HISTORICAL BIOGEOGRAPHY OF AMERICAN BEECH

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Abstract

American beech (*Fagus grandifolia*), now a centerpiece species of the eastern deciduous forest, has had a continually changing historical biogeography. This paper reviews the paleoecology, the presettlement occurrence, the modern range, and the current abundance pattern of beech. It synthesizes these four databases into maps representing the distribution and abundance of beech at specific periods from glacial maximum to the present. The post-glacial history of beech is a consistent broad northward expansion from refugia in the deep South. Beech reached its modern Canadian limits about 7,000 years ago and flourished with remarkable dominance south of the Great Lakes (regional >20% pollen) until 3,000 years ago. The contrast between presettlement (>35% witness trees) and modern beech abundance (<15% basal area) in the Northeast is just part of the regionally declining trend of beech dominance that began 2,000 years ago. The maxima of paleoecological representation, presettlement density, and current abundance are all centered in northern Pennsylvania and align in an broad axis of beech importance reaching northeast into Canada. The beech range has sharply defined boundaries and scattered southern and western populations are usually associated with riparian zones or on sheltered mesic slopes. The new distribution map extends the modern range more than 140 km north and identifies distinct outliers not found in the former mapped range. This detailed historical and geographic baseline of beech forests before it was affected by beech bark disease forms an important quantification of range, composition, and structure of beech that should be used to assess the effects of natural, land use, and new disturbances.

Introduction

American beech (*Fagus grandifolia* Ehrh.) is currently a central component of the eastern deciduous forest. Beech has great shade tolerance and is moderately long-lived and is thus, together with sugar maple (Acer saccharum Marsh), the archetypical dominant in the so-called climax "northern hardwood forest" (Tubbs and Houston, 1990). According to E. Lucy Braun's (1950) classic treatise, the deciduous forests of eastern North America are the product of differential post-glacial migration and filtering of forest composition from an original southern refugium of the last glacial maximum. Significantly, beech is widespread in all nine of Braun's (1950) forest regions, a characteristic species for four regions, including the residual mixed mesophytic core. It is also the dominant in two regions lying to the north, including the namesake beech-maple region. Furthermore, this species is a prominent component in most exemplary stands in the Northeast, and well represented in many old growth models, including the larger landscape tracts of the Great Smoky Mountains NC/TN, Five Ponds, NY, and Big Reed, ME (Whittaker, 1956; Roman, 1980; Cogbill 1996). Therefore, beech is unquestionably pivotal to both the theoretical development of the eastern hardwood forests and the empirical composition and dynamics of reference sites from Nova Scotia to Texas (Schafale and Harcombe, 1982; Greenridge, 1987; Peters, 1997). This preeminence extends to the role of beech in many realms of research: post-glacial migration and dispersal of tree species (Davis, 1983; Dexter et al., 1987); gap dynamics and hardwood regeneration processes (Forcier 1975; Woods, 1984; Runkle, 1981); and, how to conserve natural areas and significant animal habitat (Hunter, 1990; Davis, 1996). Interestingly, despite its current abundance, Siccama (1963) has observed that, at least in Vermont, beech was dramatically more abundant 200 years ago than it is today. This decline of beech is apparently not the purposeful result of land use activities (the Siccama enigma) and predates recent beech bark disease (Houston, 1975, 1994).

Postglacial Distribution and Abundance

The past range and abundance of beech is based on a collection of over 750 dated pollen cores from across eastern North America (Williams et al., 2004). Numerous summaries of beech pollen percentages from 24,000 years ago (radiocarbon dates corrected to calendar years) to the present are published, but various interpretations of the inferred pattern of tree abundance are conflicting (Davis and Webb, 1975; Lenk, 1982; Davis, 1983; Bennett, 1985, 1988; Davis et al., 1986; Delcourt and Delcourt, 1987; Webb, 1987; Dexter et al., 1987; Jackson et al., 2000; Williams et al., 2004) To establish an approximate range limit, a threshold beech pollen percentage that balances the ambiguity of occasional pollen transported long distances—pollen without local presence—and limited collection efficiency from restricted populations—local presence without pollen,. must be determined. Here a 0.5% threshold is invoked as a useful indicator (Davis et al., 1991). In addition, beech pollen is under-represented relative to tree density, but is only crudely equivalent to half of the regional proportion of trees (Davis et al., 1991). Thus, detailed reconstructions of the timing of migration and associated patterns of abundance of this tree species are still somewhat speculative (McLauchlan and Clark, 2004). This paper synthesizes various studies and reconsiders pollen profiles from specific sites, independently mapping the approximate range limit and relative regional abundance of beech at past intervals.

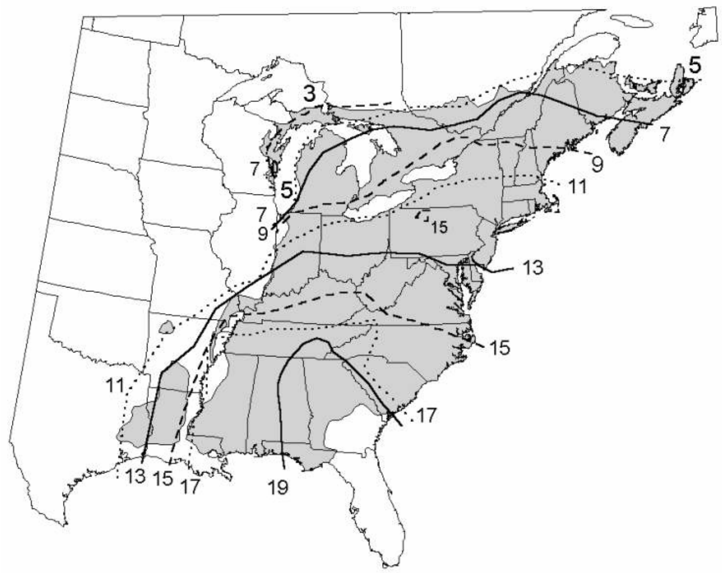

Figure 1.–Isochrones of the postglacial migration of the general northern distributional limit of beech in eastern North America. The numbers at the ends of the lines are the age in thousands of calendar years ago (Ka) inferred from pollen studies. The shaded area mapped is the resultant modern (0 yr) range of beech.

The post-glacial history of beech is clearly that of a consistent northward expansion (Fig. 1) with two major periods of flourishing and then associated declines. In summary, between 24,000 and 17,000 years ago beech was present at low levels, presumably in very localized populations, in the extreme Southeast (Delcourt and Delcourt, 1987). These southern refugia expanded rapidly, reaching a maximum of over 10% pollen across the southeastern Coastal Plain and Interior Plateaus by 14,000 years ago (Williams et al 2004). Interestingly, there was a single site in north central Pennsylvania which had possibly 15,000 year old beech pollen, indicating either rapid migration or early establishment well beyond the general range (Cotter and Crowl, 1981). The Southeast beech maximum faded from 11,000 to 8,000 years ago, but was accompanied by the continued northward spread of beech. The migration was on a broad front averaging roughly 85 m/yr (sustained 4 km per reproduction). This movement was perhaps accelerated by long-distance establishment of outliers (e.g. the jump across Lake Michigan 7,000 years ago), presumably mediated by dispersers such as passenger pigeons or blue jays (Webb, 1986; Davis et al., 1991). The present northern limits were nearly approached across Quebec as early as 7,000 years ago (Bennett, 1988). A second historic pollen maximum centered around the Great Lakes was well established 7,000 years ago and rose to more than 20% pollen at 3,000 years ago (Williams et al., 2004). At the same time, the range expanded slowly into the Maritimes and across the Upper Peninsula of Michigan, perhaps decelerated by limited ability to invade established forests (Green, 1981; Bennett, 1987; Davis et al., 1991). Starting 2,000 years ago, the widespread maximum over the Northeast dramatically shrank and lessened. By roughly the time of presettlement 500 years ago only a small restricted area of more than 10% pollen remained just south of the Lake Erie. Current pollen show the continued decline of beech to less than 5% throughout its range and only scattered remnant traces in the South (Williams et al., 2004).

Presettlement Composition

A quantitative assessment of the beech abundance unaltered by land use is based on land surveys done in anticipation of European settlement (Cogbill et al., 2002). An interpolated grid of the proportion of witness trees in 710 towns of New England and New York maps the frequency of beech in the unsettled forests (Fig. 2). In ca. 1800, beech was ubiquitous and common in the forests of the Northeast. It was found in samples from 97% of the towns and averaged 27% of the sampled trees across the northern hardwood region. Beech was only a minor component in the warmer and drier conditions south of the dramatic “tension zone” running across southern New England and northern Pennsylvania (Cogbill et al., 2002). The incredible beech dominance, first noted by Siccama (1963, 1971), is seen in a broad swath with greater than 35% proportion of beech trees from the Allegheny Plateau of Pennsylvania to mountains of northern New Hampshire. Within this zonal belt,

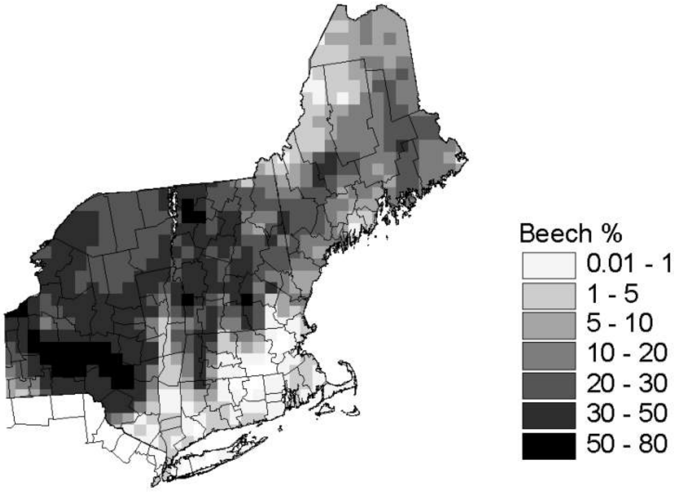

Figure 2.–Presettlement (ca. 1800) relative abundance of beech in the forests of New England and New York. Percentages are the interpolated grid proportions of beech based on witness trees cited in town-wide land surveys (Cogbill, unpublished data).

there were significant maxima in the hill country of the Green Mountains, the Catskills, and reaching a maximum abundance of 73% in west-central New York. This pattern from the presettlement tree records is reflected in the pollen record of 500 years ago with 5 to 10% beech pollen composition occurring in a zone through the mountains of the Northeast. Significantly the presettlement period pollen maximum area just south of the Great Lakes, matches the position of the presettlement tree maximum.

Modern Range

The map of beech's current geographic distribution is compiled from actual trees clearly documented in numerous land, forest, floristic, and ecological surveys. The modern range of beech is mapped as a contiguous region within which beech commonly occurs, albeit sometimes in low abundance and only on scattered sites. In addition, disjunct outliers are included where a specific beech population is restricted to a particular, often unusual, location. This new map refines the distribution map of Little's (1971) classic atlas and is brought up-to-date by incorporating recently available data. A particular advancement is the clear delimiting of the northern edge of the range, which Little based on secondary sources and was broadly generalized (Little, 1971; Farrar, 1995). The new Canadian distribution is based on observations from over 17,000 forest inventory plots in Québec (Ministère des Ressources naturelles, de la Faune et des Parcs, Direction des inventaires forestiers , Ste.-Foy, Québec, unpublished data), some 160 insect disease plots from Ontario (Canadian Forest Service, Sault-Ste.-Marie, ON, unpublished data), and floristic and ecological surveys from Ontario to New Brunswick (e.g. Rousseau, 1974; Lenk, 1983; McMahon et al., 1990; Maycock, 1994; Hinds, 2002). Details of the distribution in the Midwest of the United States are derived from presettlement forest surveys, herbarium collections, and natural history narratives (e.g., Davis et al. 1991; Iverson et al., 1999; Greenberg, 2002; Cofrin Center for Biodiversity, 2004; Missouri Botanical Garden, 2004). Changes in Little's map at the southern and western limits reflect the fine scale distribution derived from thousands of FIA inventory plots (Forestry Inventory & Analysis, United States Forest Service), county floristic checklists, and data collected in a series of ecological natural areas (e.g. FIA summarized in Prasad and Iverson, 2003; Davis, 2003; USDA Plants Database, 2004).

Beech's modern distribution covers temperate eastern United States and southeastern Canada (Fig. 3). The only exception to the compact range are Mexican stations which are disjunct by 1000 km and have been recently treated as a distinct variety (Fagus grandifolia var. mexicana (Martinez) Little) of American beech (Little, 1965). Mexican beech grow in ten restricted and very small populations in the "mesophilous" cloud forest of the mountains eastern Mexico (Williams-Linera et al., 2003). Throughout its range, beech is found on most mesic sites which have escaped fire. Beech occurs from sea level along the Atlantic Ocean to the Gulf Coast and up to 2000 m elevation in the beech gaps of the southern Appalachian Mountains (Russell, 1953). The range of beech has a sharply defined northern boundary suggesting environmental limitation, perhaps cold hardiness. On the new distribution map (Fig. 3), beech extends northward some 140 km beyond the previously mapped range (cf. Little, 1971; Hosie, 1979; Tubbs and Houston, 1990; Flora of North America Editorial Committee, 1997) and there are a few isolated populations established up to 100 km beyond the continuous range. At the northern edge of the range, beech occurs under locally moderated temperature and moisture conditions up to about 800 m on mountain slopes. It is especially abundant on well drained soils in valley sides or on hardwood ridges. The western limit of the range appears to be tied to moisture availability, with a particularly strong fidelity to river bluffs. Intriguingly

Figure 3.–Map of the modern range of *Fagus grandifolia* in eastern North America. The shaded area is the region of relatively continuous distribution of multiple populations. The dots are restricted documented outliers populations. The outlines are states of the United States, provinces of Canada and Mexico. General range is based on Little (1971) with major modifications and refinements based on various field surveys.

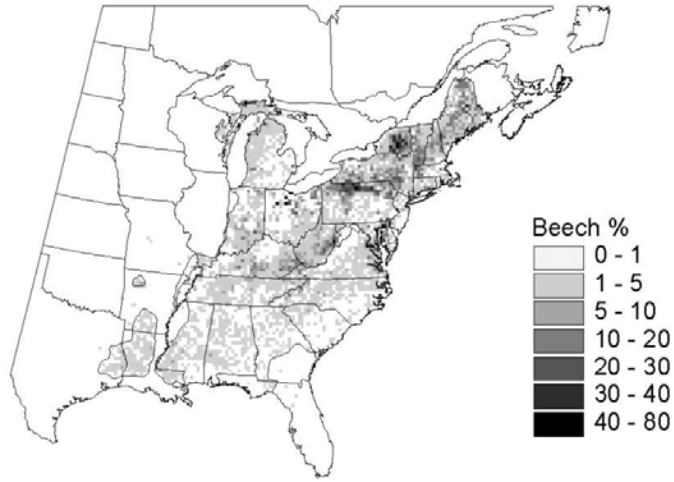

Figure 4.–Modern relative abundance of beech in the forests eastern North America. Grid map is interpolated from Forest Inventory and Analysis (FIA) plot data and adapted from Prasad and Iverson (2003). States are indicated and the additional thin line outlines the general contiguous range of beech from this study.

rivers seemingly form a hard edge to beech distribution as the range barely crosses west of the Wabash, the Mississippi (including its former channel west of Crowley's Ridge), or the Yazoo Rivers. To the southwest, the limit to the distribution is more extended, with several diffuse patches and scattered outlier populations well beyond the Mississippi River. Populations approaching the western and southern limits are usually associated with riparian zones or on sheltered mesic slopes, such as "coves". For example, beech is found in ravines around Chicago (IL), in hollows on Crowley's Ridge (AR & MO), on loess bluffs along the lower Mississippi Embayment (LA, MS, & TN), on valley floodplains (i.e. along Buffalo and Osage Rivers) within the Ozarks (AR & MO), in creek bottomlands of the Big Thicket (TX), and in hammocks (islands of isolated hardwood in bottoms) on the southern pine flatwoods (FL & GA).

Current Abundance

Beech's modern compositional importance across its United States range is most easily documented by the Forest Inventory and Analysis (FIA) program of the United States Forest Service. Averaging data from over 100,000 FIA sample plots, Prasad and Iverson (2003) have compiled a grid map of the geographic distribution of the beech's proportion of forest composition (Fig. 4). Beech averages 2.3% of the total forest basal area within its range, but the distribution across the landscape varies from less than 1% over much of the South and Midwest to being the dominant in widespread regions of the Northeast. There is a broad maximum of beech tree abundance scattered along the Appalachian Mountains from Kentucky to Maine (FIA average 11.1%), with local centers of greater than 20% (maximum 51%) beech landscape abundance in the Adirondacks (NY), northern Allegheny Plateau (PA) and central Allegheny Mountains (WV). Although Canadian forest inventory surveys have not yet been mapped, the 17.1% average beech forest proportion for its Quebec range indicates that the Northeast landscape maximum apparently continues through southern Canada almost to its northern range limit (Québec inventaires forestiers, unpublished data). This regional distribution is reiterated by modern pollen representation, in which beech pollen is found consistently, but predominantly at less than 5%, in an axis from the Great Lakes to Nova Scotia (Williams et al., 2004).

Baseline Character

The modern geographic pattern of beech on the landscape is dependent on three major factors: its

Table 1.—*Fagus grandifolia* abundance at the landscape and stand scales under different scenarios in reference sites in eastern North America.

Item	Stands/ Plots (#)	Beech Constancy (%)	Total BA (m^2/ha)	Beech BA (%)	Max. dbh (cm)	Mean dbh Dquad (cm)
Historic						
N. Hardwood region[1]	16	86	-	20	-	
Waterville, NH[2]	50ac	-	31.6	31	66	30.9
Tionesta, PA[3]	651	70	27.2	35	102	26.0
Modern outside BBD†						
Five Ponds, NY[4]	71	79	34.1	23	70	24.4
Joyce Kilmer, NC[5]	30	-	-	5	66	27.2
Walker Cove RNA§, NC[6]	18	100	33.3	18	60	26.6
Modern BBD† aftermath—no cutting						
Big Reed , ME[7]	88	89	32.4	12	60	20.9
Bowl RNA§, NH[8]	126	67	31.1	13	51	23.3
The Cape RNA§, VT[7]	28	93	28.5	2	45	19.9
Modern BBD† aftermath—managed						
Gifford Woods, VT[7]	21	76	38.2	4	61	23.0
Lords Hill, VT[7]	51	41	32.3	5	80	51.3
Hubbard Brook valley, NH[9]	431	67	29.2	11	72	24.4
Hubbard Brook W6, NH[10]	118	98	25.7	27	87	23.0

Sources: [1]Braun, 1950; [2]Chittenden, 1905; [3]Hough, 1936; [4]Roman, 1980; [5]Lorimer, 1980; [6]Dickison, 1980; [7]Cogbill, unpublished data; [8]Martin and Bailey, 1999; [9]Schwartz et al., 2003; [10]Hubbard Brook Long-term Ecological Research site, derived from data on http:www.hubbardbrook.org
†Beech Bark Disease
§Research Natural Area in National Forest

background, albeit naturally changing, regional abundance; the alterations due to centuries of land use (e.g. land clearance, agricultural regeneration, and forest management); and the recent effects of beech bark disease (BBD). The influence of these regimes on the structure of beech forests is potentially factored by historical and geographic grouping of ecological samples. In the region of current maximum beech importance, four groups of quantitative reference studies have been investigated: 1) sampled historically before local occurrence of BBD; 2) sites outside the influence of BBD; 3), unmanaged reference sites, but well after the effects of BBD or so-called aftermath forests; and 4) managed, but still primary aftermath forests (Table 1).

Discussion

The history of beech is not a simple northern migration and attenuation of the deciduous zone after glacial retreat (Braun, 1950). At glacial maximum beech was a minor species in the deep South and apparently associated with species (e.g. magnolia, oaks and pine) which are neither typical mixed mesophytic nor northern hardwoods (Delcourt and Delcourt, 1987). Later, beech migrated independently of other components of the eastern forest and was indeed a rather late northern arrival (Davis, 1983). In addition, beech has flourished twice in the past within its range, but both times its strong dominance has faded. Apparently, its abundance was not especially responsive to specific climate changes, and the movement of the range boundary appears independent of overall abundance within the range. Both the northern and western range distribution have distinct outliers which seem to be restricted to special environments, but are presumably relatively stable populations established long ago. Paleoecological and presettlement abundance records indicate that an ongoing long-term decline (but not contraction) of beech in the Northeast began some 3,000 years ago. Interestingly, the current abundance maxima in northern Pennsylvania and in upstate New York seem to be the remainders of an even greater abundance of a late-Holocene center of beech around the Great Lakes. This regional decline has certainly been accelerated by land use after settlement, but many activities such as beech being a poor timber species and its tendency to sprout after disturbance may have slowed beech decline. Recent introduction of BBD, is only adding to the strong established trends already affecting beech populations.

The dramatic contrast between beech tree abundance in the presettlement landscape (widespread >35%) and modern abundance (only locally >20%) indicates that the Siccama enigma applies to much of the Northeast. An analysis of the geographic-specific ratio of the presettlement (Fig. 2) to the FIA modern composition (Fig. 4) indicates a typical fraction of only 30% remaining from the original presettlement beech density. Similarly, parallel data from Wisconsin indicate a beech decline from 27% in presettlement (Davis et al. 1991) to less than 5% today (FIA: Prasad and Iverson, 2003). The magnitude of the historic decline varies across the region ranging from severe in northern Vermont and central New York (beech less than 10% of presettlement values and a species switch in 40% of the composition) to little change in the Adirondacks or northern Pennsylvania. For example, at Five Ponds in the western Adirondacks a presettlement witness tree survey in 1815 indicate that the 29% beech trees had changed little to the present (35% in 1975, Roman, 1980; or 32% 1993 FIA. The only areas with any consistent increase in beech abundance over the last 200 years are south of the tension zone or at the northern extremes in Maine where initial beech abundance was relatively low.

A broad perspective on the baseline compositional, size, and age structure of the deciduous forest unconfounded by BBD is derived from old databases and remnant forest stands beyond BBD. Braun (1950) found beech in 63% of 300 plots sampled across the range before 1950, with beech comprising 21% and a maximum of 63% of the stems. Similarly, a sample of 54 modern northeastern "old-growth" deciduous forest stands average 15%, with a maximum of 53% beech basal area (Cogbill, unpublished data). Regardless of its past history, northern hardwood landscapes tend to have beech found in 70 to 100% of the stands across sites and beech forms 5 and 25 % of the remarkably consistent 28 to 34 m^2/ha basal area over all forested sites (Table 1). A typical beech tree is only about 25-30 cm in diameter and forest trees over 50 to 80 cm diameter seldom survive under any conditions. Although there are speculation of up to 700 year old trees, the greatest documented ring count in any American beech is only 412 years (northwest PA, Hough 1936). Significantly, even in "old-growth" stands trees over 250 years old are only occasionally recorded (Cogbill, unpublished data). The typical 0.66% to 1.25% annual natural mortality found in old deciduous forests infers an average longevity of 80 to 150 years for beech unaffected by BBD (Runkle, 2000). Thus canopy trees are seldom expected to survive more than 150 years, presumably due to individual tree death by wind, ice, or snowload. BBD causes direct mortality as well as a predisposition to environmental disturbances shortening beech's lifespan. For example, at Lords Hill, VT some 59 beech trees followed from 1977 to 2004 display a 2.5% annual mortality indicating a 40 year turnover for beech (Cogbill, unpublished data). Despite the large size (80 cm) of remnant stems, this stand is rapidly transitioning to an aftermath forest, with reduced beech influence (Table 1). Although BBD may have accelerated beech decline the aftermath forest still maintains a sustainable forest structure albeit with an increase in smaller sprout (e.g. Siccama's so-called "beech hell" at Hubbard Brook) compensating for fewer large canopy trees (Table 1).

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