

NATURAL HISTORY FROM DENDROCHRONOLOGY: MAXIMUM AGES AND CANOPY PERSISTENCE OF RARELY STUDIED HARDWOOD SPECIES

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Abstract—Tree-ring research has made significant contributions to our understanding of environmental change and forest stand dynamics. Its application to understanding natural history, however, has been limited. Biodiversity of the central hardwood forest offers many opportunities for tree-ring based, natural history research. Recent tree-ring research examining several rarely studied hardwood species has yielded ages well beyond maximum expectations. For example, a sampling of 20 *Magnolia acuminata* trees in one population included two individuals 315 and 348 years, respectively, which are nearly two centuries more than the average life expectancy reported for this species. Also, research in recently discovered old-growth stands in western Massachusetts has illustrated the common occurrence of *Betula lenta* in *Tsuga canadensis* dominated old-growth forests with individuals frequently living beyond 320 years in these systems. These studies illustrate that tree-ring research can expand our knowledge of the natural history of central hardwood species.

INTRODUCTION

The science of dendrochronology (tree-ring analysis) has enhanced our understanding of environmental change, succession, and forest stand dynamics. In the eastern U.S., this type of research has been substantial and rich (i.e., Lorimer 1980, Foster 1988, Canham 1990, Runkle 1990, Stahle and Chaney 1994, Nowacki and Abrams 1997, Orwig and others 2001, Shumway and others 2001, Lafon and Speer 2002). In recent years, however, dendrochronology has been less frequently applied towards the understanding of natural history (cf. Dayton 2003). This type of natural history information may be more important now than ever before (Dayton, 2003; Schmidly 2005) as species and ecosystems are threatened by invasive species, land-use (development/urban sprawl), forest fragmentation and future climate change. The term 'natural history', unfortunately, is a rather nebulous term (Schmidly, 2005). In this paper we will focus on the application of dendrochronology towards determining a species' longevity and its persistence in the forest. We posit the idea, however, that dendrochronology can reveal many aspects of a species' life-history traits, which is an important part of its natural history.

Tree-ring studies in old-growth forests are valuable sources of information regarding the natural history of central hardwood species (cf. Rentch and others 2003a,b), as well as the natural disturbance dynamics, and development patterns for forest types throughout the region. This paper will highlight specific examples of new information concerning the natural history of four species. This information is derived from two recent dendrochronological studies in old-growth forests (Pederson 2005, D'Amato and others in review). The purpose of these studies was to identify the climatic sensitivity and growth history of several species in the eastern U.S. (Pederson 2005) and to estimate the amount of old-growth forest in Massachusetts (D'Amato and others in review). And yet, the ease at which new maximum ages were found highlights the fact that there are significant gaps in the natural history of many species characteristics of the central hardwood forest. Our hope is that this paper will stimulate additional research that will enrich our knowledge for many eastern U.S. species.

The first portion of this paper will focus on the longevity of four rarely studied temperate hardwood species: black birch (*Betula lenta* L.), cucumbertree (*Magnolia acuminata* L.), red maple (*Acer rubrum* L.), and shagbark hickory (*Carya ovata* (Mill.) K. Koch). New data and a review of maximum ages found

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in primary literature sources will be compared to illustrate how the ages found in our research are well beyond common maximum age expectations. There is currently no information available for any of these species in the International Tree-Ring Databank, a storehouse of dendrochronological information on hundreds of species worldwide (ITRDB 2005).

The second portion of this paper will focus on the natural history (recruitment, longevity and persistence) of black birch within eastern hemlock-mixed hardwood dominated old-growth forests in Massachusetts. Black birch is commonly reported in association with eastern hemlock (*Tsuga canadensis* (L.) Carr.) in old-growth forest ecosystems throughout the central hardwood and New England regions (e.g., Hough and Forbes 1943, Foster 1988); however, little is known about the natural history and dynamics of this species in old-growth forests. Data from eleven old-growth eastern hemlock-mixed hardwood forests in western Massachusetts are used to illustrate the surprising persistence of black birch as well as its overlooked importance in the structure and dynamics of old-growth eastern hemlock forests.

METHODS

Increment cores were collected and processed using standard tree-ring analysis techniques (Cook and Kairiukstis 1990). Generally, a minimum of twelve trees in a stand was cored, with one to two cores removed from each tree depending on the goals of the study (Pederson 2005, D'Amato and others in review). Twenty *M. acuminata* and twenty-one *C. ovata* trees representing the perceived range of age classes from a stand in George Washington National Forest in the Blue Ridge Mountains of central Virginia were selected for coring (Pederson 2005). Twenty *A. rubrum* trees in the eastern Catskills, NY equal to or greater than 10 cm dbh within two designated stands were randomly selected for coring (Charles Canham, 65 Sharon Turnpike, P.O. Box AB, Millbrook NY 12545-0129 & Paul Sheppard, 105-C1 West Stadium, Tucson, AZ 85721 USA personal communication). *B. lenta* outside of Massachusetts were sampled over two periods. In 1974, twelve individuals were sampled at the Mohonk Preserve in New Paltz, NY (Dr. Edward Cook, unpublished data). A second collection of 17 individuals was made at the Preserve in a different stand in 2002 (Neil Pederson, unpublished data). Finally, all trees equal to or greater than 10 cm dbh falling within 3-5 400 m² plots were sampled in the study examining old-growth *B. lenta* in Massachusetts (D'Amato and others in review).

Cores were glued to wooden core mounts and, in most cases, progressively sanded up to 600-grit sandpaper. *B. lenta*, *M. acuminata* and *A. rubrum* samples were often sanded using 2400 or 3200 grit sandpaper to ensure ring boundaries were visually distinct in these species with diffuse porous ring structures. Samples of *B. lenta*, *M. acuminata* and *A. rubrum* were not stained or enhanced in any way beyond sanding. Ages presented here are derived from crossdated samples. Finally, ages presented here are minimum ages; no extrapolations have been made for the number of missing rings to the center of the tree or the time it took each tree to reach coring height. Therefore, the ages presented for these trees are certainly less than their absolute age.

RESULTS AND DISCUSSION

Maximum Ages for *A. rubrum*, *B. lenta*, *M. acuminata*, and *C. ovata*

Maximum ages and comparisons for each species are summarized in table 1. Maximum age in a sample of 40 *A. rubrum* trees is 300 years. The next four oldest trees from this collection were 212, 132, 129 and 128 years old. Interestingly, this maximum age is 150 years greater than the maximum age listed for this species in Loehle (1988) and 10 years older than the oldest reported in the early Pennsylvania study by Hough and Forbes (1943). The oldest *Betula lenta* tree in a sample of 29 trees is 361 years, while the next four oldest trees were 318, 257, 169 and 166 years old. Similar to the *A. rubrum* finding, the oldest *B. lenta* in the population was far greater than the maximum age listed for this species in the current USDA Silvics manual (Burns and Honkala 1990) and Hough and Forbes (1943) (table 1). Further discussion of the age structure of *B. lenta* will be presented in the next section. The oldest *C. ovata* in a sample of 20 trees is 354 years old with the next four oldest trees in the population being 257, 255, 254 and 251 years old. The oldest individual tree is 54 years greater than the maximum age for this species listed in Loehle

Table 1—Comparison of maximum ages from the *Silvics of North America* (Burns and Honkala 1990), Hough and Forbes (1943), and recently acquired data

Species	Silvics manual ^a	Hough and Forbes	New data	Difference ^b
	----- years -----			
<i>Acer rubrum</i>	150	290	300 ^c	150
<i>Betula lenta</i>	265	265	361 ^d	96
<i>Carya ovata</i>	300	n/a	354 ^e	54
<i>Magnolia acuminata</i>	150	310	348 ^e	198

^a If no age is given in the Silvics manual, ages are substituted from Loehle (1988) or Hough and Forbes (1943).

^b Difference between new maximum age data and Silvics manual, or if no age is given, Loehle (1988) or Hough and Forbes (1943).

^c Catskill Mountains, NY.

^d New Paltz, NY.

^e George Washington National Forest, VA.

(1988). Finally, the oldest *M. acuminata* in a sample of 20 trees is 348 years old with the next four oldest trees in the population obtaining ages of 318, 215, 177 and 174 years old. The oldest individual tree is 198 years greater than the maximum age for this species listed in Burns and Honkala (1990) and 38 years greater than in Hough and Forbes (1943).

The frequency at which greater ages are found in our studies compared to the Silvics Manual of North America (Burns and Honkala 1990) or Loehle's (1988) list of known maximum longevity suggests that there is much yet to learn about the basic natural history of central hardwood and eastern US forests. Further, with the exception of *A. rubrum*, the proximity of the next oldest individuals in the recent studies either to the new or previous maximum age suggests that longevity in these species may be even greater than those reported here. This hypothesis is built upon the premise that maximum ages for each species has a normal distribution; a 'common' maximum age. It could be, however, that a species' maximum age could be significantly larger than what is reported if maximum age has an asymmetrical distribution or a long tail (*sensu* Clark and others 1998). Such a distribution could explain the 800+ year maximum age reported for eastern hemlock (*T. canadensis*) (Burns and Honkala 1990), despite the fact that a collection of more than 1000 *T. canadensis* collected from across its range has not yielded an individual greater than 600 years old (ITRDB 2005).

The similarity of the new maximum ages presented here and those ages reported in the classic study of the high plateau region of Pennsylvania by Hough and Forbes (1943) indicates that these maximum ages may represent a common maximum age. It should be noted, however, that the ages of Hough and Forbes (1943) are ring counts of stumps in the field and could be significantly off due to measurement error. Likewise, a lack of dating control might explain the extreme maximum age reported for *T. canadensis*. Crossdated samples of *A. rubrum* indicate the possibility of up to 12 missing rings per tree in extreme cases (Pederson 2005). Similarly, work on *M. Acuminata* and *B. lenta* indicates that these species can have a significant number (greater than 10) of false and missing rings (N. Pederson, unpublished data). Nonetheless, the near agreement of the Pennsylvania ages and recent studies suggest that the work of Hough and Forbes (1943) provides an excellent early estimate of the maximum ages for many of these species.

Black Birch in Old-Growth Eastern Hemlock Forests

Overall, black birch was a minor component of the old-growth stands investigated in Massachusetts, making up less than 15 percent of the overstory species composition (table 2). Within these stands, black birch was most commonly found in the intermediate and codominant crown classes and attained diameters smaller than the associated hemlock (table 2, mean hemlock diameter = 33.2 cm). Maximum ages of black birch individuals within these stands exceeded those previously reported for this species (Hough and Forbes 1943), including several individuals between 320-332 years old (table 2). In addition, only two of the eleven stands investigated did not contain at least one black birch individual greater than 210 years old (table 2).

Black birch recruitment generally occurred in episodic peaks with other species within these stands (fig. 1). These episodic recruitment patterns indicate that successful birch recruitment occurred predominantly during large disturbance events, such as the hurricane of 1893 (fig. 1). These findings are consistent with other studies that have also demonstrated the importance of moderate disturbance events in facilitating the establishment of black birch (Ward and Stephens 1996). While these recruitment events lead to an increase in the amount of black birch, the age data collected from these sites suggests that several older trees may also have become established from smaller unknown events.

Although other studies have previously reported the presence of *B. lenta* in old-growth forests (Hough and Forbes 1943, Morey 1936, Foster 1988, Orwig and others 2001), this species has traditionally been thought of as an associate of younger forest ecosystems (e.g., Stephens and Waggoner 1970, Trimble 1970). The findings from our research indicate that black birch commonly plays a prominent role in the structure and dynamics of old-growth hemlock stands attaining ages well beyond previous expectations. In the populations examined in this study, most *B. lenta* were less than 150 years old; however, 58 percent of those individuals greater than 180 years old have lived beyond 250 years illustrating the ability of this species to consistently persist within the canopy of these old-growth stands. Interestingly, *B. lenta* is often the species replacing eastern hemlock in stands infested with hemlock woolly adelgid in southern New

Table 2—Summary table for attributes of black birch populations in 11 old-growth mixed eastern hemlock stands in western Massachusetts

Study area	Importance value ^a	Age ^b	Diameter cm
Mt. Everett	9.4	65 (77)	18.2
Grinder Brook	5.7	175 (218)	27.3
Bash Bish Falls	2.8	172 (211)	28.3
Cold River A1	11.0	127 (251)	28.9
Cold River A2	9.0	169 (326)	30.3
Cold River B	9.0	146 (238)	32.0
Cold River D	8.6	165 (261)	21.4
Manning Brook	7.2	87 (158)	24.0
Wheeler Brook	10.4	203 (284)	27.5
Black Brook	12.5	182 (328)	30.3
Todd Mountain	6.9	163 (332)	28.4
Average	8.4	150	27.0

^a Importance value = (relative basal area + relative density)/2.

^b Average age with maximum found at site in parentheses.

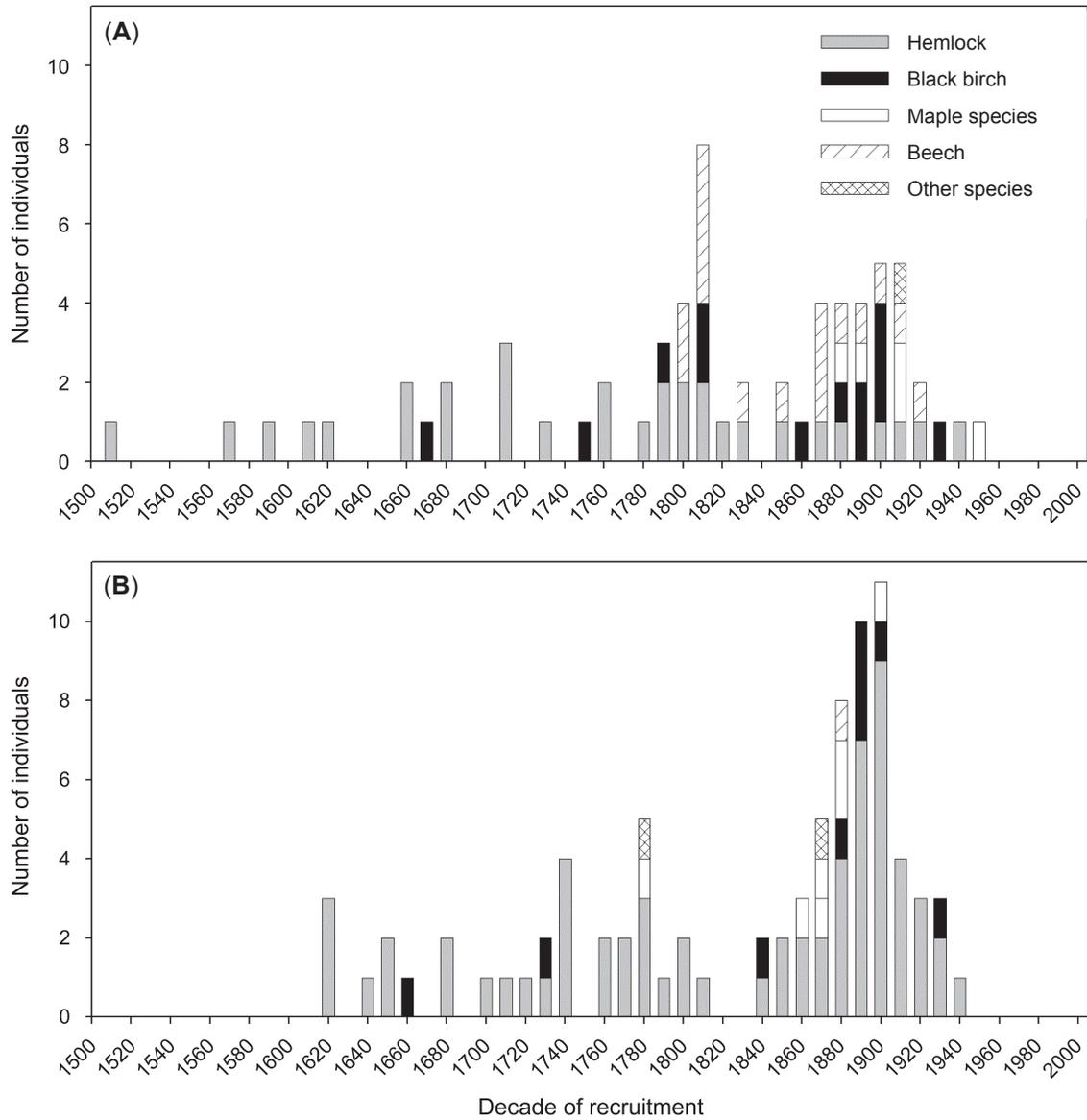


Figure 1—Example age structures from two eastern hemlock-mixed hardwood dominated old-growth forests, (A) Cold River A2 and (B) Todd Mountain, in western Massachusetts. N = 74 (13 *B. lenta*) and 88 (9 *B. lenta*) for (A) and (B), respectively.

England (Orwig and Foster 1998). In light of our findings, it is likely that *B. lenta* may persist in these affected stands longer than previously expected.

CONCLUSIONS

Data presented here suggests that rarely studied trees species can live much longer than previously thought. Our results also show how dendrochronology is an excellent tool to deepen our knowledge of the natural history of central hardwood tree species. Besides maximum age, tree-ring analysis can reveal other facets of natural history such as how long a species can remain suppressed in the understory, how they respond to disturbance events or how long they can sustain high levels of productivity. Not only will this dendrochronology-derived information help expand our knowledge of natural history, it will provide

important data for simulation models to produce realistic estimations of tree longevity. Future studies of other central hardwood species will be critical for future efforts aimed at modeling long-term forest dynamics, as well as for predicting the population and system responses to the effects of environmental changes and novel disturbances such as the hemlock woolly adelgid, on future forest structure and composition (Dayton 2003; Schmidly, 2005).

The ‘accidental’ discovery of new maximum ages for four species typical of central hardwood forests and the surprising persistence of *B. lenta* suggests the lack of natural history knowledge for many eastern U.S. tree species. We hope this presentation emphasizes the need for more research. Such research would be an excellent avenue for inspiring motivated undergraduate and graduate-level students to incorporate the field of natural history into their studies.

ACKNOWLEDGMENTS

N. Pederson greatly acknowledges support of the Department of Energy’s Global Change Education Program for support during his dissertation research. Many thanks to Drs. Charles Canham and Paul Sheppard for collecting and sharing the *A. rubrum* samples and Ed Cook for collecting and sharing the New Paltz *B. lenta* samples. This is Lamont-Doherty Earth Observatory Contribution Number 6869.

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