

# Dendrochronology of two butternut (*Juglans cinerea*) populations in the southeastern United States

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## Abstract

Butternut (*Juglans cinerea*) has been an important component of eastern hardwood forests in North America since the last ice-age, but an exotic fungal pathogen (*Sirococcus clavigignenti-juglandacearum*) has been devastating the species throughout its native range since the late 1960s. Restoration strategies have not been widely adopted in the southern part of the species' range, in part due to lack of information on disease and stand dynamics in the region. We initiated a study in 2004 to determine the feasibility of using butternut in tree ring analysis and to determine effects of climate and competition on growth and mortality of butternut trees. We studied the tree ring characteristics and population dynamics of butternut populations in southwestern Virginia and in central Tennessee. Butternuts in both populations were found to be relatively sensitive to annual variation of climate, particularly Palmer Drought Severity Indices, and had easily distinguishable tree ring boundaries. Overstory tree competition appeared to be accelerating butternut decline in a stand originating from a clearcut, while old-field succession was benefiting a butternut population in another stand. Our results indicate that potential exists to use dendrochronology as a tool in understanding the dynamics between butternut canker disease, exogenous factors (climate, disturbance), and endogenous factors (tree age, genetics) that will affect butternut population restoration efforts. These results should be tested in other parts of the species' range.

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## 1. Introduction

Butternut (*Juglans cinerea* L.) is a hardwood species native to eastern North America valued for its attractive wood, edible nuts, and as a mast source for wildlife (Clark, 1958; Rink, 1990; Ostry and Pijut, 2000). In the southern part of its range, butternut has comprised 1–3% of arboreal pollen since the last ice-age (Delcourt, 1979) and was an important component of species diversity in pre-settlement and early settlement forests (Campbell, 1989; Shuler, 1997). Butternut was once abundant enough to be used as a dye for Confederate Army uniforms in the Civil War and was used by Native Americans for medicinal purposes (Ostry and Pijut, 2000).

Butternut populations have been declining throughout the species' range due to a disease caused by a recently introduced

fungus [*Sirococcus clavigignenti-juglandacearum* (Nair, Kostichka, and Kuntz)] (Anderson and LaMadeleine, 1978; Nair et al., 1979; Furnier et al., 1999). Spores of the butternut canker disease first cause branch dieback on twigs in the lower canopy, spores are later carried to the trunk and exposed roots through rainfall, and multiple stem cankers will weaken and can eventually kill the tree (Tissert and Kuntz, 1983, 1984). Butternut is currently listed as a “species of concern” under the federal Endangered Species Act of 1973, and mortality from the canker has exceeded 80% throughout most of its range (Prey and Kuntz, 1981; Ostry and Pijut, 2000). The species was also negatively impacted during the 20th century by damming and channeling of riparian areas where the butternut typically grows. The tree grows best on loamy soils in riparian forests, but can also be found on drier soils derived from limestone parent material (Ostry et al., 1994).

Butternut is a fast growing and shade intolerant species (Rink, 1990; Ostry et al., 1994) and is considered early successional due to low plasticity to leaf absorbance of light

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and establishment dynamics in forest stands (St. Jacques et al., 1991; Doyon et al., 1998). In addition to butternut canker disease, natural succession in remnant populations causes butternut replacement due to its relatively short longevity, ca. 70–80 years (Ostry and Pijut, 2000). However, little empirical evidence exists on establishment and stand dynamics for this species, particularly in the southern portion of its range.

The tree rings of butternut have been characterized as semi-ring porous with distinct ring boundaries (Miller, 1976). However, no research has been conducted to determine the species' sensitivity to high-frequency variations in annual growth caused by climatic fluctuations, a characteristic preferred in dendrochronology research (Douglass, 1920; Fritts, 1976). Reconstruction of stand history dynamics using dendrochronology would allow identification and understanding of processes controlling mortality, including the butternut canker, succession, or other external factors, such as drought or disturbance. Land managers could better guide restoration efforts if they had information on life history, competition effects, and butternut canker impacts on growth and survival.

Genetic analysis, resistance testing, and observational evidence indicate that the butternut canker disease was introduced sometime before 1967 when it was first distinguished from native fungi (Nair et al., 1979; Furnier et al., 1999; Schlarbaum et al., 1997). The disease generally infects all sizes and age classes of trees on a variety of sites (Anderson and LaMadeleine, 1978; Prey and Kuntz, 1981; Ostry et al., 1994). Genetic diversity of butternut is currently low and the species may have low adaptability to changes in the environment, including the ability to withstand the butternut canker (Morin et al., 2000).

Butternut restoration efforts and silvicultural prescriptions should be based on a knowledge of successional processes needed to ensure a natural regeneration component in addition to resistance and breeding programs (Ostry et al., 1994; Ostry and Pijut, 2000). Dendrochronology and subsequent analysis involving variation in tree ring growth can be used to study the stand dynamics of species and populations, including relationships between growth, climate, and competition (cf. Douglass, 1920; cf. Lorimer, 1980). To date, no tree ring database exists for *Juglans* species in North America (Grissino-Mayer and Fritts, 1997) and no previous studies have examined butternut in natural stand conditions using dendrochronology.

We conducted a preliminary examination to determine the feasibility of using butternut in tree ring analysis and to reconstruct development of two butternut populations in the southern portion of the species' range in the United States. We hypothesized that: (1) butternut will be a problematic species to use in dendrochronology due to its semi-ring porous pattern and low variability in annual growth related to climate, and (2) butternut populations may be recruiting during periods of old-field succession and following clearcutting, but are negatively impacted by competition.

## 2. Study area

We chose two populations of butternut in the southeastern United States for sampling based on personal accounts and

preliminary vegetation surveys that identified an unusually high abundance of butternut in these areas (Fig. 1). Both stands would be considered typical of other butternut stands surveyed in the southeastern United States (S.E. Schlarbaum, unpublished data) in that butternut at both sites are found close to drainages. However, both stands are atypical in the high abundance of butternut at each site. The first population is located on private property in Dekalb County (approximately 36°N, –86°W) in a valley located in the Interior Low Plateau, Highland Rim Section of the Eastern Broadleaf Forest Province (Bailey, 1995). This population, hereafter referred to as Butternut Valley, is located on 430 acres of mixed hardwood and riparian forests interspersed with old fields that have been largely undisturbed since the late 1940s. Elevation averages 250 m. Butternut Valley may contain the highest known concentration of butternut trees in the southeastern portion of the species' range.

The second population is located in a 30 acre hardwood cove on the Clinch Ranger District of the George Washington-Jefferson National Forest, Wise County, Virginia, hereafter referred to as the Clinch site. The Clinch site is located in the Northern Cumberland Mountain Section of the Central Appalachian Broadleaf Forest Province (approximately 37.1°N, –82.7°W) (Bailey, 1995). The cove is predominately east facing, averages 18% slope, 600 m elevation, and originates from a clearcut in the early 1970s (exact year unknown).

## 3. Methods

### 3.1. Field sampling

In 1998 and in 2004, all butternut trees (>6 cm dbh) at the Butternut Valley site were examined and 90% of live butternuts were cored at this site ( $n = 61$ ). Trees that had obvious sign of internal bole rot were not cored. At the Clinch site, we subjectively placed three 0.04 ha circular plots so that each plot included concentrations of live butternut trees in order to sample as large a population of butternuts and their competition as possible. We collected increment cores from all trees  $\geq 10$  cm dbh within each plot and we also collected increment cores from butternut trees located outside the plots for a total of 23 butternuts cored at the Clinch site. At both sites, cores were collected from the longest axis of the tree at a height of 1.4 m and all trees were measured for dbh. Multiple cores were sometimes collected if pith was not intercepted. At the Clinch site, we identified five dead and downed butternut logs and collected a cross-section from the base of the log for tree ring analysis. Increment cores were rinsed in an alcohol solution between core sample collections to reduce risk of disease infection.

### 3.2. Sample processing and laboratory methods

Each core was dried, mounted and glued to a wooden core mount. Cores were sanded with progressively finer grades of sandpaper (100, 200, 320, 400 and 600 grit) until the cellular

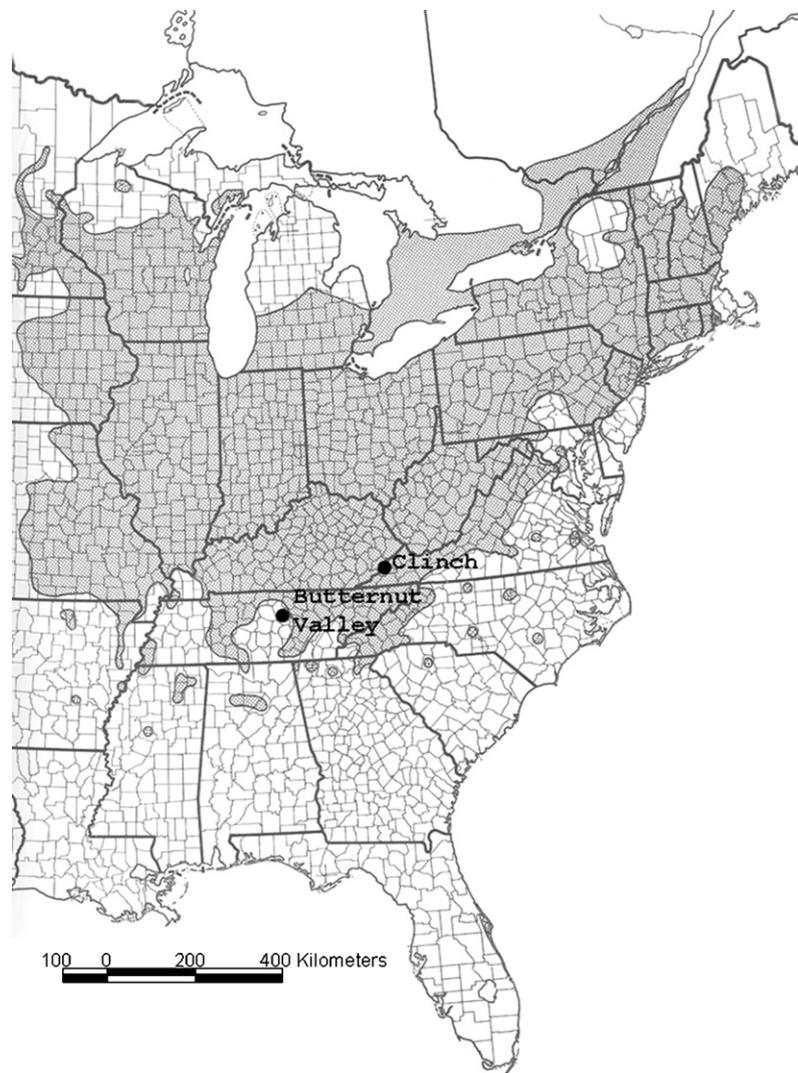


Fig. 1. Range of butternut in southeastern United States, as adapted from Rink (1990), and locations of study areas.

structure of the tree rings was distinguishable under a stereomicroscope (10–50 $\times$ ). Cross-sections were dried, planed and sanded (80, 100, 200, 400 grit). Variations in year to year ring widths for each core were plotted onto graph paper and then pooled to create a visual live-tree chronology of each species at each site and to ensure accurate aging of each core to an exact calendar year (Douglass, 1941; Stokes and Smiley, 1996). Phloroglucinol was sometimes applied to yellow-poplar (*Liriodendron tulipifera* L.) and basswood (*Tilia americana* L.) cores collected from the Clinch site to increase distinction of tree ring boundaries. For dead tree cross-sections, year of death was unknown, and cross-sections were dated using visual crossdating with the live tree chronology. Variations in yearly tree ring widths from the butternut dead tree cross-sections were plotted onto graph paper and visually matched with the live butternut tree chronology to date each ring to an exact calendar year (Douglass, 1941; Stokes and Smiley, 1996).

For butternut cores and cross-sections, tree ring widths were measured to the nearest 0.001 mm using a Velmex stage micrometer. If multiple cores were collected from a tree, we measured the core that came closest to pith. For butternut cores

in which the pith was missed by an estimated 5 years or more, a graphical technique was used to estimate the pith date; otherwise, a visual estimation of number of years to pith was made (Villalba and Veblen, 1997; Clark and Hallgren, 2004). For all other tree species, we visually estimated number of years to pith by examining tree rings nearest the pith and visually estimating number of years to pith. For cores and cross-sections with the pith missing due to rot, regression equations were developed for each site and used to predict pith date using DBH or diameter of cross-section (Clark and Hallgren, 2004).

### 3.3. Tree ring analysis and climate data

We used the program COFECHA, version 6.06P, to check the accuracy of core and cross-section dating (Holmes, 1983; Grissino-Mayer, 2001). COFECHA is used to test correlations between successive segments of each tree ring series against the master chronology, and identifies segments that have a significantly low correlation at the 0.01 significance level. For Butternut Valley cores, we used the default settings for correlations to be computed successively in 50-year segments,

lagged at 25 years. For the younger Clinch trees, we shortened the segment length to 30 years, lagged at 15 years. If a segment of a series fell below the default critical value (0.32 for 50-year segments; 0.42 for 30-year segments), the segment was flagged as potentially inaccurately dated. The accuracy of dating for each flagged segment was inspected by reexamining the core under the stereo-microscope to identify measurement errors, miscounts or missing or false rings. If the problem flagged by COFECHA could not be identified and corrected by reexamining the tree rings of the series, the core was not used in further tree ring analysis. Some flagged segments were identified as correctly dated after inspection and were used in further analysis despite their low correlation with the master chronology.

After all series were correctly dated and measured, we used COFECHA to check the accuracy of crossdating the dead tree cross-sections from the Clinch site with the live tree master chronology. COFECHA matches segments of the undated dead tree cross-sections against segments of the dated master chronology and computes the 11 highest correlation values for each segment. If a high correlation ( $>0.32$ ) predicted in COFECHA matched the dating determined through visual crossdating, then accuracy of visual crossdating was confirmed and each ring of the cross-section was assigned a calendar year. If a high correlation predicted using COFECHA did not match our dating made through visual crossdating, the cross-section was not considered accurately dated to an exact calendar year, and ring counts could only be used to make age determinations.

After all cores had been dated accurately, we used the actual or estimated (for cores in which the pith was missed or rotten) pith date for all butternuts to characterize the age structure of butternuts at Butternut Valley. For the Clinch site, we used the sample of trees cored within the 0.04 ha plots to characterize the age structure of all species within the stand.

COFECHA was used to calculate standard descriptive statistics of tree ring data including mean raw tree ring growth, series autocorrelation, mean sensitivity, and mean correlation of each series with the master chronology. Autocorrelation is a measure of the persistence of 1 year growth to the next year growth and low values indicate low levels of persistence in year to year growth. Sensitivity is used to describe the degree of annual variation within a tree ring series and ranges between 0 (least sensitive) and 1 (most sensitive) (Fritts, 1976).

We used program ARSTAN (version 3.02 V) to produce an ARSTAN tree ring indices chronology for each site (Cook, 1985; Cook and Holmes, 1999). We used all correctly dated core and cross-section butternut samples at each site confirmed through COFECHA to produce the ARSTAN chronology. The ARSTAN indices chronology represents a robust estimation of exogenous climate and endogenous growth dynamics in the tree ring series and is considered to contain a strong climate signal (Cook, 1985). The ARSTAN chronology is produced through an autoregressive modeling technique that contains the persistence common among a large portion of each series (Cook and Holmes, 1999).

Climatic data were obtained for the Butternut Valley and Clinch localities. Monthly total precipitation and average

monthly temperature data were obtained from the National Oceanic and Atmospheric Administration's (NOAA) National Climatic Data Center (NCDC) for weather stations within 8–13 km of each study site (NOAA, 2004a). Climate variables were averaged across six weather stations in the National Weather Service's Cooperative Station Network for Butternut Valley (station IDs: 405216, 405882, 407811, 408404, 408405, and 409866); and variables were averaged across six weather stations for the Clinch site (station IDs: 151119, 441808, 441825, 154236, 154236, and 449215). Weather stations used for each locality had significant positive correlations with one another in precipitation ( $0.59 < r < 0.94$ ) and temperature values ( $0.85 < r < 0.94$ ). Palmer drought severity index ranges from  $-4$  (extreme drought) to  $+4$  (extreme wet) and represents several environmental variables that affect tree growth, including drought duration, soil water holding capacity, temperature, and precipitation (Palmer, 1965). The PDSI values were obtained from the NOAA's NCDC using data for Virginia, Division 6 for the Clinch site, and Tennessee, Division 2 for Butternut Valley (NOAA, 2004b).

We computed means and Pearson correlations among annual ARSTAN index values, annual total precipitation, average annual temperature, and average annual PDSI values using PROC CORR in SAS (SAS, 2004). Means and Pearson correlations were computed when tree core sample size was at least 4; 1946–2004 for Butternut Valley and 1974–2004 for the Clinch. The Butternut Valley location was the only chronology with sufficient length to perform monthly weather analysis using Dendroclim software (available at <http://woods.geography.unr.edu/dendrosite/software/DendroClim.html>). This analysis used correlation and response function analysis to determine which months have significant correlations among mean weather data and tree ring growth patterns. Input weather data were temperature, precipitation, and PDSI monthly values from the current January through the current December for 1950–2003. Input tree response data was the ARSTAN chronology for the same period. Significance was set at the 0.05 level for all analyses.

## 4. Results

### 4.1. Tree ring analysis and suitability for crossdating

Butternut cores and cross-sections in this study were semi-porous with relatively distinguishable tree ring boundaries (Fig. 2). False rings occurred on approximately 19% of trees sampled and occurred in the first 10 years of growth 58% of time. The false rings appeared as a dark tangential band usually in the middle of the growth ring (Fig. 2), and were easy to distinguish from the sharper boundary demarcating the latewood boundary of a true growth ring. Averages of raw tree ring widths ranged from 3.29 to 5.04 mm, depending on site (Table 1). Average mean sensitivity was greater than 0.300 for both sites.

We were able to accurately date 54 (88%) and 21 (91%) of the live tree butternut cores from Butternut Valley and the Clinch site, respectively, using graphical techniques and

Table 1  
Descriptive statistics for tree ring and weather data at the Butternut Valley and Clinch sites

Variable	Site	
	Butternut Valley	Clinch
Number of cores used in tree ring analysis	54	21
Average age	43	32
Average dbh (cm)	29.5	29.2
Average ring width (mm) ± standard deviation	3.29 ± 1.562	5.02 ± 2.365
Mean sensitivity	0.308	0.338
Auto correlation	0.564	0.459
Mean correlation with master chronology	0.653	0.655
Annual precipitation (cm)	141	119
Average daily temperature (°C)	15	12

verification through COFECHA. Based on the relatively high correlations with the live tree chronology, we were able to crossdate all dead tree samples from the Clinch. In two of the five samples, crossdating was confirmed with the highest correlation predicted by COFECHA ( $r > 0.45$ ). In the remaining 3 samples, our visual crossdating was confirmed with the second highest correlation predicted by COFECHA ( $r > 0.33$ ).

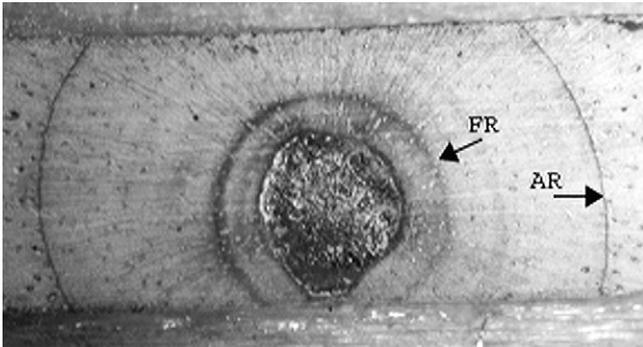


Fig. 2. Pith and first annual growth ring boundary (AR) of a butternut increment core sample. False ring (FR) is shown as a dark tangential band within the annual ring.

#### 4.2. Population age structure and dynamics

Butternut Valley butternuts averaged 43-year-old, and the oldest tree originated in 1929 (Table 1 and Fig. 3). Butternuts have had relatively continuous recruitment at this site over the last 70 years (Fig. 3). Average dbh of butternuts was approximately 29 cm for both sites. At the Clinch, the live trees averaged 32-year-old and the dead trees were slightly younger at 26-year-old at time of death (Table 2). The butternut trees at this site recruited during a 9-year period following the clearcut in the early 1970s and several trees recruited prior to the clearcut (Fig. 3). Yellow-poplar was the primary competitor with butternut at this site, and basswood and black birch (*Betula lenta* L.) were secondary competitors. Most species had similar regeneration patterns as butternut (Fig. 4), regenerating just after the clearcut. The oldest trees at this site were a 36 cm red maple (*Acer rubrum* L.) (inner ring ca. 1934) and a 13 cm northern red oak (*Quercus rubra* L.) (inner ring ca. 1935).

#### 4.3. Climate analysis

Butternut Valley had slightly higher annual precipitation and temperature values, but slightly lower mean annual growth than the Clinch (Table 1). None of the correlations between annual values of tree ring growth and climate were significant for each site. However, when monthly climate variables were correlated to annual tree growth at Butternut Valley, monthly PDSI had significant relationships to tree growth. In particular, current year July, August and September PDSI values were most strongly related to ARSTAN indices ( $r < 0.45$ ). Current year April temperature ( $r = 0.32$ ) and June ( $r = 0.30$ ) and July ( $r = 0.43$ ) precipitation were also significantly correlated with ARSTAN values. The positive relationship between summer PDSI (July–September) and annual tree growth is shown in Fig. 5. At Butternut Valley, years 1952, 1954, 1988, 2000, and 2002 were drought years with relatively narrow tree ring widths. At Clinch, years 1976, 1984, and 1988 were years of relatively small tree growth and low PDSI values. However, ARSTAN index values did not always mirror PDSI values, particularly when sample sizes were small. For example, at

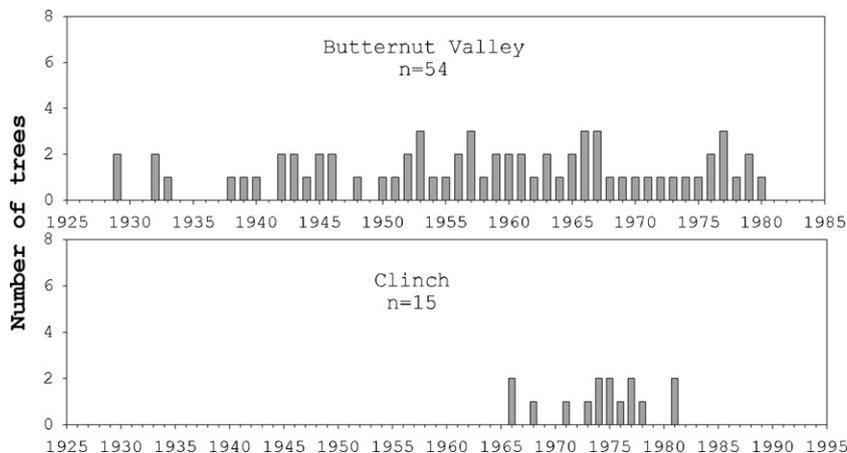


Fig. 3. Age structure of butternut trees cored at 1.4 m height at the Butternut Valley and Clinch sites.

Table 2  
Life history information on dead butternut tree cross-sections at the Clinch site

Tree	Pith date	Outer ring date	Estimated age at death
1	1971	1997	27
2	1971	2001	31
3	1979	1997	19
4	1970	1995	26
5	1980	2003	23

Butternut Valley, 1945 had the lowest ARSTAN index value, but relatively normal precipitation values.

## 5. Discussion

### 5.1. Feasibility of using butternut in tree ring analyses

Our first hypothesis that butternut cores would be problematic for dendrochronology research was not supported by the results. Mean sensitivity of Butternut Valley and Clinch cores would be considered relatively high according to standards for tree ring dating (Douglass, 1920; Fritts, 1976; Grissino-Mayer, 2001). This result was surprising given that sites were located in riparian areas near drainages, where trees typically exhibit lower sensitivity ( $<0.30$ ) than trees on drier sites (Douglass, 1920; Fritts, 1976). Additionally, high mean series correlation with the master chronology and distinctive tree ring boundaries allowed for chronology development using live tree cores and accurate visual crossdating of dead trees. Although false rings were common, they were easily distinguishable from the sharp demarcation of the latewood ring boundary.

Our success at crossdating butternut samples was due to a significant relationship between tree growth and climate, as detected in the analyses between climate variables and tree ring growth. A primary factor controlling tree growth appeared to be growing season drought and precipitation, similar to other deciduous species growing in temperate climates (Fritts, 1962, 1966). This relationship was weak in certain years, probably due to exogenous disturbances or localized weather events. These results demonstrate the need to locate a relatively large number of older trees for use in tree ring analysis, which may be difficult with species like butternut that are being progressively decimated by an exotic pest. Despite these limitations, potential exists for future studies to use dendrochronology as a tool in understanding the pathology of butternut canker disease that will aide in restoration of this species.

### 5.2. Population dynamics of butternut

Our second hypothesis that clearcutting and old-field succession favors butternut recruitment was supported by the results. Butternut recruitment increased following clearcutting at the Clinch and then declined in abundance due to competition from other species. The 10-year range in post-clearcut recruitment dates of butternut trees at the Clinch is likely due to the error in age determination related to missing the pith during coring or coring at 1.4 m versus at ground level. If exact

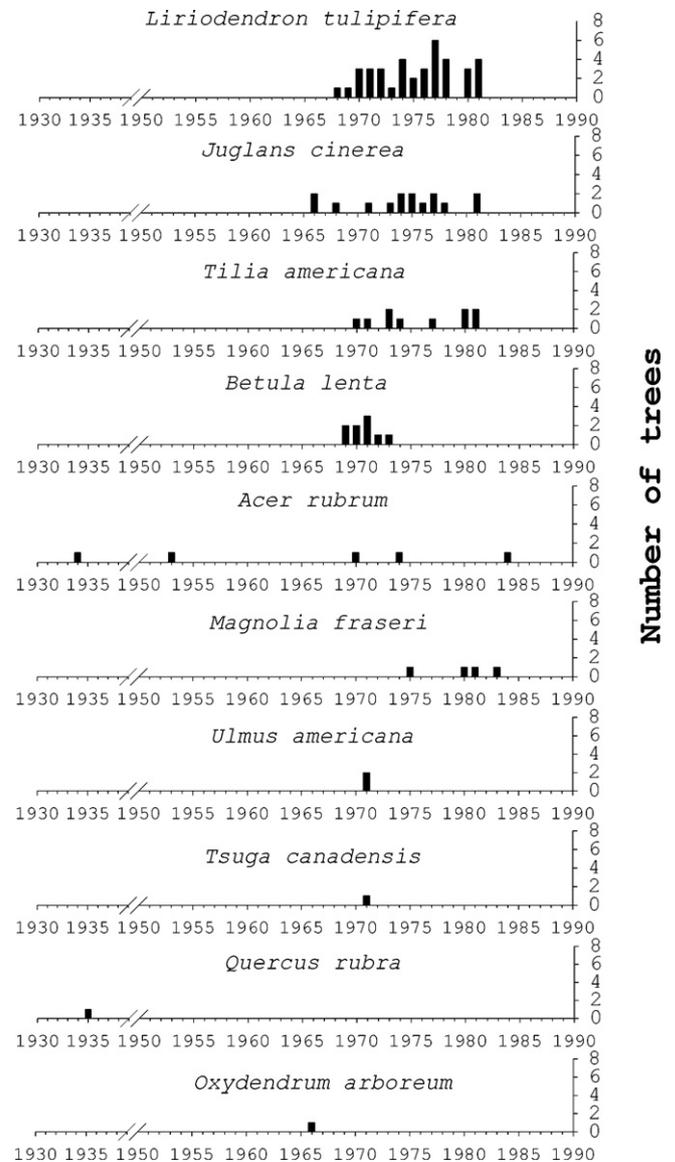


Fig. 4. Age structure by species of trees cored at 1.4 m height within three 0.4 ha plots at the Clinch site.

ages of trees could be determined, we would expect that the majority of trees likely recruited within 1 or 2 years of the clearcut disturbance; however, off-center increment cores and sampling above ground level can underestimate age (Villalba and Veblen, 1997). Butternuts appeared to benefit from disturbances in a closed canopy stand (Ostry et al., 1994); however, our inferences are limited because we did not sample prior to clearcutting. Butternut trees at the Clinch site died prior to reaching the maximum ages attained in living trees on site and compared to the older trees found at Butternut Valley. A cursory examination of dead trees at the Clinch did not reveal any canker development, although further analysis is needed. We speculate that these trees died primarily from shading effects of primary competitors such as yellow-poplar and basswood and butternut canker disease was only a minor contributor to mortality. Butternut exhibits low plasticity to shading and may not survive without release from competitors

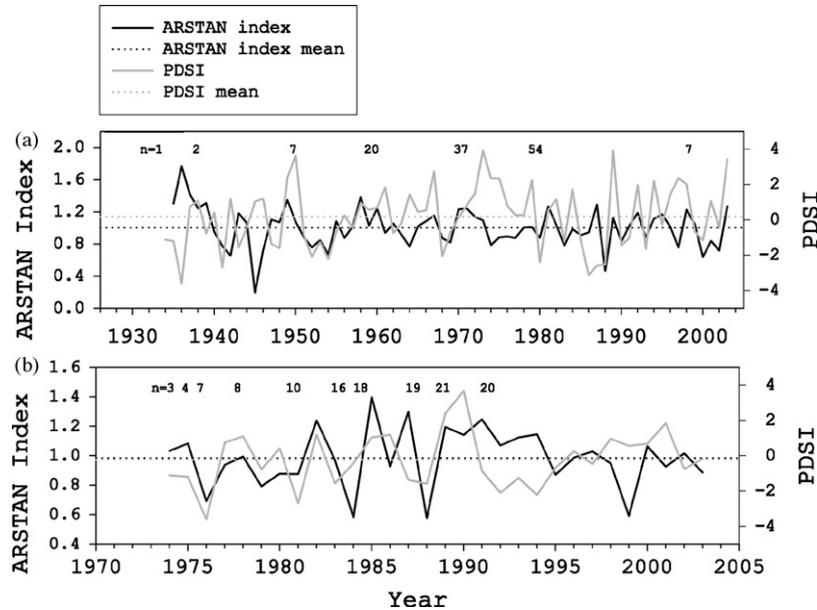


Fig. 5. Butternut ARSTAN index chronology and Palmer Drought Severity Index (PDSI) chronology for Butternut Valley (a) and Clinch (b). The ARSTAN chronology represents a robust estimation of climate and growth dynamics across tree ring series, and PDSI is a measure of drought intensity ranging from  $-4$  (extreme drought) to  $+4$  (extreme wet).

(St. Jacques et al., 1991). However, additional analysis of stem sections from the dead trees is needed to confirm this hypothesis.

Butternut Valley may contain the most intact population of butternuts in the southeastern United States, and this population does not appear to be currently declining due to the butternut canker. We speculate that old-field succession from abandoned pasture and agricultural fields throughout Butternut Valley has allowed butternuts to become established in relatively open canopy conditions, conducive to growth of this species (Ostry et al., 1994). As old fields succeed to closed canopy forests, we would expect the butternut population in this area to decline without continued disturbance that promote increased light availability. Crossdating of dead tree stems with the live tree chronology appears promising, and future studies at this site could include historical reconstruction of canker development over the last century. This type of information would add to the knowledge base of butternut canker development that currently exists for stands in the northern portion of the species range (Kuntz et al., 1979).

## 6. Conclusions and implications for future research

Results show that butternut has potential for dendrochronology studies even in relatively mesic areas where yearly annual growth fluctuations related to climate is typically low. Despite the geographic limitations of this study, our results provide evidence that this species has potential for future research involving dendrochronology. Our results should be tested in other parts of the species range prior to initiating large-scale research experiments using tree ring analysis. If cross-dating dead tree sections can be accomplished as in this study, cankers could be dated to an exact calendar year and stem analysis of butternut trees could be conducted. Disease

development within individual trees and the epidemiology of butternut populations could be reconstructed, providing important information on rate of disease spread, changes in genetic resistance over time, and examination of relationships between canker development on tree growth and mortality.

In southern butternut populations, damage from butternut canker disease appears to be periodic (R.L. Anderson, personal communication), suggesting that the disease is related to climatic conditions, including stress from drought. Identification of weather-related variables related to disease development would be important in resistance testing and breeding strategies and may have relevance to management of surviving populations. Specific information on how long a tree or genotype can withstand infestation of the butternut canker also would enhance restoration efforts.

A large-scale research project on butternut that includes dendrochronology could eventually help refine restoration efforts by helping to predict growth response given local climatic conditions and disease presence. Despite a lack of observational or empirical evidence in this study that coring live butternut trees may contribute to mortality or disease spread, coring of butternuts should be done with caution to reduce risk of fungal infestation (Grissino-Mayer, 2003). Locations with relatively old intact populations, such as Butternut Valley, show the greatest potential for dendrochronological studies. However, older stands of butternut will be difficult to locate because most butternut populations were likely decimated from the canker and through deforestation activities to convert forest lands to agriculture and pasture following European settlement. Similar to the American chestnut (*Castanea dentata* [Marsh.] Borkh.) (Jacobs, 2007), potential for butternut restoration through afforestation is probably greatest on pasture and agricultural lands where butternut was once present.

Although more research is needed, the limited evidence presented in this study indicates that butternut mortality may be related to competition in addition to butternut canker disease. Competition control should be considered when attempting butternut restoration in forested conditions. Thinning, crop tree release, or regeneration harvesting is recommended for butternut stands (Ostry et al., 1994) and may be necessary for restoring butternut on mesic sites in the southeastern United States where competition from other tree species is often intense. Enhanced knowledge of species life history and pathological responses of the butternut canker coupled with predictive modeling to locate potential restoration sites (van Manen et al., 2002; Thompson et al., 2006) will be powerful tools to enhance restoration of this species. Restoration of butternut should be an important part of conservation planning where the species occurs naturally because of the species' increasing rarity, its ecological importance to biodiversity, and its utilitarian values.

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### References

- Anderson, R.L., LaMadeleine, L.A., 1978. The distribution of butternut decline in the eastern United States. USDA Forest Service Northeastern Area State and Private Forestry, Forest Insect and Disease Management Survey Report S-3-78.
- Bailey, R.G., 1995. Description of the Ecoregions of the United States, Second ed. USDA Miscellaneous Publication, 1391.
- Campbell, J.J.N., 1989. Historical evidence of forest composition in the Bluegrass Region of Kentucky. In: Rink, G., Budelsky, C.A. (Eds.), Proceedings of the Seventh Central Hardwood Forest Conference. USDA Forest Service General Technical Report NC-132, pp. 231–246.
- Clark, F.B., 1958. Silvical characteristics of butternut. USDA Forest Service Central States Forest Experiment Station Miscellaneous Release 28.
- Clark, S.L., Hallgren, S.W., 2004. Age estimation of *Quercus marilandica* and *Quercus stellata*: applications for interpreting stand dynamics. Can. J. Forest Res. 34, 1353–1358.
- Cook, E.R., 1985. A time-series analysis approach to tree ring standardization. Ph.D. Dissertation. University of Arizona-Tuscan.
- Cook, E.R., Holmes, R.L., 1999. User's manual for Program ARSTAN. Laboratory of Tree ring Research, University of Arizona, Tuscan, AZ.
- Delcourt, H.R., 1979. Late quaternary vegetation history of the eastern highland rim and adjacent Cumberland plateau of Tennessee. Ecol. Monogr. 49, 255–280.
- Douglass, A.E., 1920. Evidence of climatic effects in the annual rings of trees. Ecology 1, 24–32.
- Douglass, A.E., 1941. Crossdating in dendrochronology. J. Forest. 39, 825–831.
- Doyon, F., Bouchard, A., Gagnon, D., 1998. Tree productivity and successional status in Quebec northern hardwoods. Ecoscience 5, 222–231.
- Fritts, H.C., 1962. The relation of growth ring widths in American beech and white oak to variations in climate. Tree Ring Bull. 25, 2–10.
- Fritts, H.C., 1966. Growth-rings of trees: their correlation with climate. Science 154, 973–979.
- Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, New York.
- Furnier, G.R., Stolz, A.M., Mustaphi, R.M., Ostry, M.E., 1999. Genetic evidence that butternut canker was recently introduced into North America. Can. J. Bot. 77, 783–785.
- Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree Ring Res. 57, 205–211.
- Grissino-Mayer, H.D., 2003. A manual and tutorial for the proper use of an increment borer. Tree Ring Res. 59, 63–79.
- Grissino-Mayer, H.D., Fritts, H.C., 1997. The International Tree ring Data Bank: an enhanced global database serving the global scientific community. The Holocene 7, 235–238.
- Holmes, R.L., 1983. Computer-assisted quality control in tree ring dating and measurement. Tree Ring Bull. 43, 69–78.
- Jacobs, D.F., 2007. Toward development of silvical strategies for forest restoration of American chestnut (*Castanea dentata*) using blight-resistant hybrids. Biol. Conserv. 137, 497–506.
- Kuntz, J.E., Prey, A.J., Jutte, S., Nair, V.M.G., 1979. The etiology, distribution, epidemiology, histology and impact of butternut canker in Wisconsin. In: Kessler, K.J., Jr., Weber, B.C. (Tech. Coords.), Proceedings of the Walnut Insects and Diseases Workshop, USDA Forest Service General Technical Report NC-52, pp. 69–72.
- Lorimer, C.G., 1980. Age structure and disturbance history of a southern Appalachian forest. Ecology 61, 1169–1184.
- Miller, R.B., 1976. Wood anatomy and identification of species of *Juglans*. Bot. Gaz. 137, 368–377.
- Morin, R., Beaulieu, J., Deslauriers, M., Daoust, M., Bousquet, J., 2000. Low genetic diversity at allozyme loci in *Juglans cinerea*. Can. J. Bot. 78, 1238–1243.
- Nair, V.M.G., Kostichka, C.J., Kuntz, J.E., 1979. *Sirococcus clavignenti-juglandacearum*: an undescribed species causing canker on butternut. Mycologia 71, 641–646.
- National Oceanic and Atmospheric Administration's National Climatic Data Center, 2004a. World wide web address accessed July 2004: <http://ols.nndc.noaa.gov/plolstore/plsql/olstore.pubdetail?prodnum+C00096-PUB-S0001&subset=004&pubchoice=44>.
- National Oceanic and Atmospheric Administration's National Climatic Data Center, 2004b. World wide web address accessed July 2004: <http://www.ncdc.noaa.gov/oa/climate/onlineprod/drought/xmrg3.html>.
- Ostry, M.E., Pijut, P.M., 2000. Butternut: an underused resource in North America. Hort. Technol. 10, 302–306.
- Ostry, M.E., Mielke, M.E., Skilling, D.D., 1994. Butternut—strategies for managing a threatened tree. USDA Forest Service General Technical Report NC-164.
- Palmer, W.C., 1965. Meteorological drought. US Department of Commerce Weather Bureau Research Paper 45.
- Prey, A.J., Kuntz, J.E., 1981. The distribution and impact of butternut canker. Ann. Report-Northern Nut Growers Assoc. 72, 81–85.
- Rink, G., 1990. *Juglans cinerea* L. Butternut. In: Burns, R.M., Honkala, B.H. (Tech. Coords.), Silvics of North America, vol. 2. Hardwoods. USDA Forest Service Agricultural Handbook 654, pp. 386–390.
- SAS, 2004. SAS/STAT User's Guide, Version 9, Second ed. SAS Institute Inc., Cary, NC.
- Schlarbaum, S.E., Hebard, F., Spaine, P.C., Kmalay, J.C., 1997. Three American tragedies: chestnut blight, butternut canker, and Dutch elm disease. In: Britton, K.O. (Ed.), Proceedings of the Exotic Pests of Eastern Forests, Tennessee Exotic Pest Plant Council, Nashville, TN, April 8–10, pp. 45–54.
- Shuler, T.M., 1997. Temporal variation in woody species composition from 1922 to 1996 in a second-growth Appalachian forest. In: Pallardy, S.G., Cecich, R.A., Garret, H.E., Johnson, P.S. (Eds.), Proceedings of the Eleventh Central Hardwood Forest Conference, USDA Forest Service General Technical Report NC-188, p. 352.

- St. Jacques, C., Labracque, M., Bellefleur, P., 1991. Plasticity of leaf absorbance in some broadleaf tree seedlings. *Bot. Gaz.* 152, 195–202.
- Stokes, M.A., Smiley, T.J., 1996. *An Introduction to Tree ring Dating*. The University of Arizona Press, Tucson, AZ.
- Thompson, L.M., van Manen, F.T., Schlarbaum, S.E., DePoy, M., 2006. A spatial modeling approach to identify potential butternut restoration sites in Mammoth Cave National Park. *Restor. Ecol.* 14, 289–296.
- Tissert, N., Kuntz, J.E., 1983. The etiology and epidemiology of butternut canker. *Ann. Report-Northern Nut Growers Assoc.* 74, 30–36.
- Tissert, N., Kuntz, J.E., 1984. Butternut canker: development on individual trees and increase within a plantation. *Plant Dis.* 68, 613–616.
- van Manen, F.T., Clark, J.D., Schlarbaum, S.E., Johnson, K., Taylor, G., 2002. A model to predict the occurrence of surviving butternut trees in the southern Blue Ridge Mountains. In: Scott, J.M., Heglund, P.J., Morrison, M.L. (Eds.), *Predicting Species Occurrences-Issues of Accuracy and Scale*. Island Press, Washington, DC, pp. 491–498.
- Villalba, R., Veblen, T.T., 1997. Regional patterns of tree population age structures in northern Patagonia: climatic and disturbance influences. *J. Ecol.* 85, 113–124.