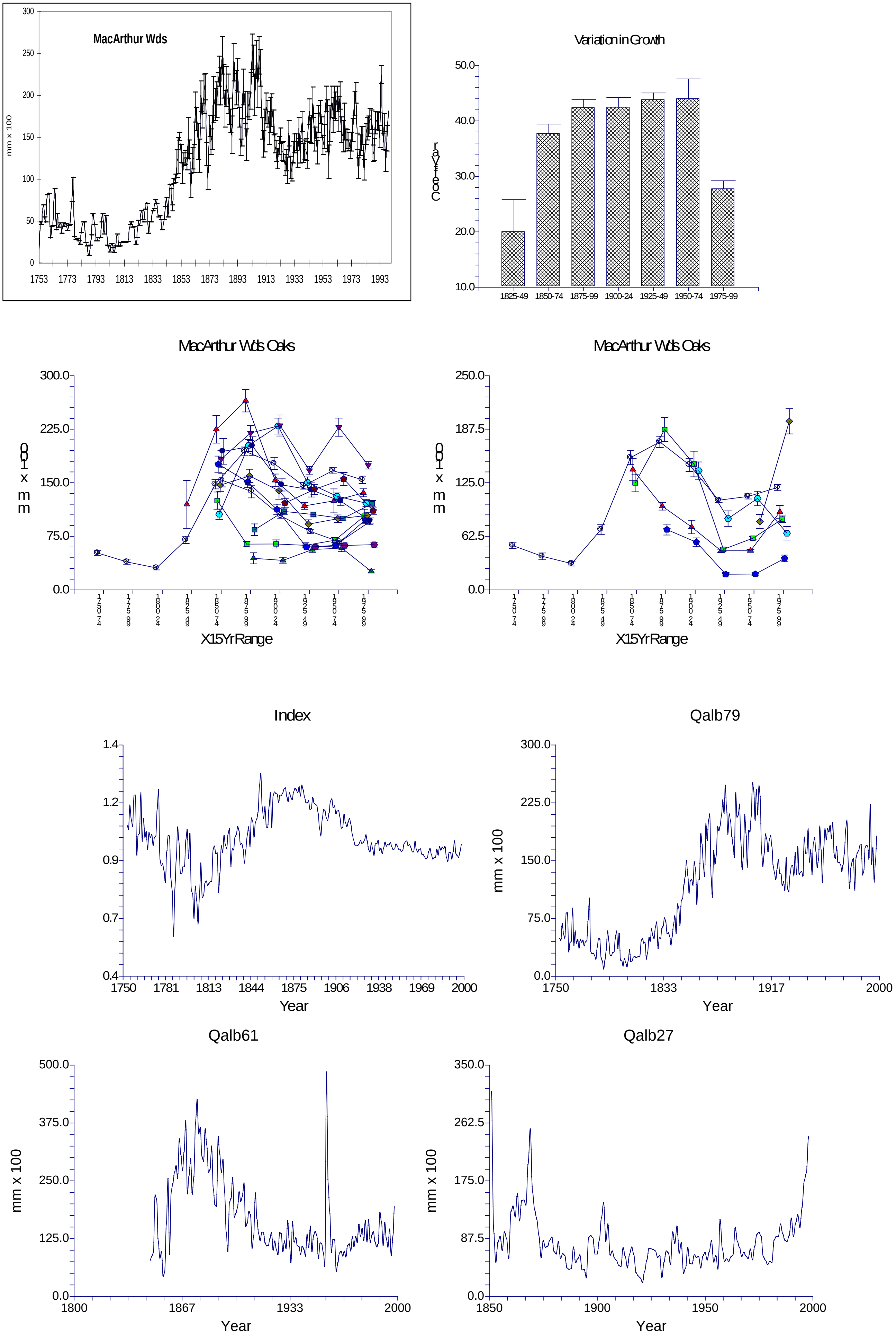
Appendix II. Thorn Creek Woods stand chronology; Coefficient of Variation, oak and non-oak variation (compared to oak mean) in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



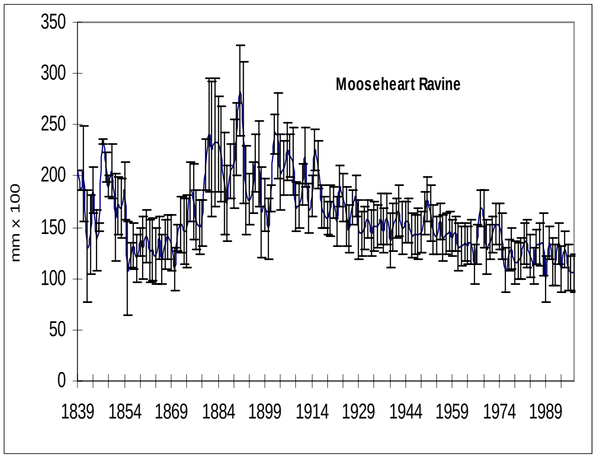
Appendix II. Elburn Forest Preserve stand chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

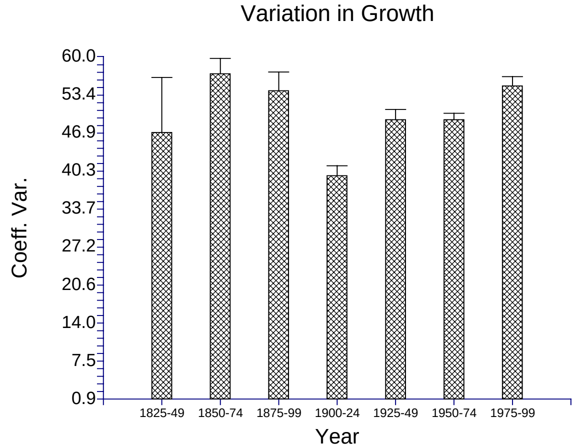


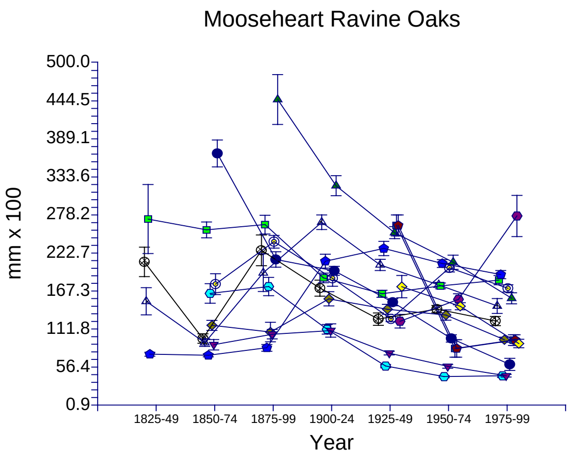
Appendix II. Helms Woods stand chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

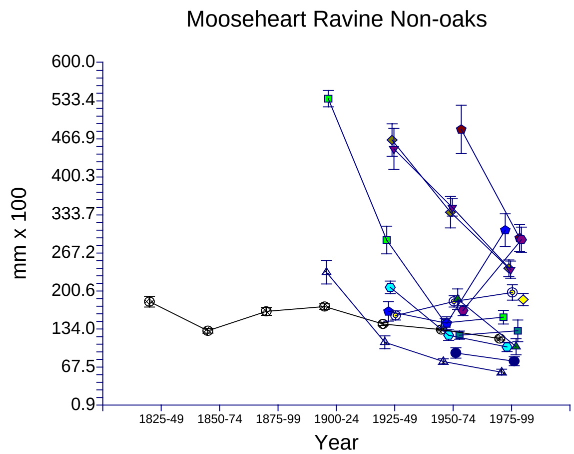


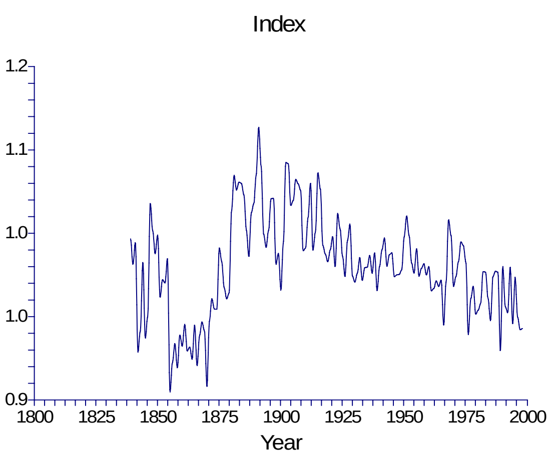
Appendix II. McArthur Woods stand chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

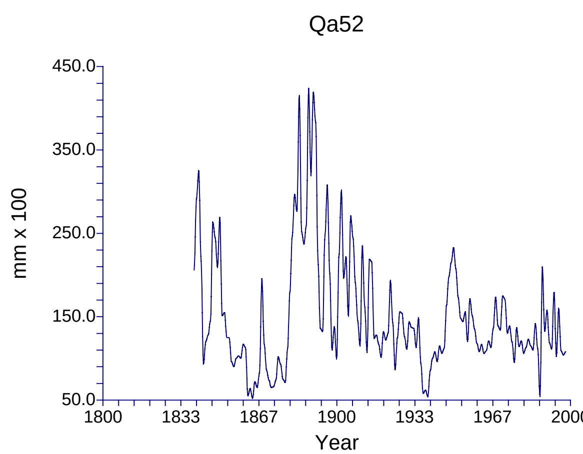


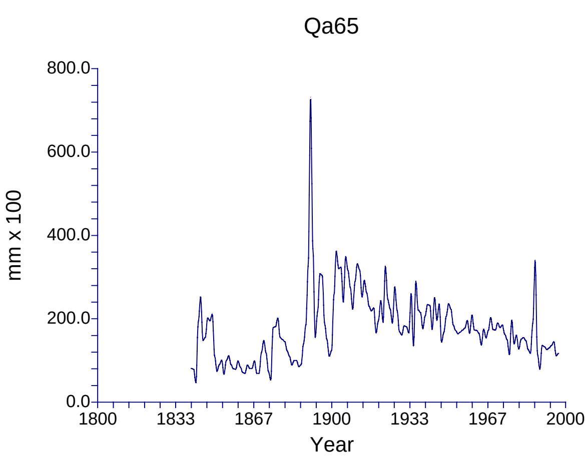


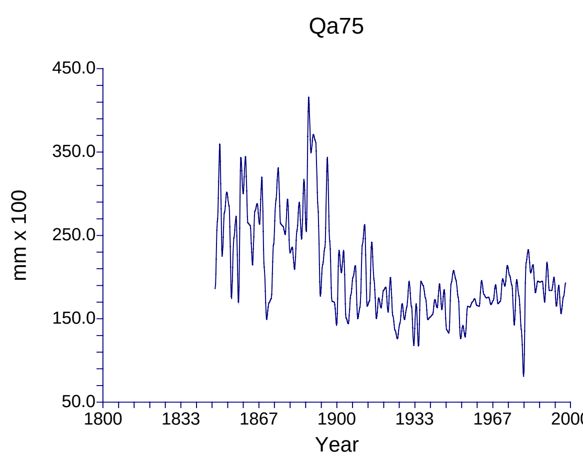




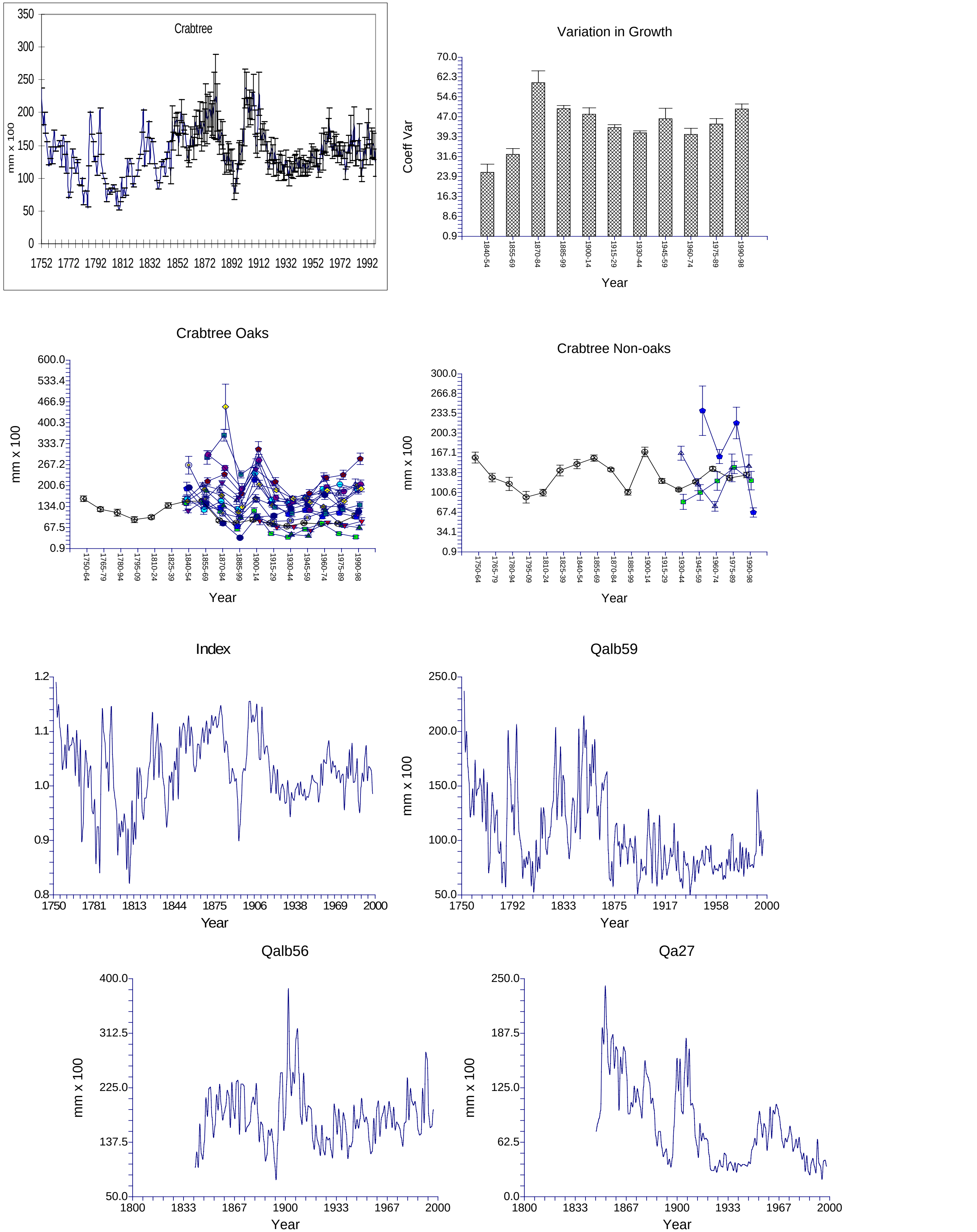




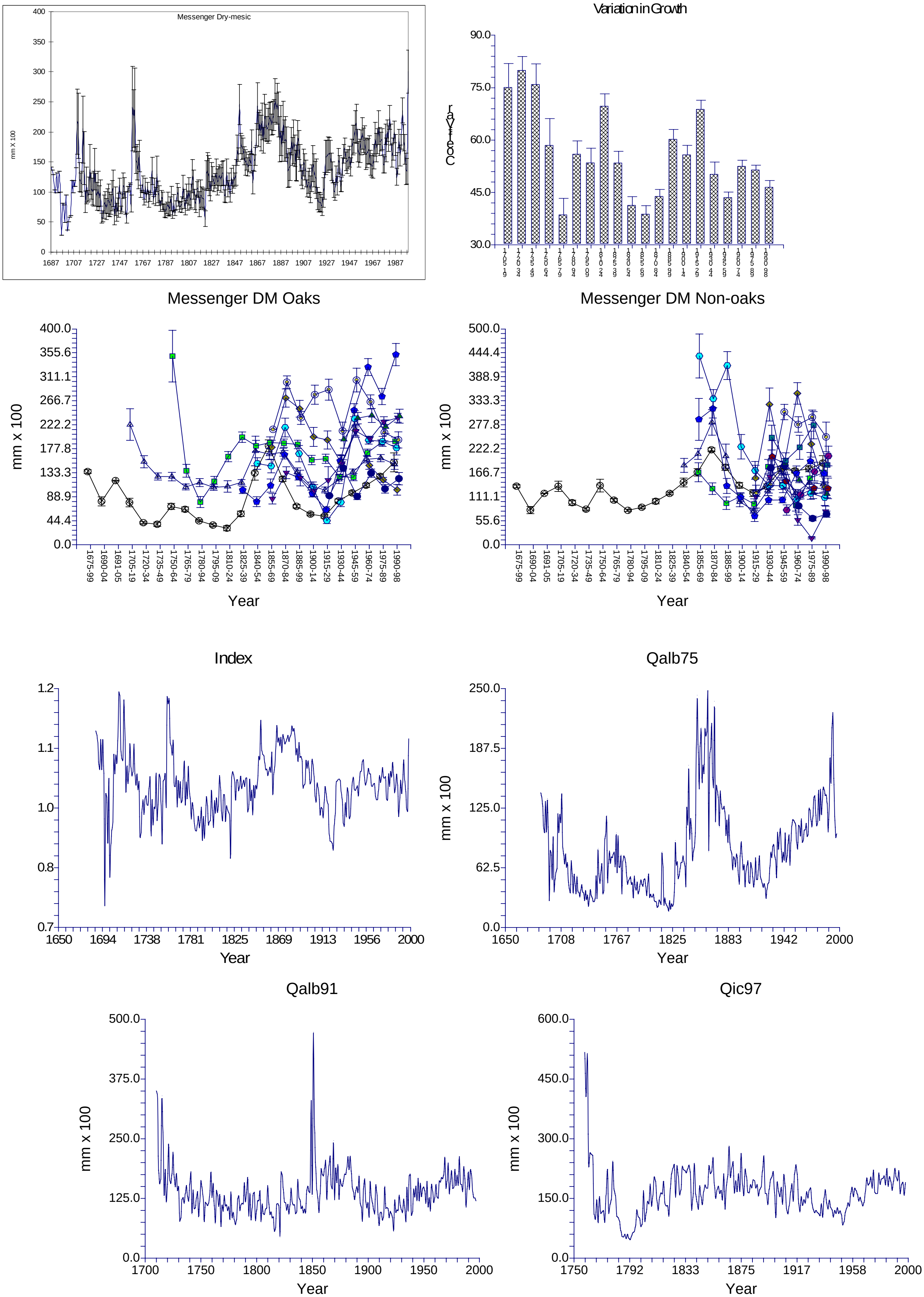




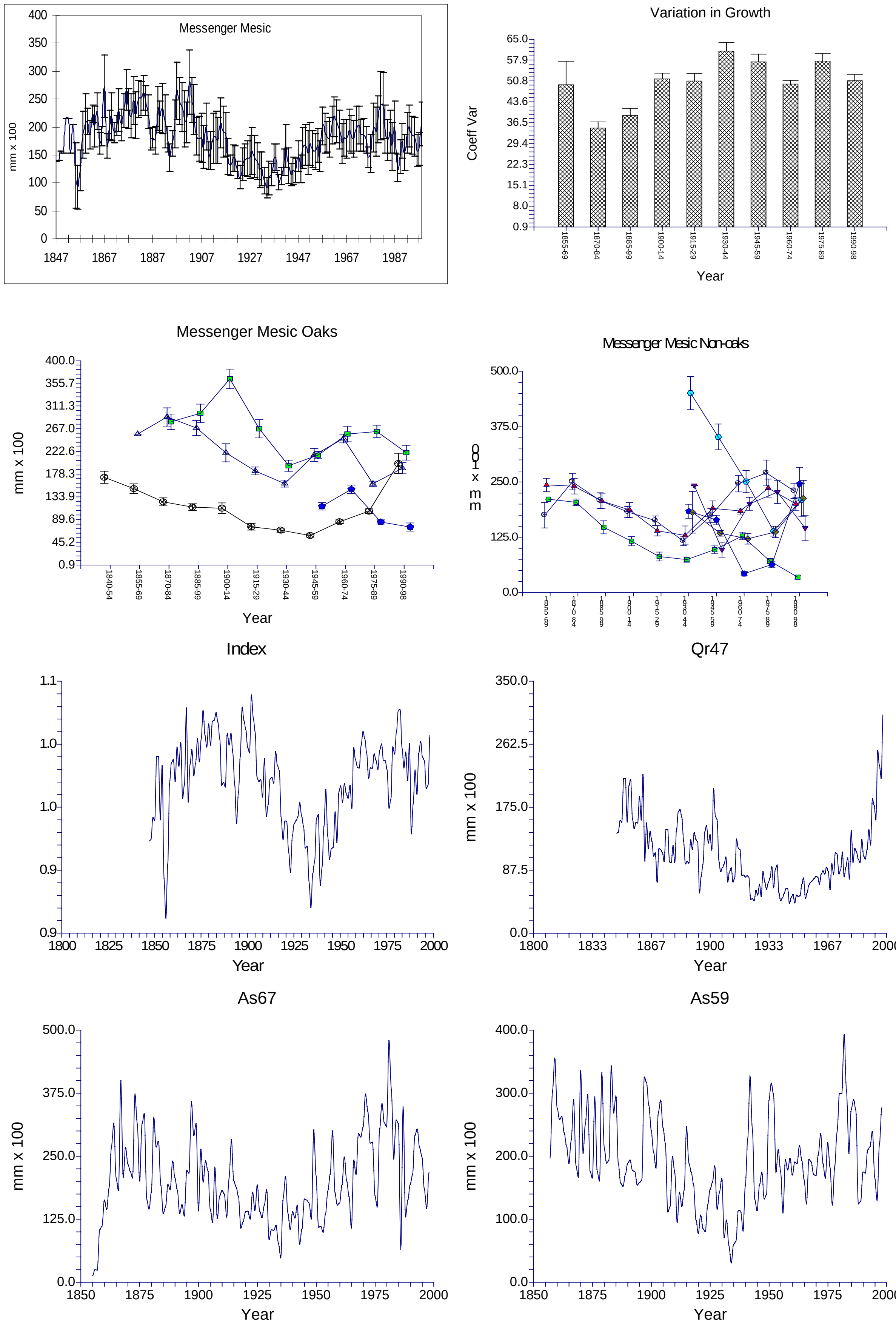
Appendix II. Mooseheart Ravine chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



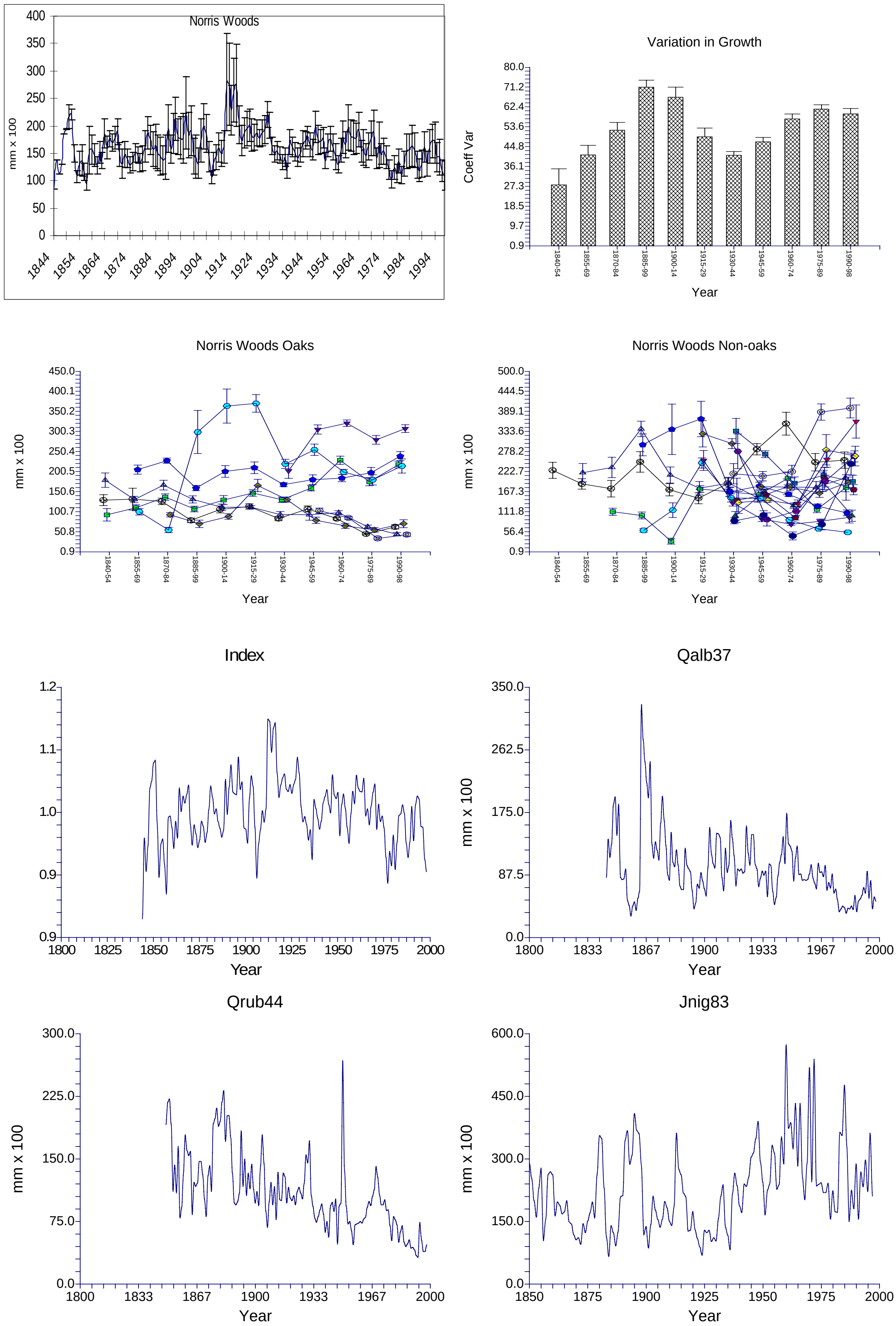
Appendix II. Crabtree Woods chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



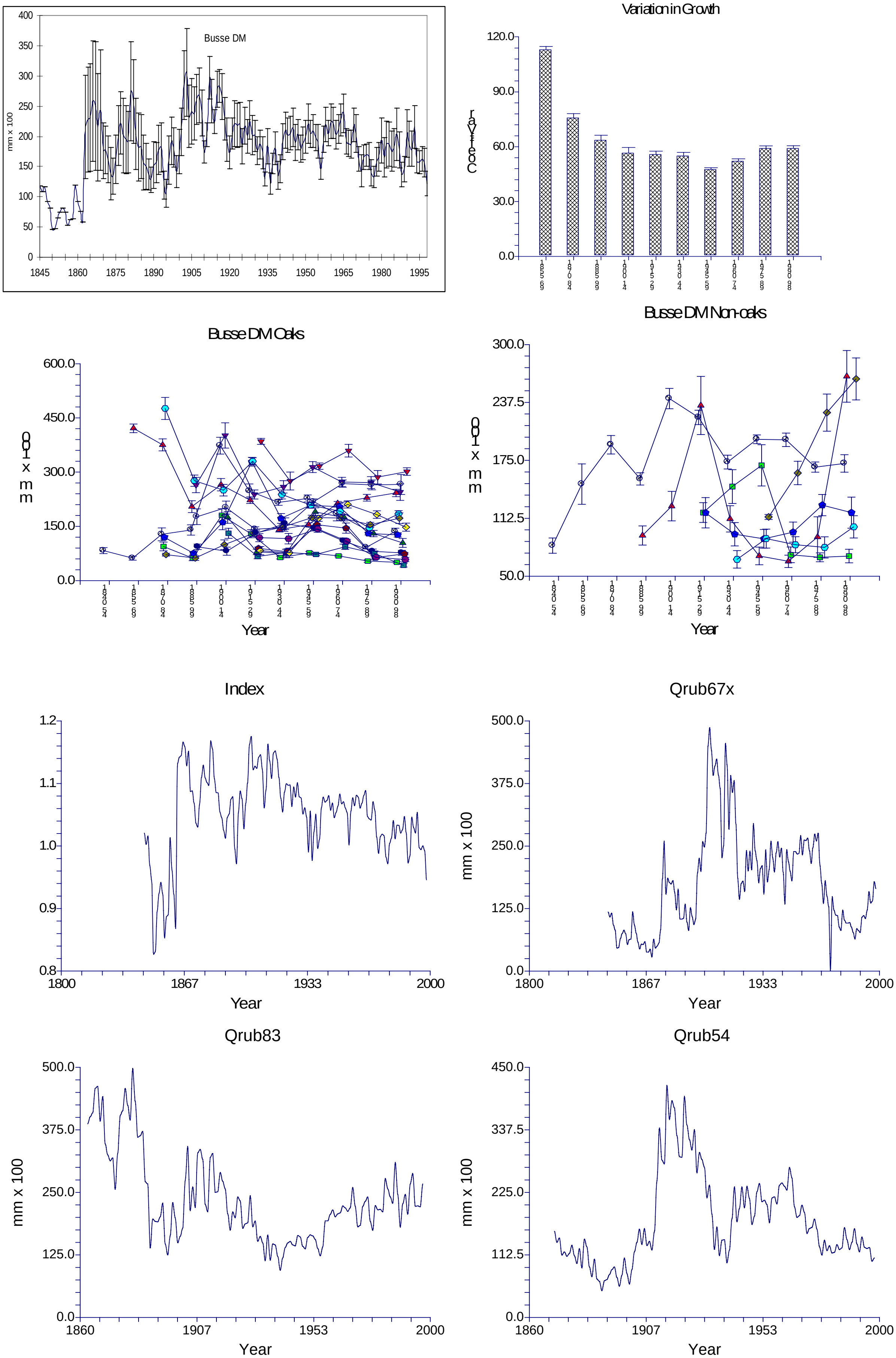
Appendix II. Messenger Woods dry-mesic chronology; Coefficient of Variation, oak and non-oak variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



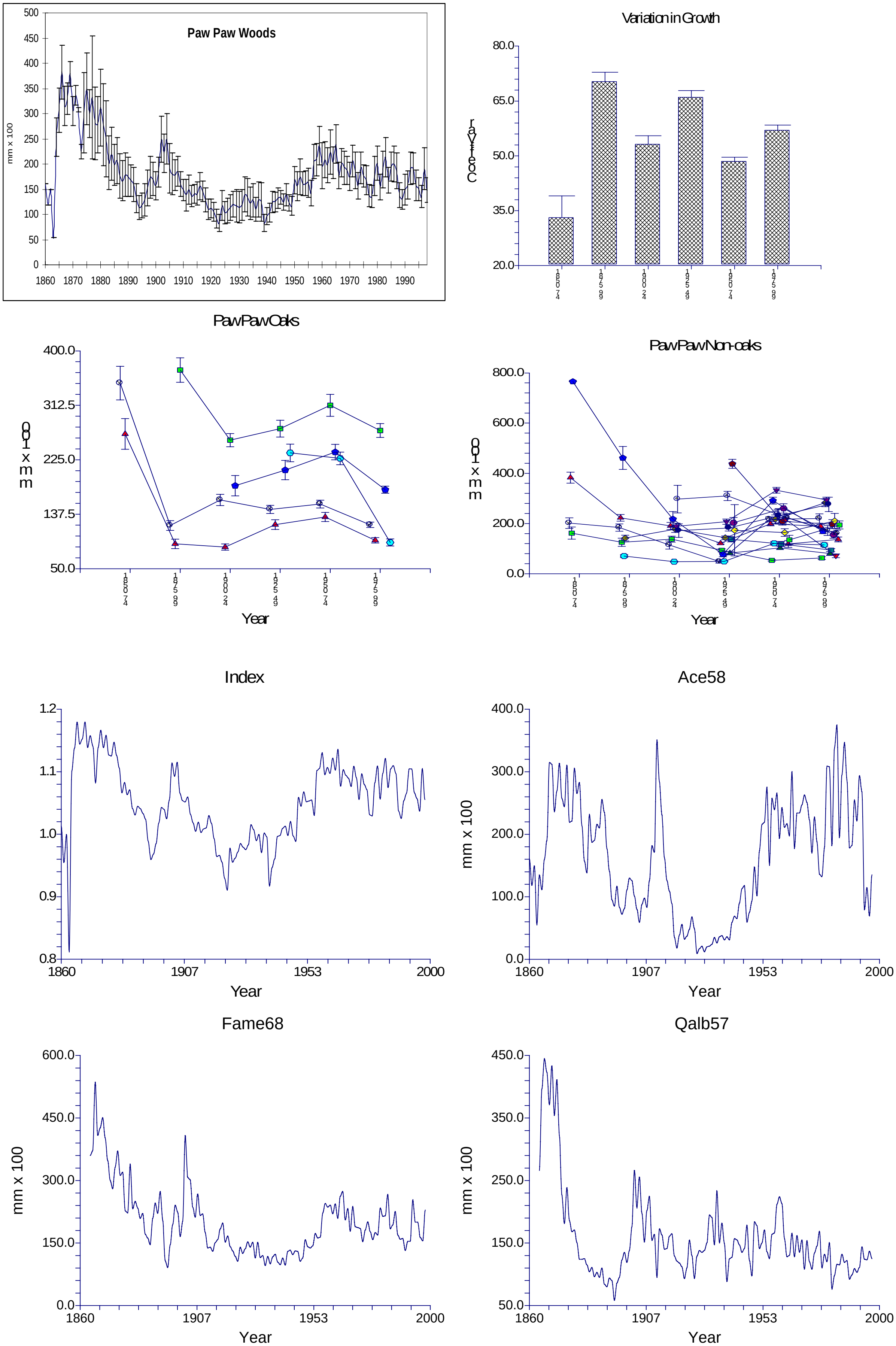
Appendix II. Messenger Woods mesic chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



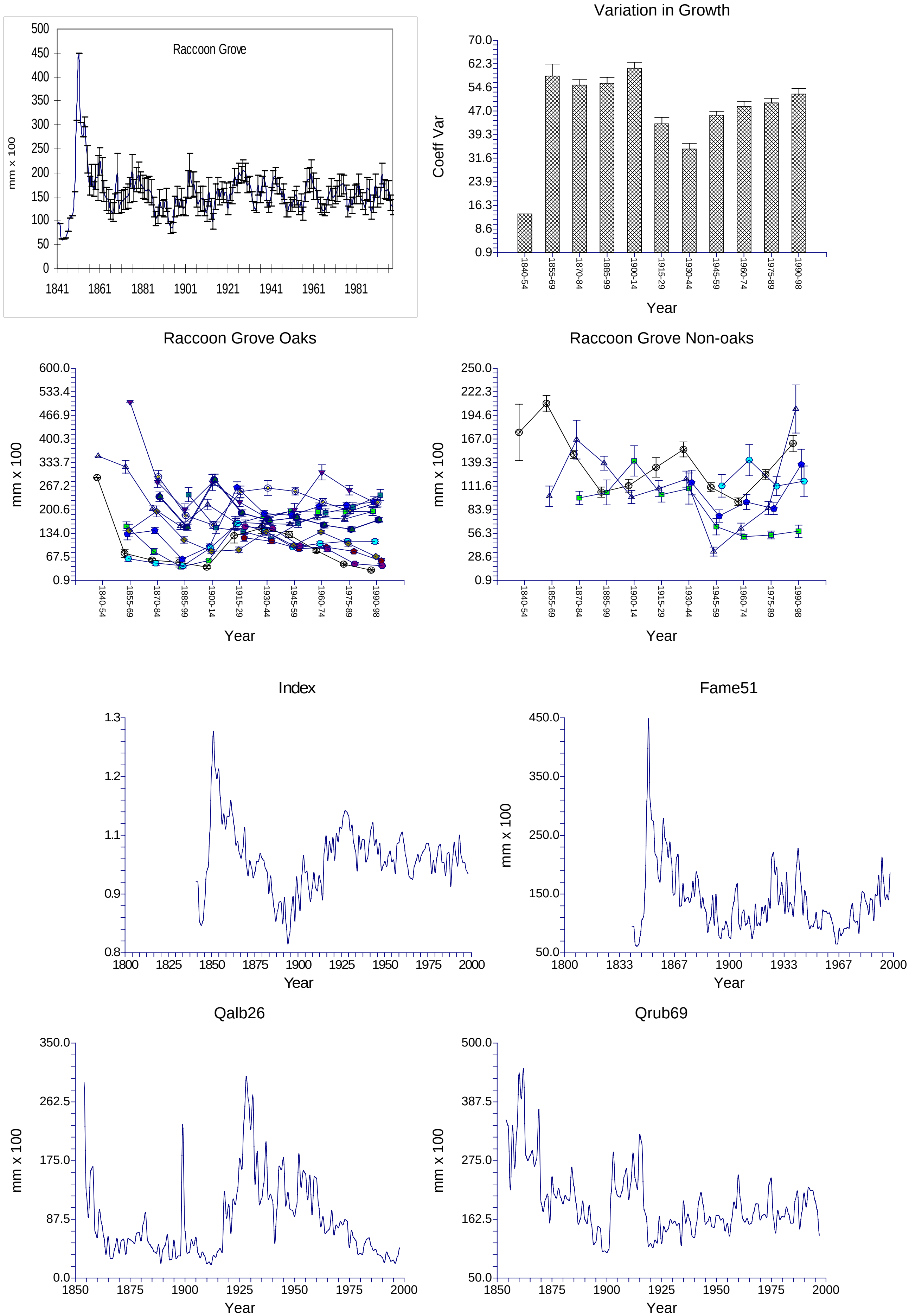
Appendix II. Norris Woods chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



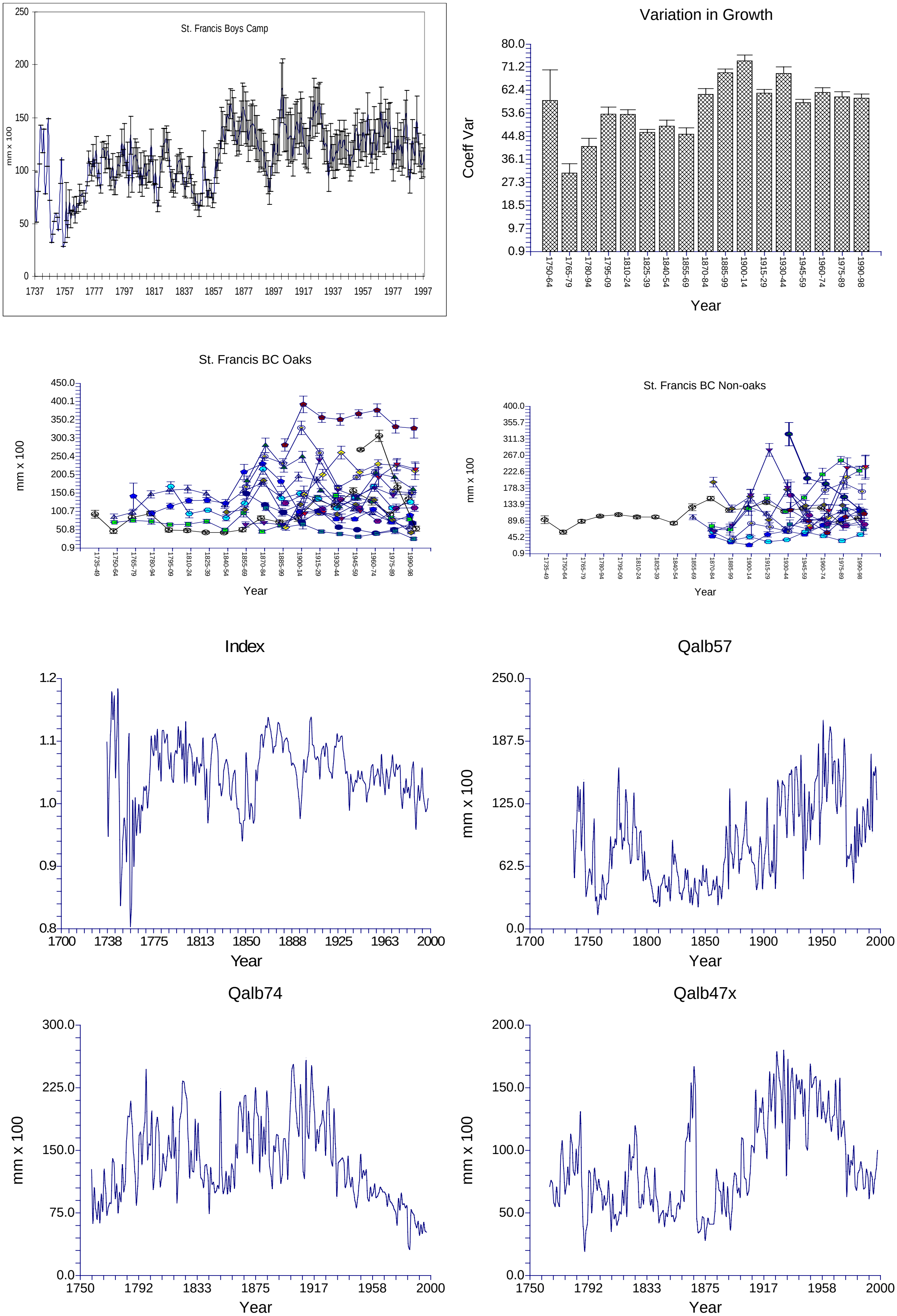
Appendix II. Busse Woods dry-mesic chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



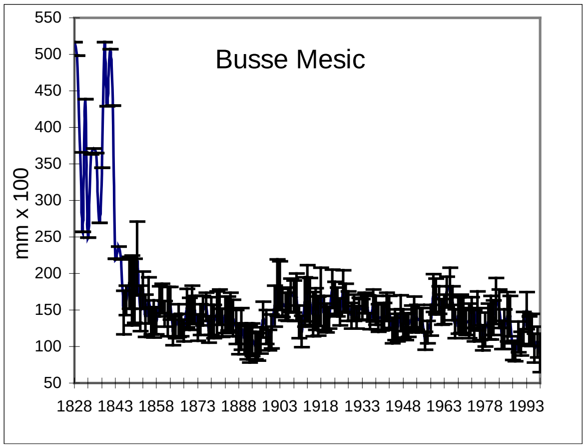
Appendix II. Paw Paw Woods chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

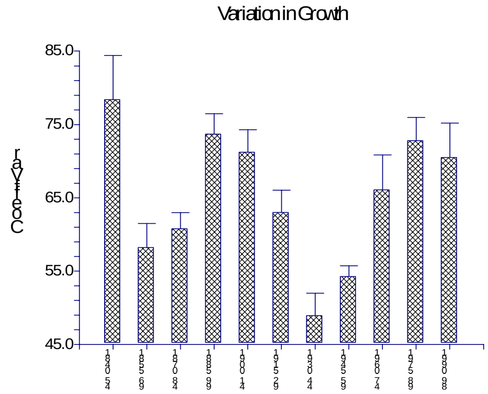


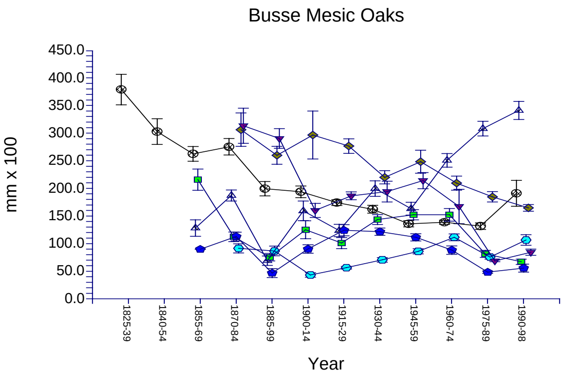
Appendix II. Raccoon Grove chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

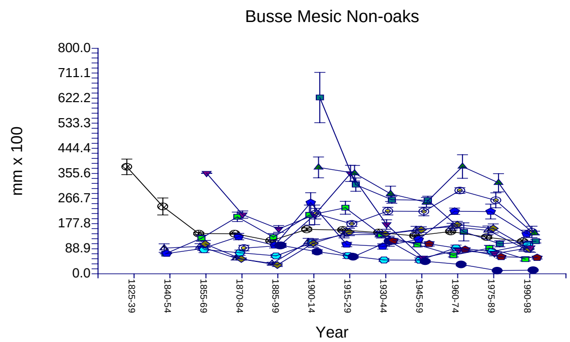


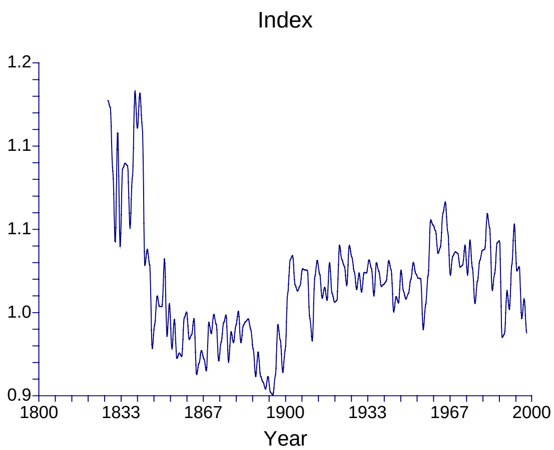
Appendix II. St. Francis Woods chronology; Coefficient of Variation, oak and non-oak variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

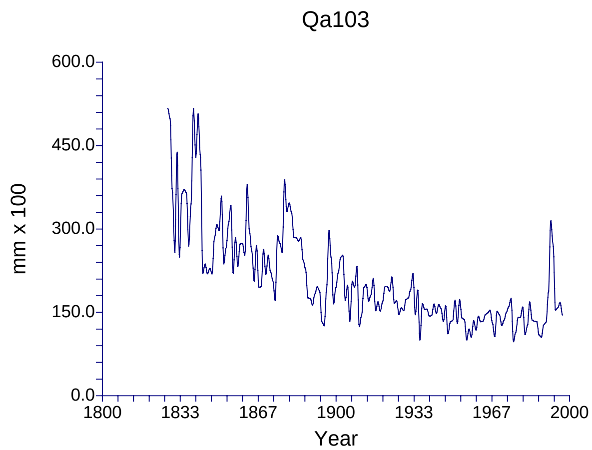


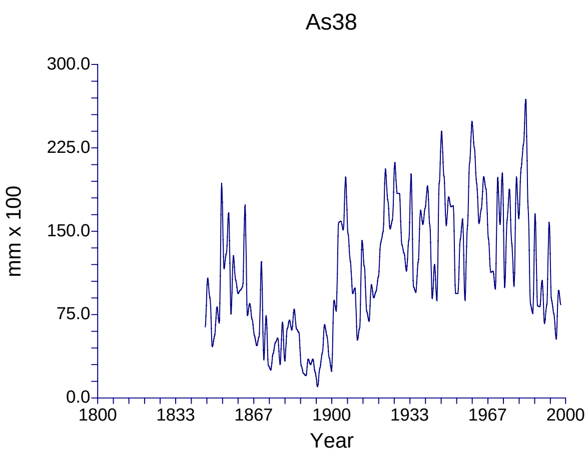


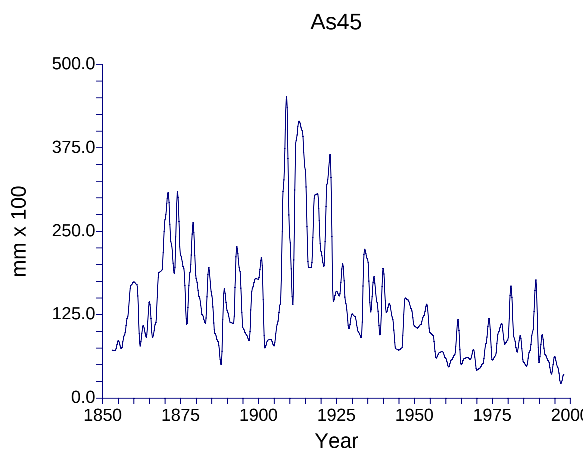




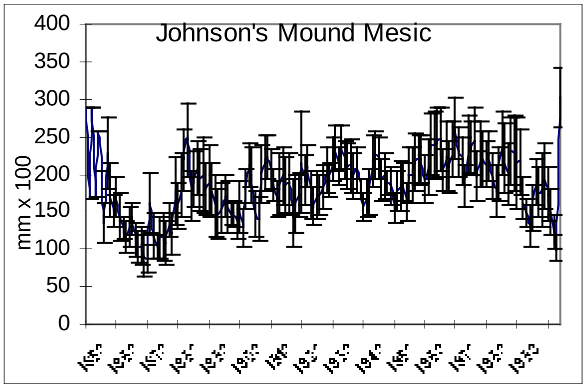


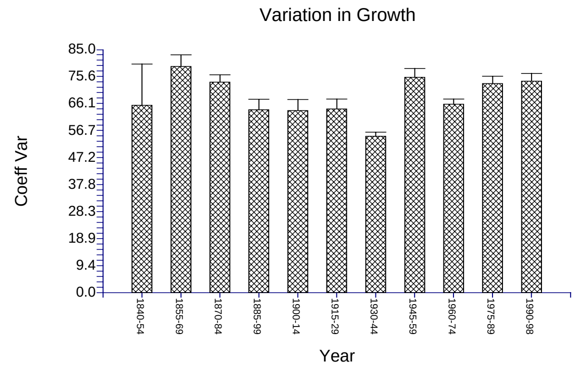


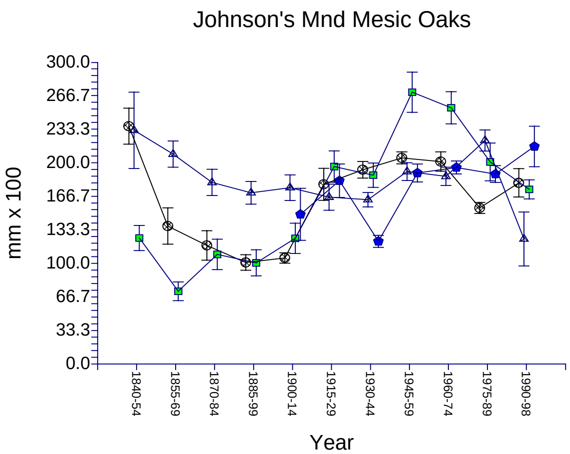


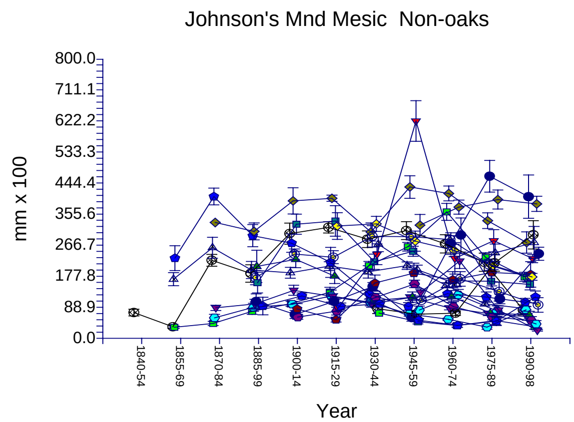


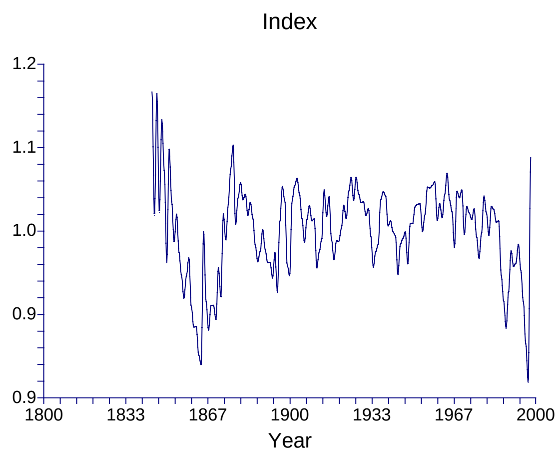
Appendix II. Busse Woods mesic chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

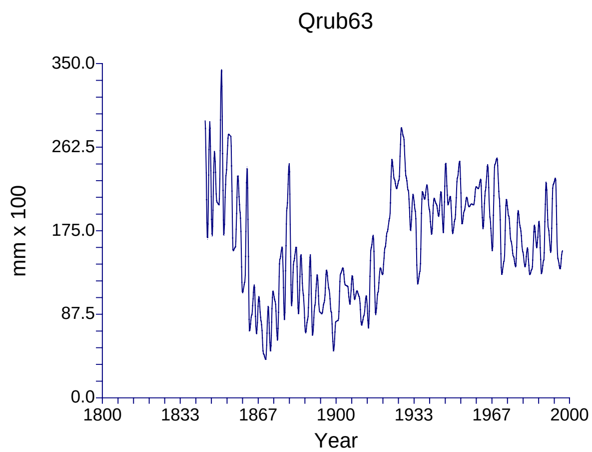


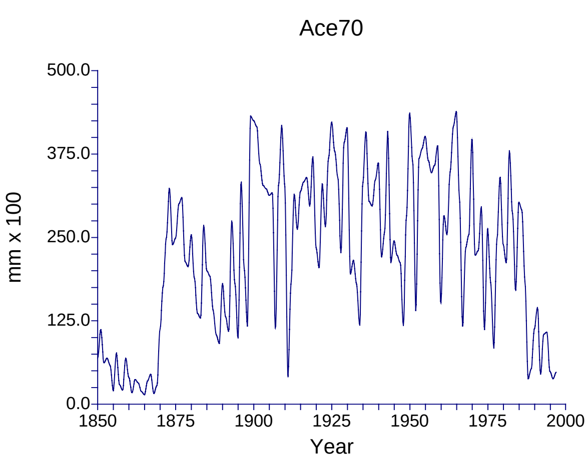


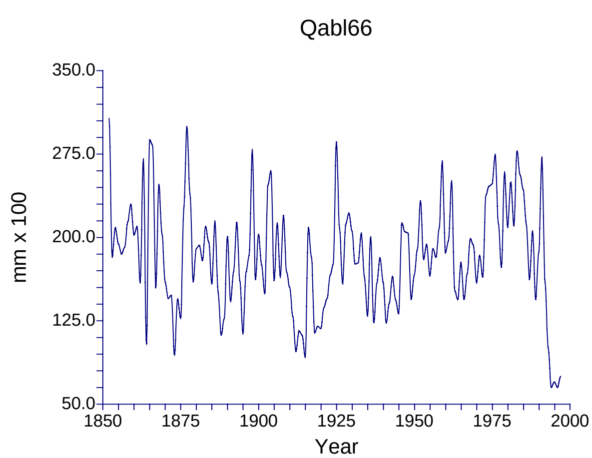




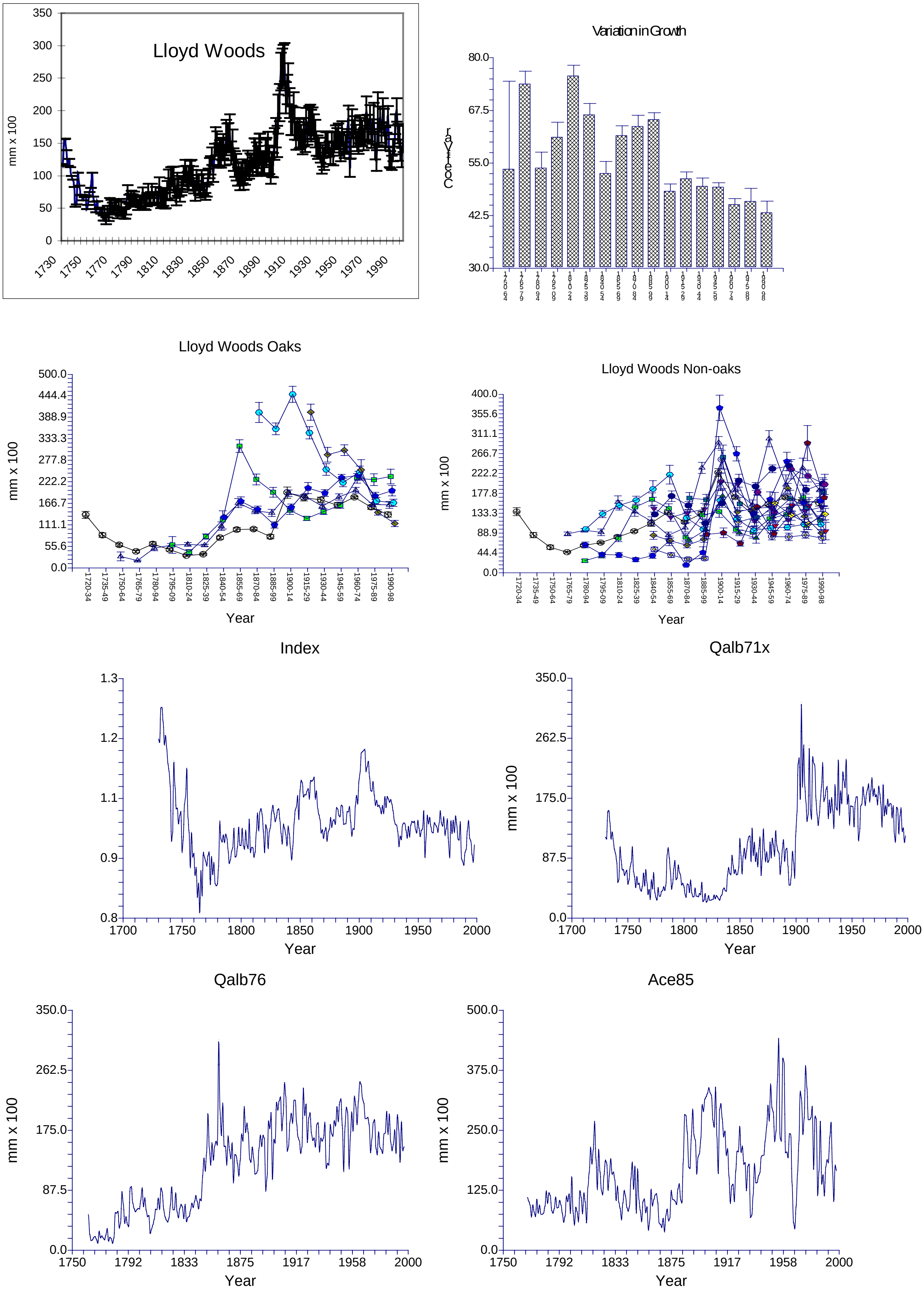




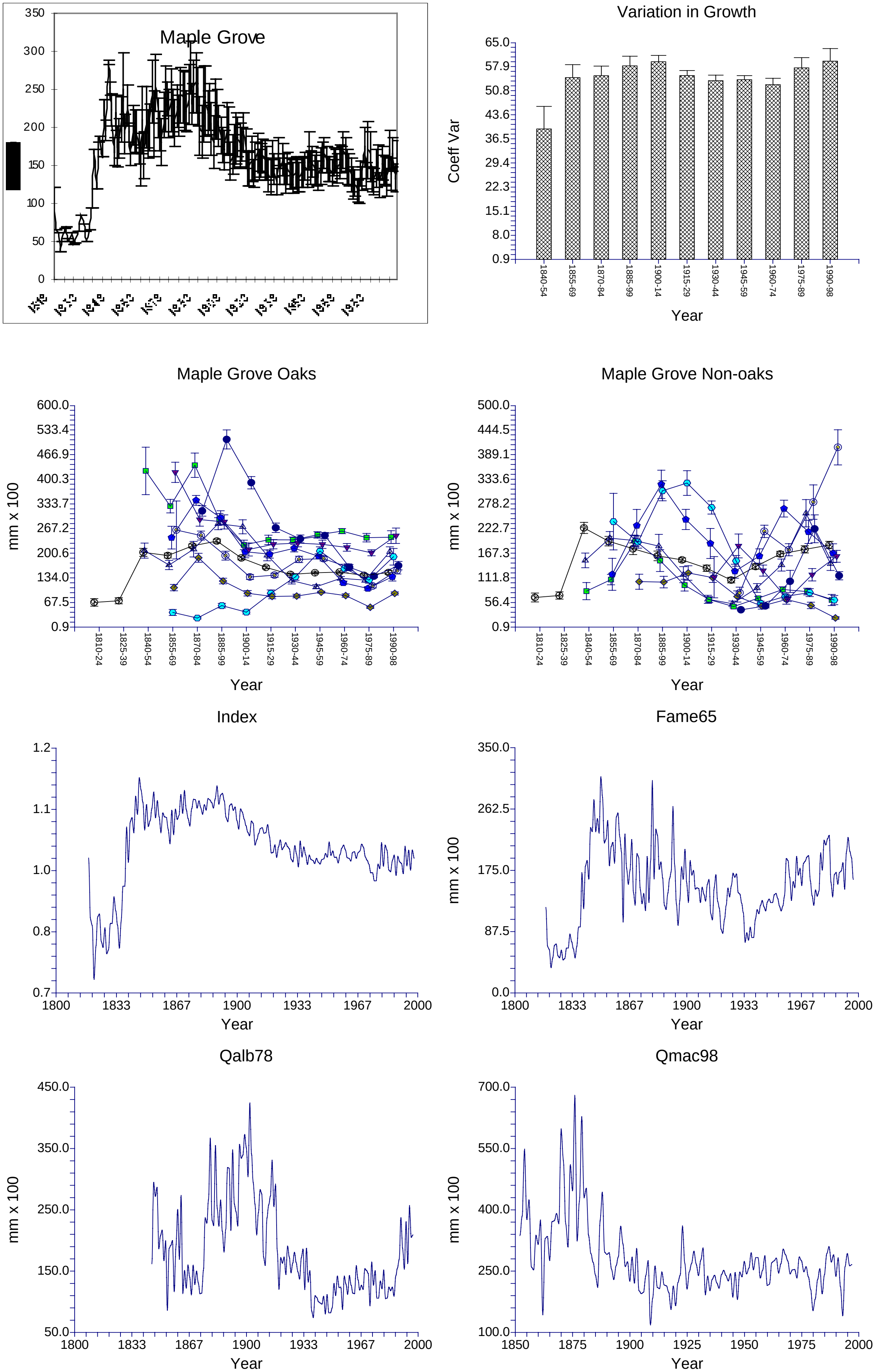




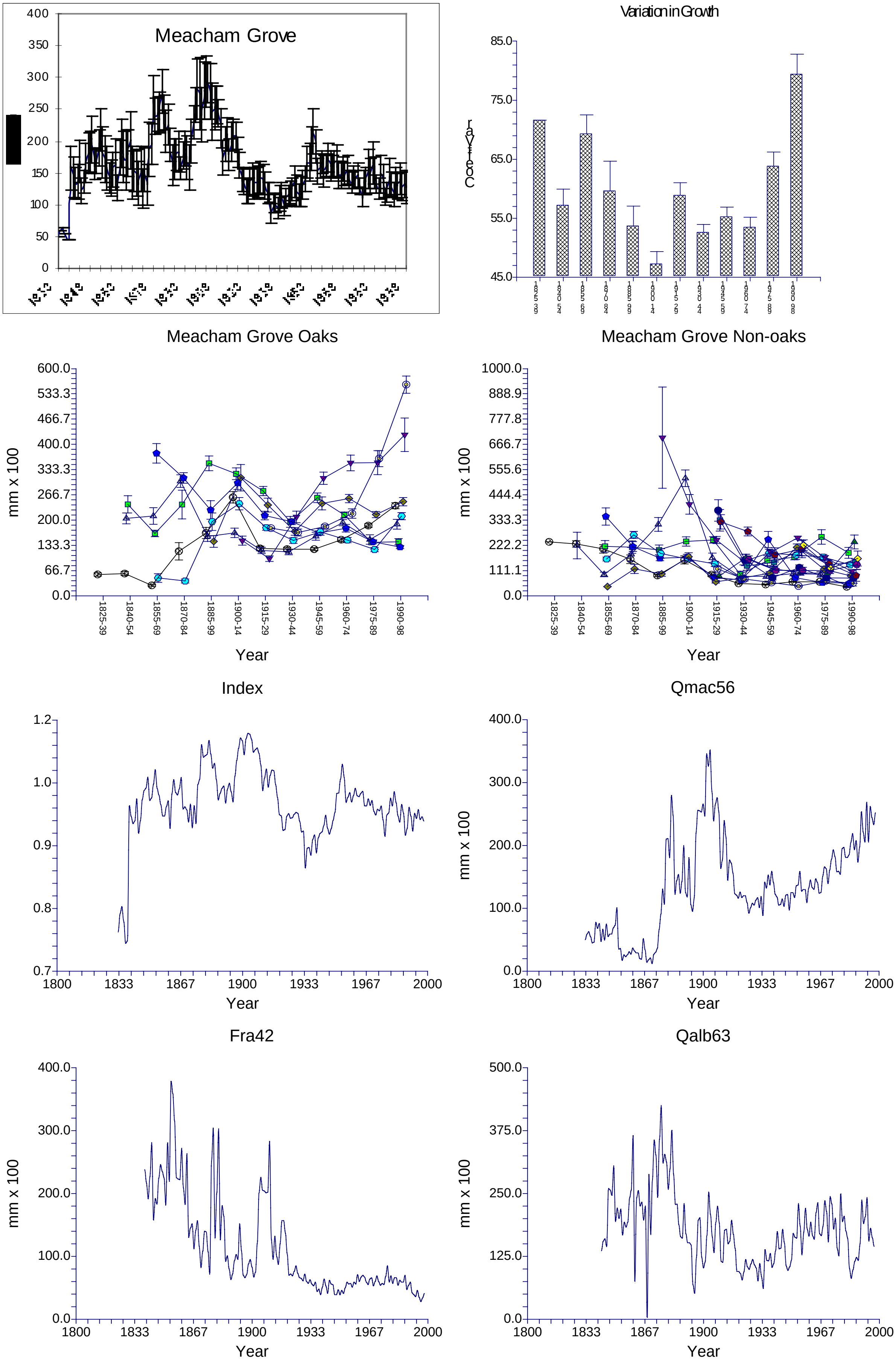
Appendix II. Johnson's Mound mesic chronology; Coefficient of Variation, oak and non-oak variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



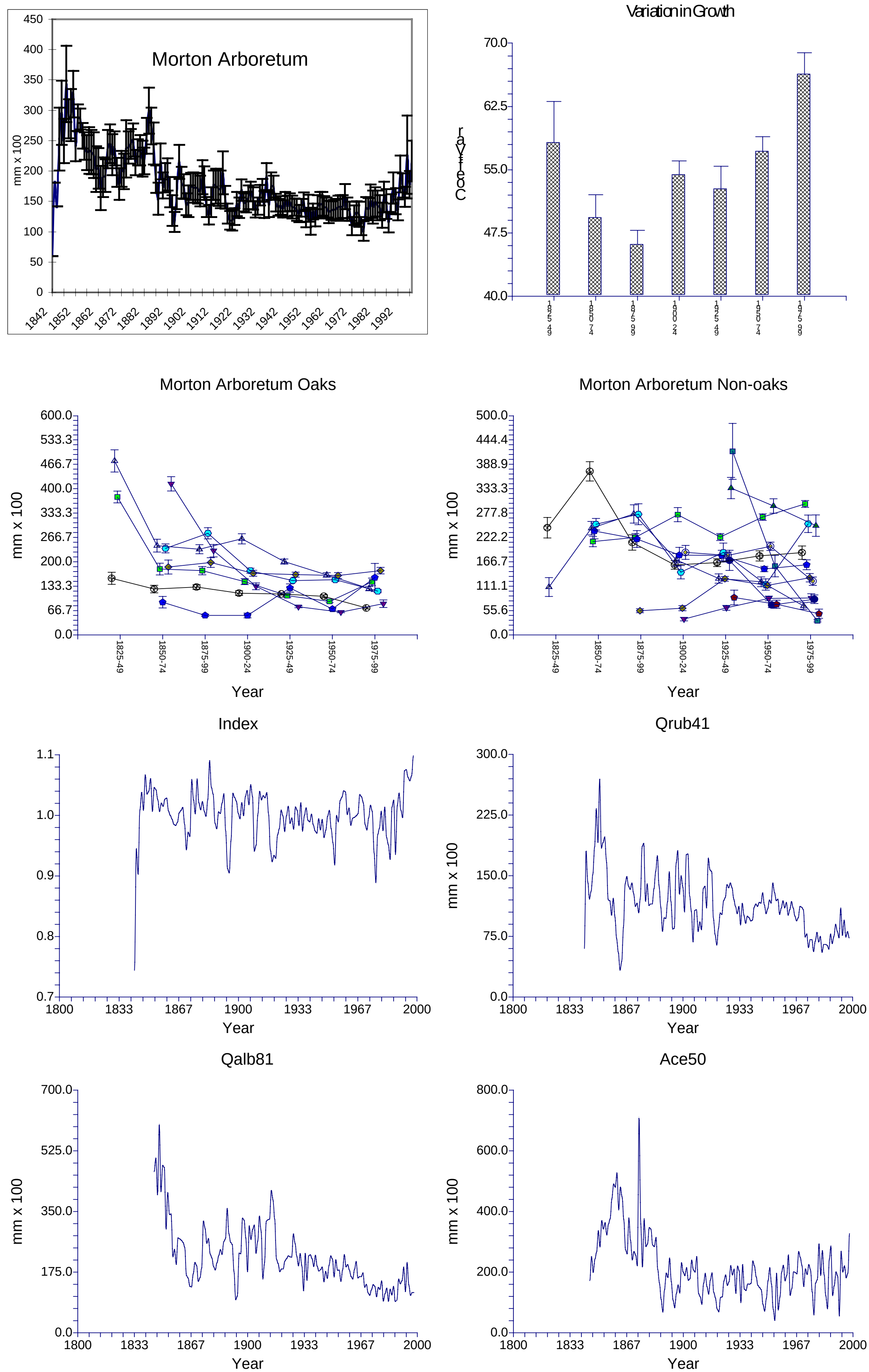
Appendix II. Lloyd Woods chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



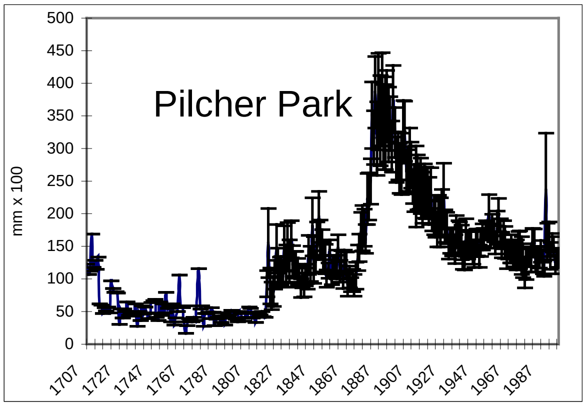
Appendix II. Maple Grove chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

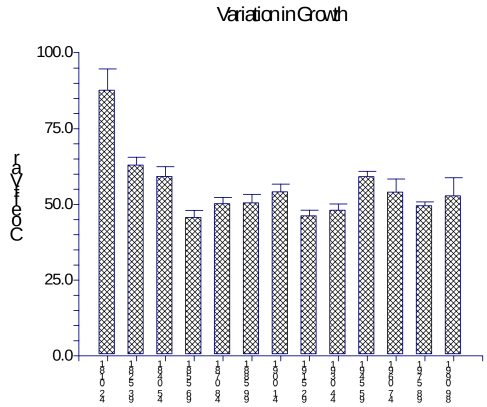


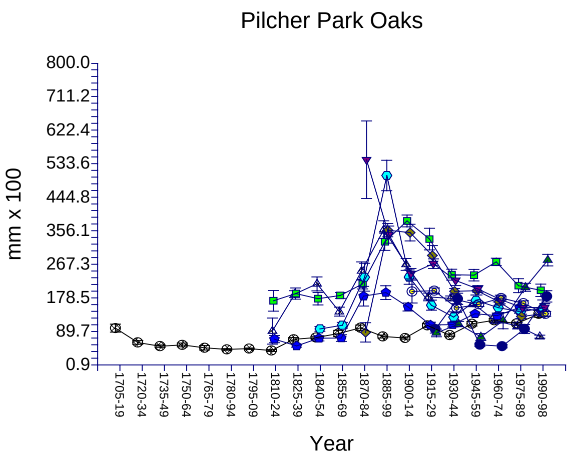
Appendix II. Meacham Grove chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

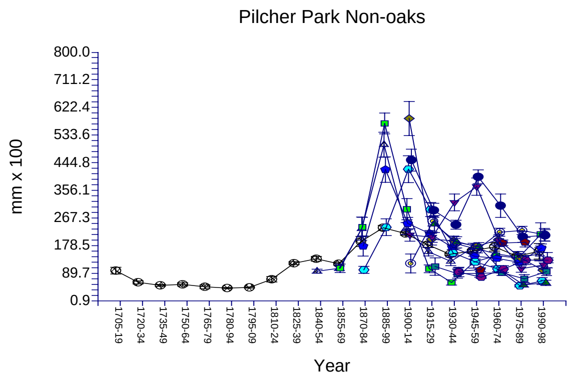


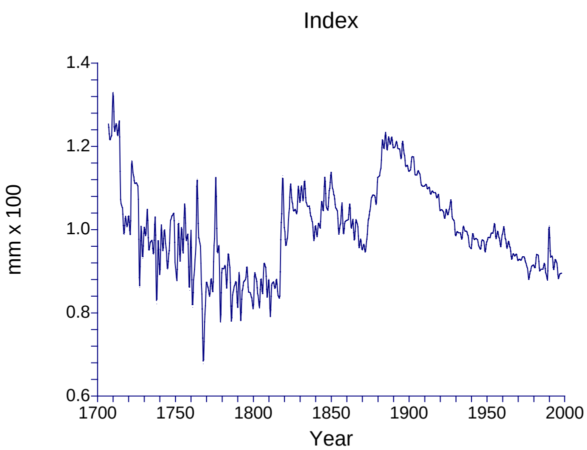
Appendix II. Morton Arboretum Grove chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

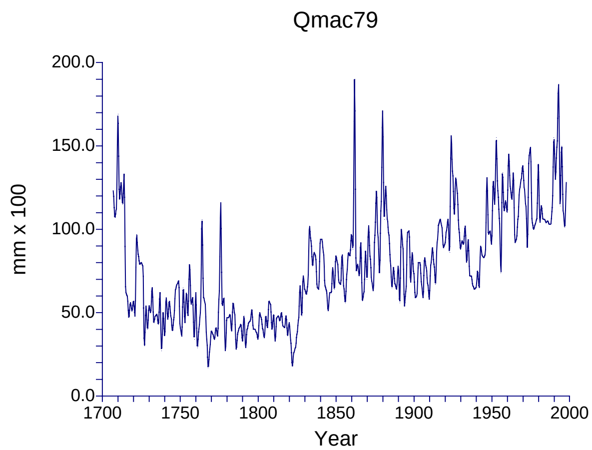


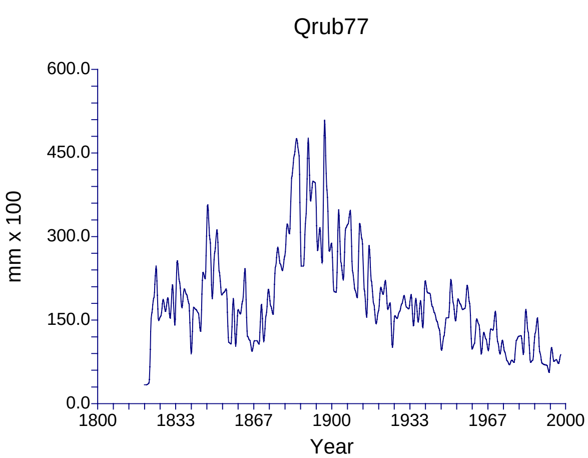


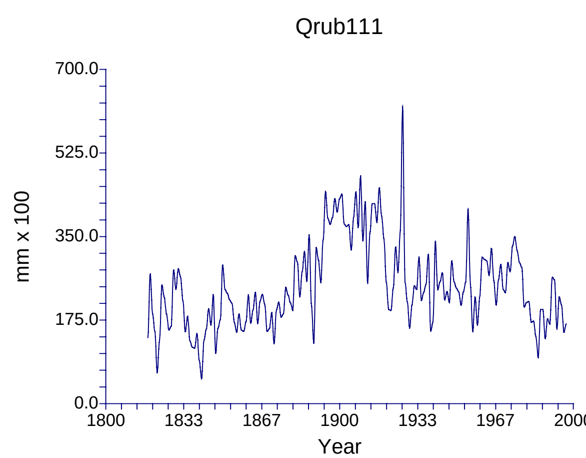




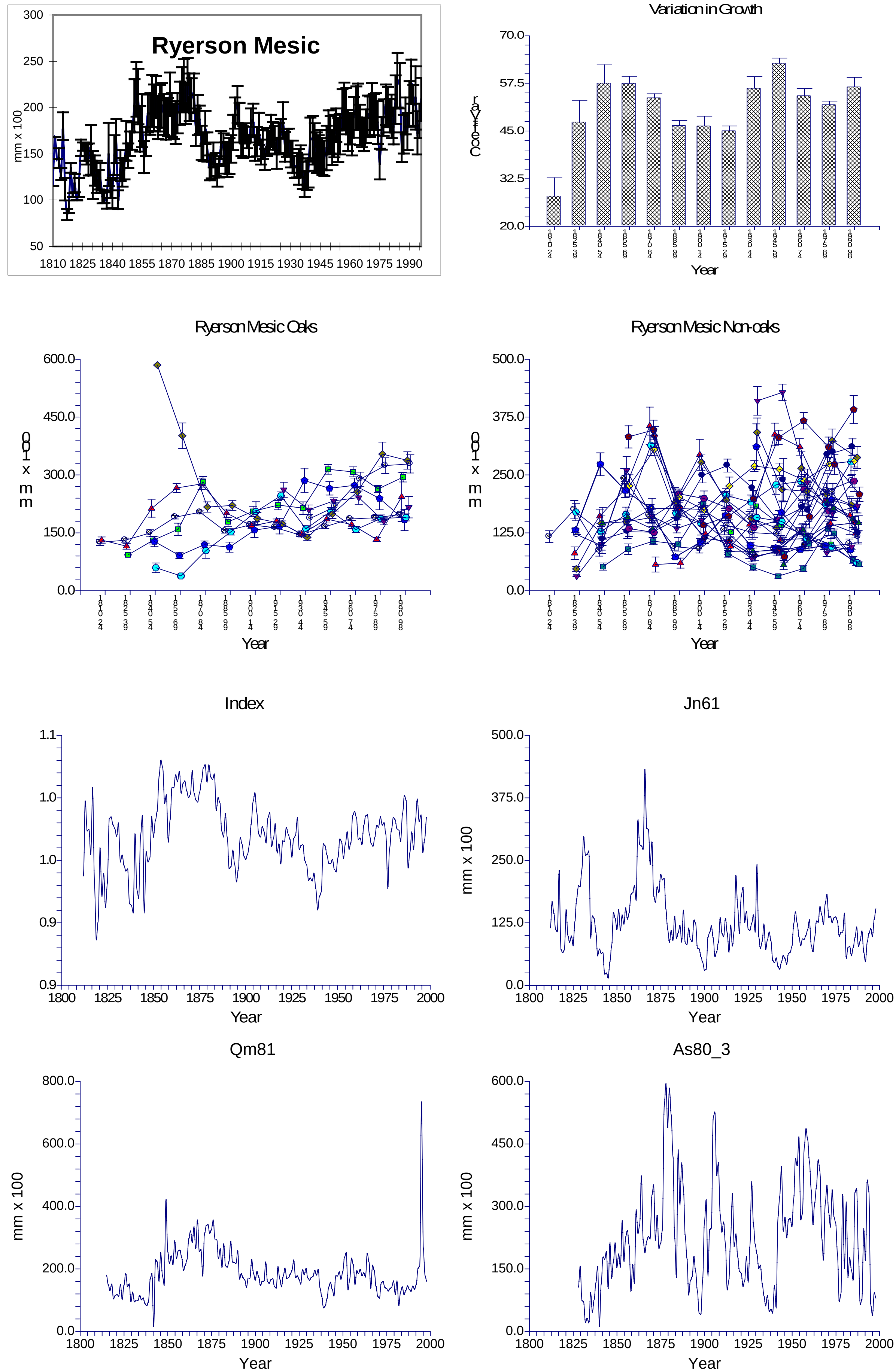




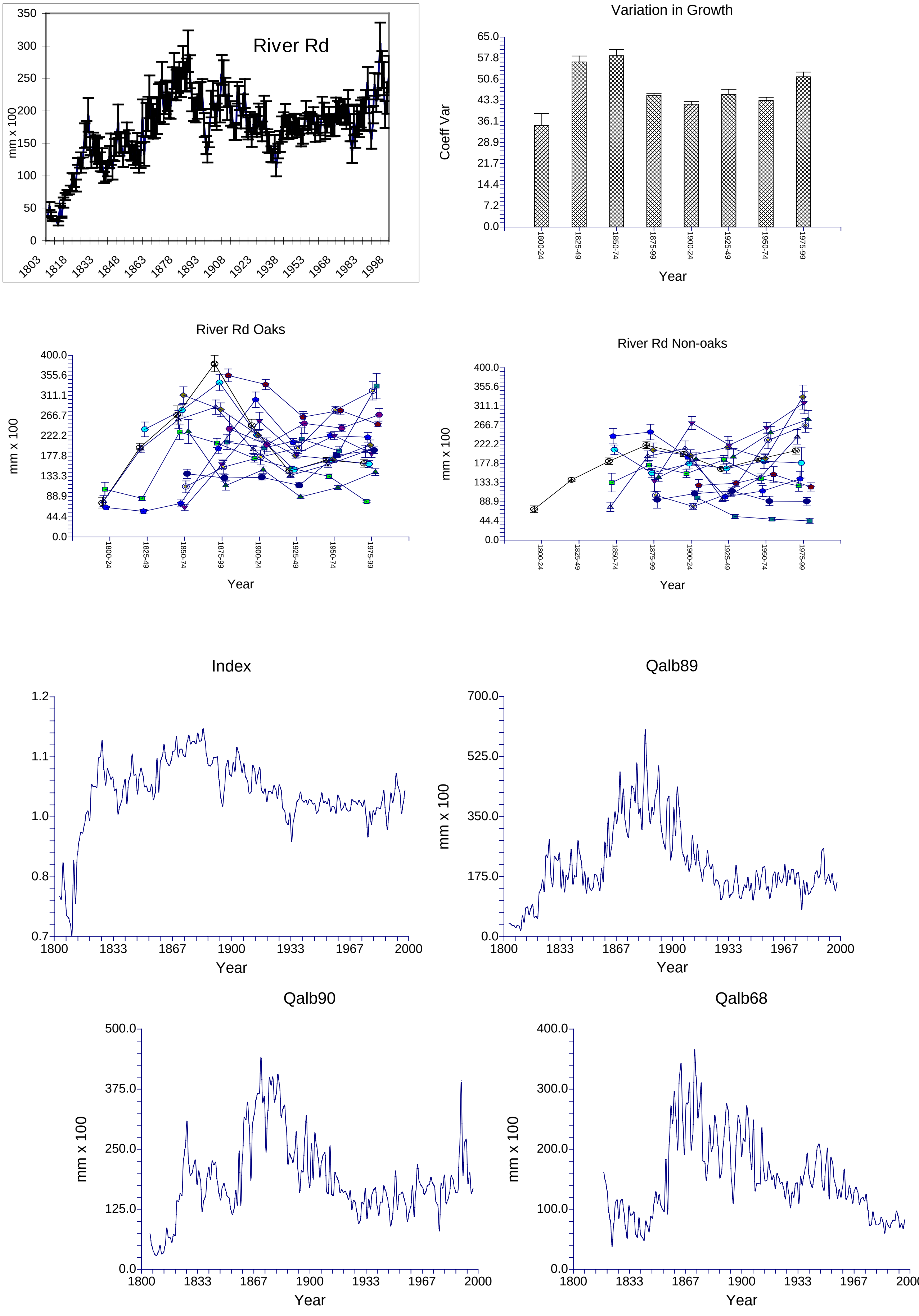




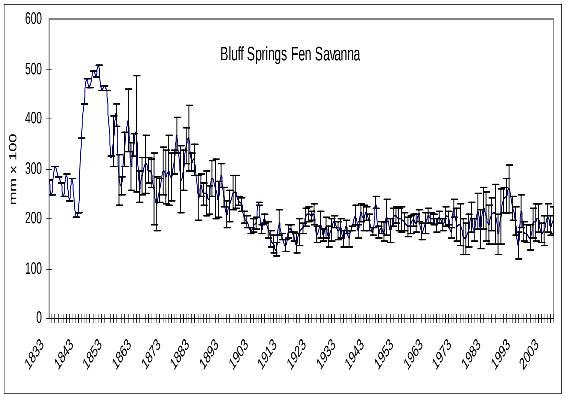
Appendix II. Pilcher Park chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

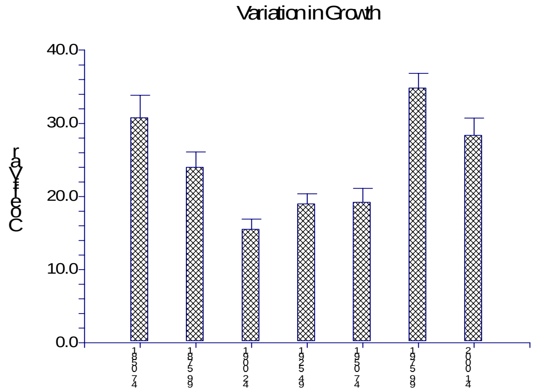


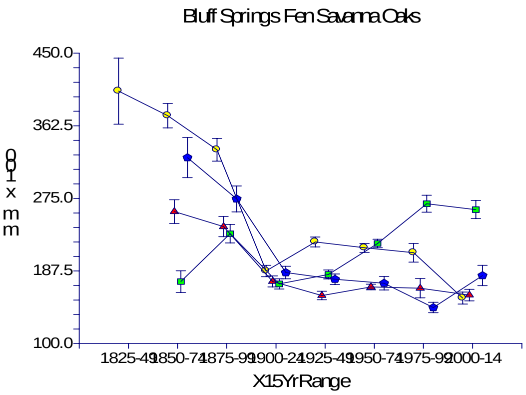
Appendix II. Ryerson Forest Preserve chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

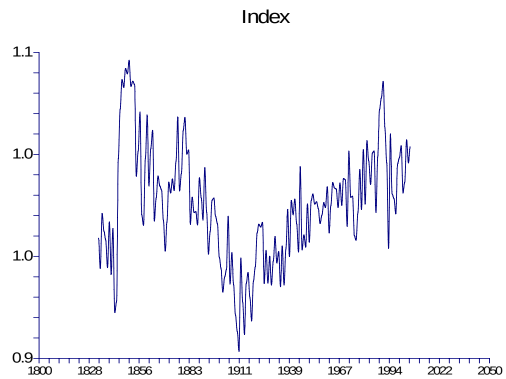


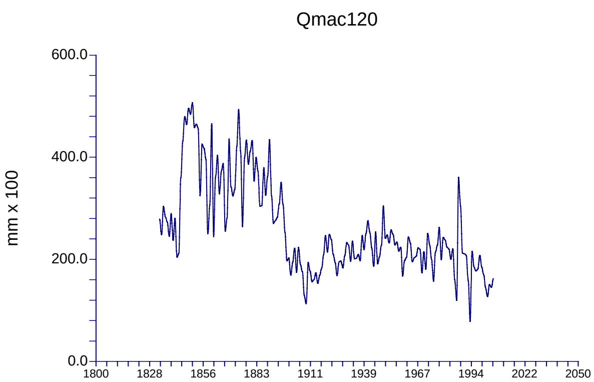
Appendix II. River Road Forest Preserve chronology; Coefficient of Variation, oak and non-oak (compared to oak mean) variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.

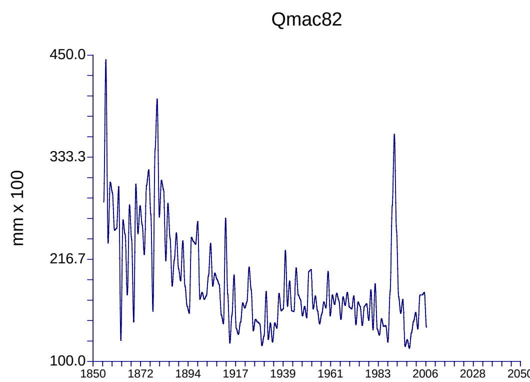


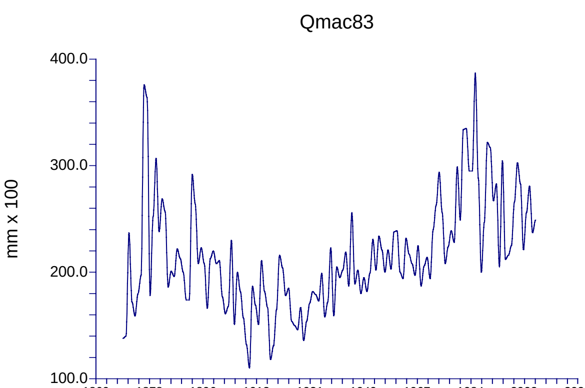


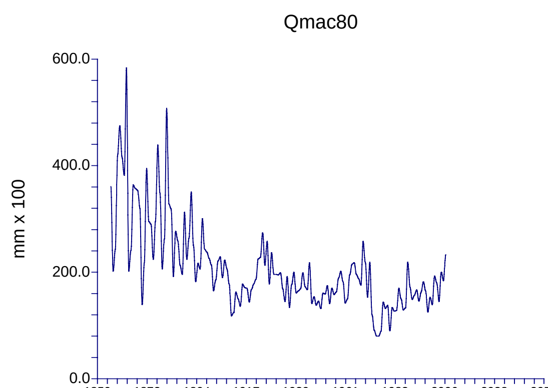




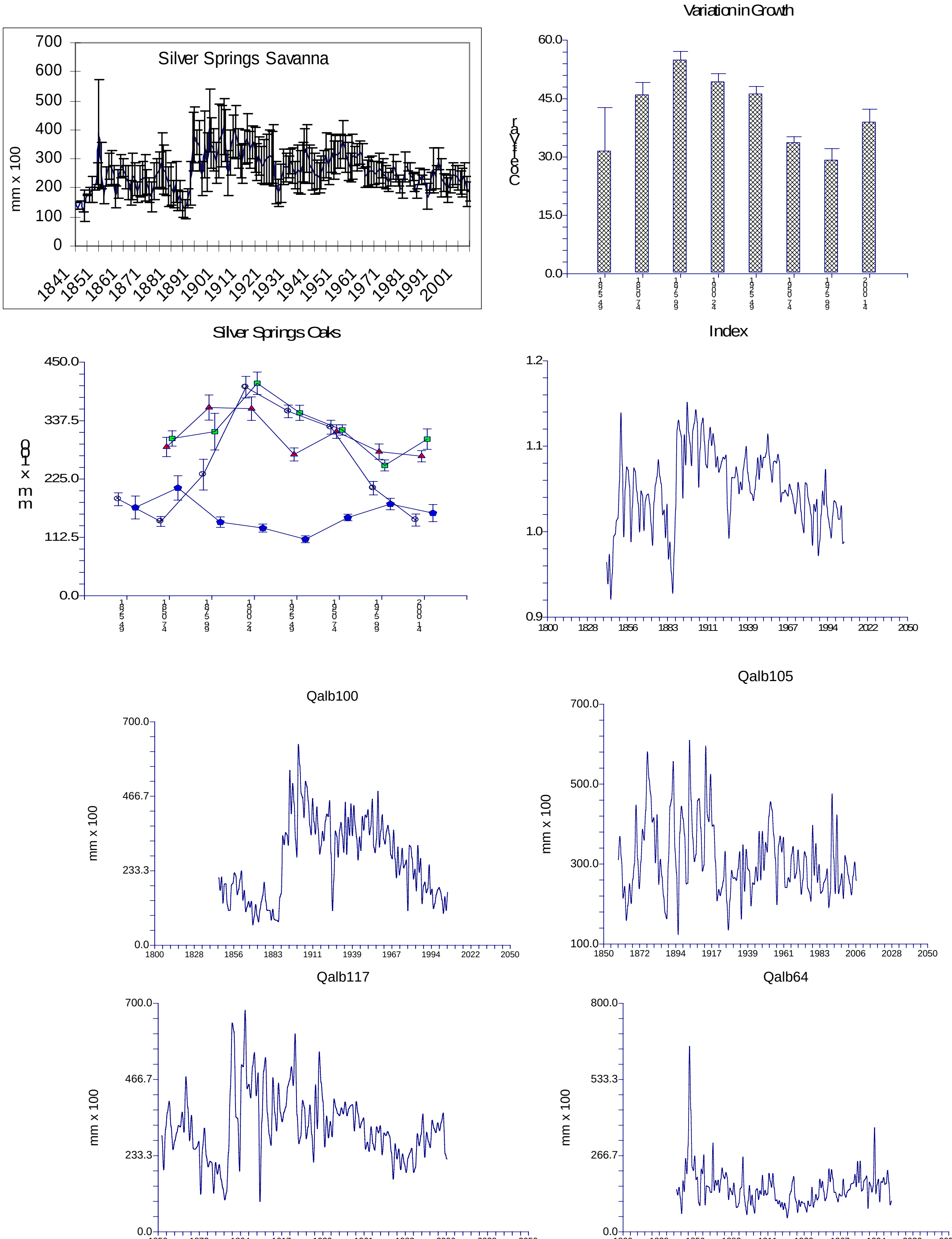




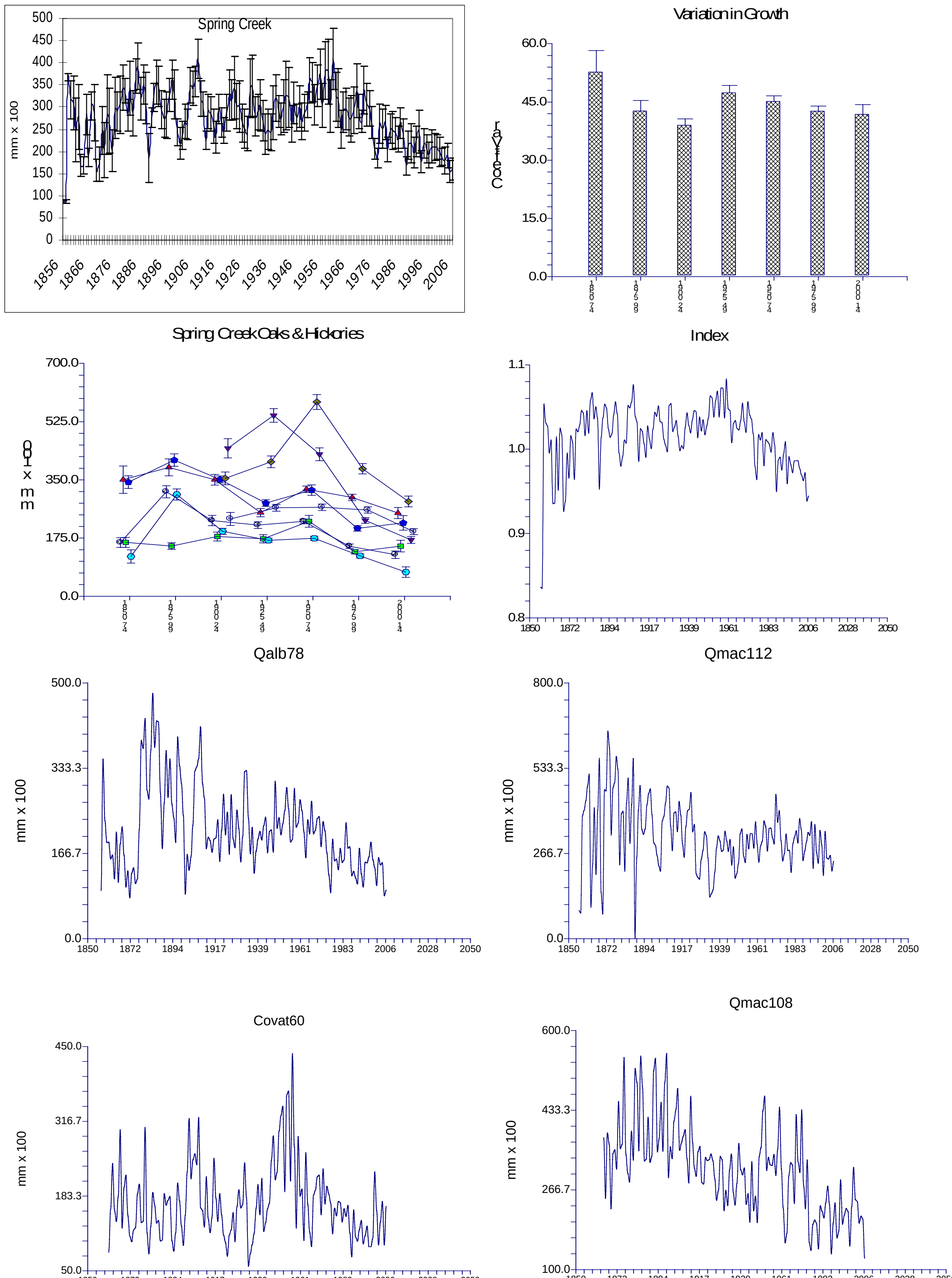




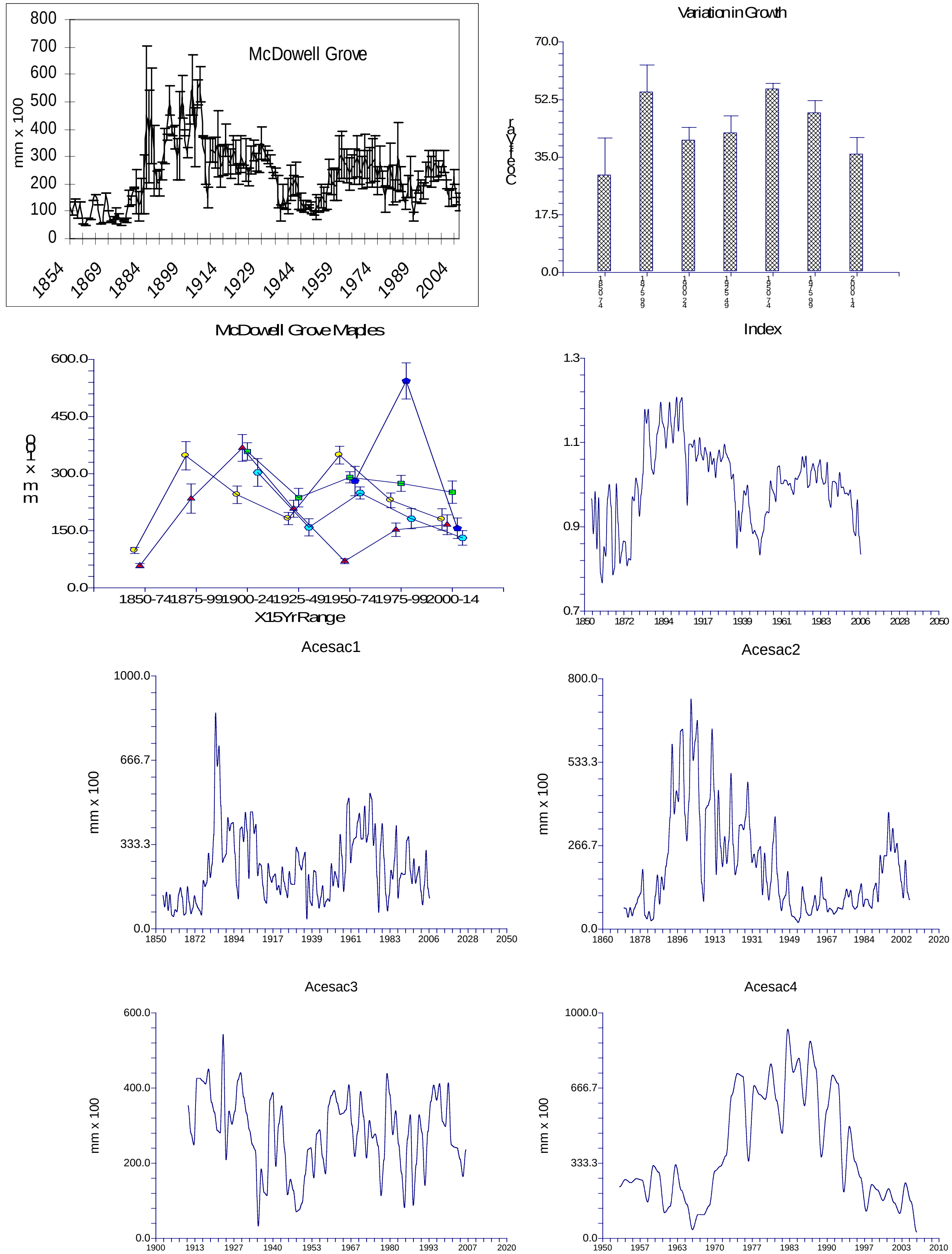
Appendix II. Bluff Springs Fen Savanna chronology; Coefficient of Variation, individual tree variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



Appendix II. Silver Springs Savanna chronology; Coefficient of Variation, individual tree variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



Appendix II. Spring Creek Savanna chronology; Coefficient of Variation, individual tree variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.



Appendix II. McDowell Grove Savanna chronology; Coefficient of Variation, individual tree variation in growth at fixed time intervals; standardized index; and annual growth of three oldest trees. Tree dbh follows tree abbreviation.