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Abstract: We reviewed literature in the fields of anthropology, archaeology, ethnobotany, palynology and ecology to try to determine the impacts of Native Americans as active and passive promoters of mast (nuts and acorns) and fruit trees prior to European settlement. Mast was a critical resource for carbohydrates and fat calories and at least 30 tree species and genera were used in the diet of Native Americans, the most important being oak (*Quercus*), hickory (*Carya*) and chestnut (*Castanea*), which dominated much of the eastern forest, and walnut (*Juglans*) to a lesser extent. Fleshy tree fruits were most accessible in human-disturbed landscapes, and at least 20 fruit- and berry-producing trees were commonly utilized by Native Americans. They regularly used fire and tree girdling as management tools for a multitude of purposes, including land clearing, promotion of favoured mast and fruit trees, vegetation control and pasturage for big-game animals. This latter point also applies to the vast fire-maintained prairie region further west. Native Americans were a much more important ignition source than lightning throughout the eastern USA, except for the extreme Southeast. First-hand accounts often mention mast and fruit trees or orchards in the immediate vicinity of Native American villages and suggest that these trees existed as a direct result of Indian management, including cultivation and planting. We conclude that Native American land-use practices not only had a profound effect on promoting mast and fruit trees but also on the entire historical development of the eastern oak and pine forests, savannas and tallgrass prairies. Although significant climatic change occurred during the Holocene, including the 'Mediaeval Warming Period' and the 'Little Ice Age', we attribute the multimillennia domination of the eastern biome by prairie grasses, berry-producing shrubs and/or mast trees primarily to regular burning and other forms of management by Indians to meet their gastronomic needs. Otherwise, drier prairie and open woodlands would have converted to closed-canopy forests and more mesic mast trees would have succeeded to more shade-tolerant, fire-sensitive trees that are a significantly inferior dietary resource.

Key words: Indian diet, fire, land-use history, cultivation, oak, hickory, mast, fruit trees, Holocene.

Introduction

Vegetation is forever dynamic because the environment in which it grows is constantly altered by changing climate, edaphic conditions, disturbance regimes and anthropogenic impacts. If vegetation is always changing, a central question in ecology is 'what is natural vegetation?' (Lorimer, 2001; Williams, 2002). It may be argued that the natural vegetation of the USA is what existed immediately prior to European settlement – after which severe resource exploitation produced radical changes in community composition and structure (Fuller *et al*., 1998; Abrams, 2003; Schulte *et al*., 2007). Our ability to discern or approximate the pre-European settlement forest via the wide availability of witness-tree data from public-land surveys partially explains this bias. Nevertheless, the European settlement legacy or ecological footprint in the USA is very large (Rees, 1992). In contrast, early Native Americans lacked European technology and may have had a much lighter touch on the landscape and thus a more harmonious, less intrusive relation with vegetation, leaving a smaller ecological footprint. But is this true?

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Several researchers have concluded that climate is the primary driver of vegetation change in the eastern USA (Parshall and Foster, 2002; Shuman *et al*., 2004). While we agree with the importance of climate, we also believe that the impact and extent of early Native American land use in shaping vegetation types is more substantial than previously thought. The large disparity in presettlement vegetation expression between climax forests (set by climatic controls) and that of shade-intolerant, disturbance-based vegetation types strongly points toward human intervention (Stewart, 2002; Nowacki and Abrams, 2008). Indeed, vegetation modification by Native American burning and agricultural land clearance has been particularly well documented (Cronan, 1983; Pyne, 1983; Williams, 1989; Whitney, 1994; Bonnickson, 2000). For example, forests dominated by oak, chestnut, hickory and pine prior to European settlement are thought to require periodic fire for continued recruitment and long-term success (Abrams, 1992; Lorimer, 2001). Bromley (1935) concluded that Native American populations in southern New England were of sufficient size to burn most of the landscape on a recurring and systematic basis. Indians regularly used broadcast burning to clear forest undergrowth, prepare croplands, facilitate travel, reduce vermin and weeds, increase mast production and improve hunting opportunities by stimulating forage and driving or encircling game (Whitney, 1994; Stewart, 2002; Williams, 2002). Accidental wildfires also occurred from escaped camp and signal fires and burned into the surrounding forests. Once fires were set, there was little incentive or means by which to put them out (Stewart, 2002).

During the latter part of the Holocene, Native Americans planted a wide variety of crop species in well-managed agricultural fields adjacent to their villages (Trigger, 1978; Fogelson, 2004). MacDougall (2003) lists a total of 35 herbaceous plant species cultivated by eastern Native Americans. By the sixteenth century, the most abundant crops were maize, beans and squash, known as the ‘Three Sisters’ when planted together (Martinez, 2007). In contrast to our understanding of Native American use of fire and the cultivation of crops, we know very little about their direct and indirect impacts on the distribution of the mast and fruit trees that were important in their seasonal diet. If Native Americans had the skills to develop sophisticated systems of agriculture, did they possess similar skills to manage forests?

The promotion of mast and fruit trees would have involved active silviculture and horticulture such as reducing competing vegetation via girdling, cutting or prescribed fire and the planting and tending of beneficial tree species, possibly even creating fruit or mast orchards (Delcourt and Delcourt, 2004). The passive promotion of certain trees could have stemmed from various land uses intended for other purposes, such as broadcast fire for reducing undergrowth for security and travel, game management and general land clearance. It also could have resulted from village and agricultural field abandonment. Important mast trees used by Native Americans in the eastern USA included oak, hickory, beech (*Fagus*), chestnut and walnut (*Juglans*), species that dominated many presettlement forests. Prairies dominated much of the Central Plains and Midwest prior to European settlement, also as result of Indian burning (Sauer, 1975; Stewart, 2002). Prairie sustained huge populations of large ungulate species of *Bison*, deer (*Odocoileus*) and elk (*Cervus*) that were vital to the Indian diet. In any given part of the eastern USA, various vegetation types or stages may exist depending on the climate, site conditions, disturbance regime and successional status. It is important to know to what extent the dominance of mast trees and prairie were a result of Native American land use and disturbance, whether either directly or indirectly, and to what extent these were created and maintained to meet dietary needs.

The purpose of this paper is to explore the role of Native Americans in the active and passive promotion of dietary mast and fruit trees and prairie in the eastern USA, and to determine to what extent their practices shaped the overall vegetation prior to European settlement. We explore the hypothesis that Native American land-use management was focused on the creation of large expanses of specific forest and prairie to meet their dietary needs. This will be accomplished by:

(1) synthesizing palaeoecological information on the long-term vegetation dynamics and climate during the latter part of the Holocene;
(2) comparing Native American ignitions to natural (lightning) sources;
(3) exploring ethnobotany and anthropology studies on the dietary uses of mast and fruit trees by Native Americans;
(4) reconstructing vegetation composition at the time of European settlement and ascertaining to what extent it was a result of Native American activities;
(5) documenting Native American land-use and vegetation management that has played a direct (active) or indirect (passive) role in promoting dietary mast and fruit trees in the USA.

Human–vegetation–fire relations in the palaeoecological record

Humans have long affected their surrounding environment, to the point of being considered an ecological factor, an ecological change agent or a ‘keystone’ species (Day, 1953; Kay, 2000; Bonnicksen *et al*., 2000). Although humans do not have the same antiquity in the New World as in the Old World, they were firmly in place across North America by the end of the last Ice Age some 11 500 yr ago and participated in the dramatic postglacial changes over the continent (Pielou, 1991; Meltzer, 2003). With glacial retreat, plants and animals migrated outward from refugia, intermingling and forming new dynamic communities along the way (Pielou, 1991; Delcourt, 2002).

Postglacial vegetation changes have generally been attributed to climate (Woods and Davis, 1989; Prentice *et al*., 1991; Foster *et al*., 1998). A dynamic equilibrium set up over time as the location and configuration of species niches shifted with climate. Furthermore, as climate and vegetation concomitantly changed, so did disturbance regimes. For instance, shifts towards warmer and drier conditions were often accompanied by increased fire and *vice versa*. As such, a close relationship existed among vegetation, climate and disturbance (fire). Anomalies occur when these factors were out of sync. These anomalies resulted from ecological inertia (lags related to vegetation and established feedbacks; Pielou, 1991) or human activities (eg, burning). It is through these anomalies that human-caused vegetation changes can be ferreted out.

To detect palynological anomalies, genera must be classified by preferred climate regime (eg, cool dry, cool wet, warm dry, warm wet; Iverson *et al*., 1999), pollen frequencies tracked across multiple climate intervals (with climate being established independent of vegetation), and mismatches identified between a genus’ preferred climate and the actual recorded climate (see Shuman *et al*., 2002). Likewise, charcoal abundance (an indicator of fire) can be tracked across multiple climate intervals and anomalies identified. In particular, a constant level or increase of fire and/or fire-adapted species during an increasingly moist and cool climate is probably the most definitive signature of human activity.

For the Northeast, six postglacial climatic intervals were identified by Shuman *et al*. (2004). Climatic periods included cold dry (14 600–12 900 yr BP), cold (12 900–11 600 yr BP), cool dry (11 600–8200 yr BP), warm wet (8200–5400 yr BP), warm dry (5400–3000 yr BP) and cool wet (3000 yr BP onward). Two climate–vegetation anomalies were apparent among the mast-producing genera of chestnut (preferred climate = warm wet), hickory (warm dry), and oak (warm dry): (1) the late arrival and rise of chestnut during the most recent cool wet period (3000 yr BP to present) and (2) the stability (opposed to decline) of hickory during the same period. Since these genera are fire-adapted, they may have benefited from Native American burning in the region and, in the case of chestnut, through active dispersal by Natives (Abrams, 1992; Foster *et al*., 2002; MacDougall, 2003; Pederson *et al*., 2005). Indeed, based on palaeocharcoal data, the occurrence of fire was unusually high for this cool wet period (Foster *et al*., 2002), at least up until the 'Little Ice Age' (Pederson *et al*., 2005). Alternatively, the late arrival of certain heavy-seeded species such as chestnut may also be due their slow migration rate following glacial retreat (Davis *et al*., 1991), although it is still unusual that expansion took place during suboptimal (cooler) conditions.

In their evaluation of palaeoecological studies, Abrams (2002) and Lorimer and White (2003) remarked how stable oak has been over the past 9000 years in the eastern forests and that recurring surface fires were important prior to European settlement. Natives must have been the principal ignition source as lightning-based ignitions are uncommon in the humid northeast and most other regions of the eastern biome (Stewart, 2002; Lorimer and White, 2003). Moreover, a strong linkage exists between the distribution of fire-adapted oak at low elevations and Native villages of the Northeast (along coastlines and in broad interior valleys; Fuller *et al*., 1998). In New England, palaeocharcoal levels dating to 2500 years ago were lowest in northern hardwood forests, intermediate in oak and pine forests and highest in pitch pine and oak forests (Parshall and Foster, 2002). Oak-dominated forests in the Hudson Highlands of southeastern New York were developed and maintained throughout most of the Holocene as a result of Native American fires (Maenza-Gmelch, 1997). Although scientists generally agree that Native pyro-activities did affect northeastern vegetation, the scale at which it happened (local versus regional) is still being debated (cf. Patterson and Sassaman, 1988 and Parshall and Foster, 2002).

Strong human–fire–vegetation relations have been found in central and southern Appalachian Mountains through coupling palaeoecological (pollen analyses and charcoal stratigraphy) with archaeological data. In eastern Kentucky, a dramatic increase of oak, hickory, chestnut and pine after 3000 yr BP corresponded to increased fire and anthropogenic activity (Delcourt *et al*., 1998). Since lightning-ignited fires are relatively infrequent in the Appalachian Mountains, a direct cause-and-effect relationship was inferred between human-set fires and vegetation change. At the rain-saturated Horse Cove archaeological site in western North Carolina, the constancy of oak dominance over the past 4000 years was attributed to Native American burning (Delcourt and Delcourt, 1997). Native populations along the Lower Little Tennessee River had strong impacts on surrounding vegetation. Through land clearance and abandonment, the proportions of disturbance-based taxa increased to the detriment of bottomland taxa (Chapman *et al*., 1982). Furthermore, the increase in the extent of open lands and forest edge might have enhanced the abundance and diversity of food resources and ultimately the carrying capacity of the land.

Using lake-sediment cores, Camill *et al*. (2003) reconstructed climate, vegetation and fire regimes along the prairie-forest ecotone of south-central Minnesota. Four broad climatic periods were identified: cool humid (11 250–8250 yr BP), warm dry (8250–4250 yr BP), warm humid (4250–2450 yr BP) and cool humid (2450–0 yr BP). Grassland expansion corresponded with warm dry conditions and increased fire in the mid Holocene (8250–4250 yr BP); thereafter oaks expanded as the climate shifted to a moister regime (4250 yr BP onward), which seemingly removed water-stress limitations to tree recruitment. Two climate–vegetation–fire anomalies were: (1) a curious increase of fire during the warm/humid period (4250–2450 yr BP) and (2) a continuation of fire, albeit at a decreased level, during the subsequent cool/humid period (2450–0 yr BP). The former was attributed to productivity-driven increases in fine herbaceous fuels. Regarding the latter, perhaps the area's down-wind proximity to the Great Plains allowed regular fire entry from the west. Alternatively, local Natives may have maintained a burning regime amidst deteriorating climatic conditions (McAndrews, 1968; Grimm, 1983). In the Big Woods region of south-central Minnesota, pre-European settlement forests were dominated by elm (*Ulmus*), basswood (*Tilia americana*) and sugar maple (*Acer saccharum*) on infrequently burned sites, or oak and aspen (*Populus*) on frequently burned sites (Grimm, 1984). This author concluded that lightning fires were rare in this region and that the vast majority of fires were set by Native Americans. A recent shift to mesophytic 'Big Woods' vegetation (within the last 300 yr) corresponds to even wetter and cooler conditions associated with the 'Little Ice Age' (Grimm, 1983) along with possible decreased ignitions due to Indian depopulation (McAndrews, 1968).

Grasslands are one of the few ecosystems whose occurrence is dictated by human-caused fire rather than climate (Gleason, 1913; Moore, 1972; Sauer, 1975; Nuzzo, 1986; Stewart, 2002). This is especially true for the tallgrass prairies of the Midwest – Transeau's prairie peninsula (Transeau, 1935; Williams, 1981). Here a climate–vegetation anomaly exists whereby cool and moist climate capable of supporting forests prevailed since the end of the Hypsithermal (Anderson, 2006). The fact that the prairie peninsula historically extended across multiple temperature (north–south) and precipitation (east–west) gradients and across contrasting soils strongly implicates fire as the primary cause (Lindsey, 1961; Dorney, 1981). Here, presettlement woodlands and forests were largely restricted to the leeside of firebreaks (Gleason, 1913; Neuenschwander, 1957; Grimm, 1984). The fire dependence of tallgrass prairies and affiliated systems (oak savannas) is illustrated by the near-universal conversion to shrubs and trees upon European fire suppression (Cottam, 1949; Abrams, 1986; Nuzzo, 1986). Although lightning ignitions may have been important on the dry Great Plains (Higgins, 1984; but see Moore 1972), it was Native Americans who dominated ignitions in the humid Midwest where rainfall usually accompanies lightning storms (Sauer, 1975; Stewart, 2002; Anderson, 2006). Moreover, the dominance of dormant-season burns strongly points to Native American origin (McClain and Elzinga, 1994). The term 'Indian Summer' was specifically derived from the red smoky appearance of the sky associated with regular Native burning in the Autumn (Foot, 1836; Williams, 1981). Grazers may have influenced the patterning and structure of prairie-savanna landscapes, but they were not the primary determinants of its character; it was fire (Olson, 1996). The conscious use of fire by Midwest Indians to create grazing habitat and partially control large herbivores probably represents the most extensive form of prehistoric management anywhere in the USA (Auclair, 1976).

One possible way of distinguishing anthropogenic impacts on fire regimes is by evaluating vegetation-fire conditions with and without humans during similar climatic periods. However, opportunities are practically non-existent during the Holocene (past 12 000 yr BP) as humans rapidly spread across and colonized the North American continent after deglaciation (Meltzer, 2003). This restriction forces the use of long-term pollen and charcoal records that extend back to previous interglacial periods. The longest continuous pollen record east of the Rocky Mountains comes from Pittsburg Basin, Illinois (Teed, 2000), which includes the Sangamon Interglacial Period (*c*. 130 000–120 000 yr BP). In comparing the last two interglacial periods, Teed found different vegetation compositions and fire regimes. The dominant temperate deciduous forests of the Sangamon Interglacial had greater tree diversity (based on pollen equitability and abundance) than that of the dominant oak-hickory forests of the Holocene. Correspondingly, the Sangamon had a much more subdued fire regime than the Holocene based on charcoal analysis. The dissimilarities of vegetation between these two periods were probably more due to differences in fire regimes than climate (Teed, 2000). One obvious difference between the Sangamon and Holocene interglacial periods is the presence of humans, an important igniter of fires.

Taken collectively, the above palaeoecological studies indicate a divergence of fire–climatic relations over the Holocene presumably due to increasing human ignitions. Changes in causal mechanisms may be a continent-wide phenomenon, as Brown and Hebda (2002) found a similar trend along the West Coast. There climate strongly controlled the early-Holocene fire regime but gradually dissipated towards the cool and moist late Holocene when humans ignitions became important.

Native American versus lightning ignitions

There has been long-running debate whether humans were primary igniters of presettlement landscapes or merely supplemented lightning ignitions. In the distant past, natural fire regimes were intimately linked to wet and dry cycles, with combustibles growing during wet periods and burning during dry periods from natural ignitions (Pyne, 2001; Brown and Hebda, 2002). However, things began to change upon the arrival of humans roughly 12 000 years ago. Asians who crossed the Bering Land Bridge were vastly familiar with fire for subarctic survival (eg, for warmth, cooking). As such, fire accompanied humans as they spread across the North American continent. Over time and space, Natives reshaped the ‘natural’ geography of fire by increasing ignitions and fire frequency and extending burning windows past the ‘normal’ thunderstorm season, thus lessening the dependence of lightning ignitions and the rhythmic tie to wet–dry cycles (Pyne, 2001). By the time Europeans arrived in the New World, many of the landscapes they encountered were pyrogenic (Nowacki and Abrams, 2008) – a product of both human- and lightning-caused fire.

Although the relative importance of human versus lightning ignitions on presettlement fire regimes might never be truly deciphered, several lines of evidence strongly point to humans as the principal cause of fire in the eastern USA.

First, ignition sources are not created equal! Humans represent a unique ignition source by being mobile and persistent ‘keepers of the flame’. As such, Native Americans could light fires whenever and wherever conditions permitted, and did so for many reasons. Lewis (1993) chronicled over 70 reasons why Natives burned. Human ignitions were not spatially or temporally encumbered as with lightning, which is restricted to times of atmospheric instability that generate air-to-ground electrical discharges (ie, thunderstorms). In the humid East, lightning is usually accompanied by rain, hence greatly retarding its effectiveness as an ignition source. Furthermore, lightning storms are largely restricted to the summer growing season when humidity is high and vegetation flammability is low (Higgins, 1984; Ruffner and Abrams, 1998; Peterson and Drewa, 2006; Stambaugh and Guyette, 2008). Lastly, fuels need to be sufficiently dry to allow lightning-caused ignitions to spread, oftentimes requiring drought conditions (Rorig and Ferguson, 2002; Mitchener and Parker, 2005; Petersen and Drewa, 2006). For instance, Mitchener and Parker (2005) estimated that drought of up to 12 months is necessary for lightning-caused fires to erupt in the southern Appalachians. The most favourable fire conditions occur in the spring and autumn when vegetation is dry and most flammable. This period lands within the year-round burning potential of humans but outside the range of peak lightning activity (Guyette *et al*., 2006).

Lightning-strike density does not adequately explain the predominance of fire-adaptive vegetation types in presettlement times. Modern lightning strikes (assuming they approximate the presettlement era) are disproportionately concentrated in the Southeast, Florida in particular (http://www.lightningsafety.noaa.gov/lightning_map.htm). The combination of high lightning-strike density, rapid fuel accumulation, conifer dominance and periodic summer drought predisposes this region to a high incidence of lightning-caused fires currently (Mitchener and Parker, 2005) and probably in the past. Outside the Southeast, lightning strike density wanes, and its distribution does not correspond well with the large fire-based vegetation formations that extended from southern Minnesota to New England in presettlement times (tallgrass prairie-oak savanna, northern pineries, oak and oak-pine forests) (see Nowacki and Abrams, 2008). In the central USA, human-ignited fires influenced vegetation at all scales: local, landscape and regional.

Tree fire-scar research has gone a long ways in determining the intricacies among fire, humans and lightning. By combining tree fire-scar, topographic and climatic data with human population and cultural data, Richard Guyette (University of Missouri-Columbia) and associates have been able to elucidate the significance of human ignitions on local and regional fire regimes. For instance, a non-linear relationship exists between human population and fire frequency in the Missouri Ozarks, in part, because of fuel conditions (availability and continuity) and cultural behaviour (Guyette *et al*., 2002). At low population levels, a positive correlation exists between humans and fire, indicating that background levels of natural ignitions were inherently low. Even though fire occurrence is associated with drought, the fire-scar record indicates that drought-induced fires are not fully realized without broad-scale human ignitions (Guyette *et al*., 2006). The fact that the vast majority of fire scars (~95%) occurred during the dormant season strongly implicates humans as the driving force, not lightning (Guyette *et al*., 2006). Using highly conservative estimations of Native American population and ignition rates, these authors demonstrated that Natives provided the level of ignitions needed to explain presettlement fire-scar histories over the eastern USA. In their modelling of eastern US presettlement mean fire intervals, mean maximum temperature and human population density were two key predictor variables, whereas lightning ignition rates did not enter the stepwise regression. Subsequent models have found topographic roughness, human population density and river distance as primary variables in mapping mean fire intervals (Stambaugh and Guyette, 2008). Most telling is Mitchener and Parker’s (2005) work in the lightning-rich Southeast, where drought was universally the most important explanatory variable in wildfire models, strongly muting the contribution of lightning flash density. Loope and Anderton’s (1998) fire-scar work adds further credence to the pre-eminence of Native American ignitions, which exceeded by an order of magnitude the number of fires expected by lightning ignitions in presettlement northern Michigan.

Acceptance of humans as important fire igniters has been hampered by two longstanding concepts regarding the ‘balance of nature’ and indigenous people living ‘in harmony of nature’ (Briggs *et al*., 2006). In actuality, through use of fire, humans were behaving as keystone species by disproportionately manipulating the environment and component species relative to their own abundance (Bonnicksen *et al*., 2000; Guyette *et al*., 2006). The timely release of Stewart’s (2002) comprehensive treatise decades ago would have helped immeasurably overcome ecological and social impediments to understanding the gravity of Native American controls over the environment (Lewis and Anderson, 2002). Indeed, most of the recent literature supports the idea that Native American burning was a recurring and pervasive force in the historical development of the eastern forest and prairie biomes (Sauer, 1975; Cronon, 1983; Pyne, 1983; Whitney, 1994; Bonnicksen, 2000; Williams, 2002). Early explorers, surveyors and settlers commonly referenced an open forested landscape throughout much of the eastern USA, which was thought to be a result of Indian burning (Rostlund, 1957; Lorimer, 2001; Faison *et al*., 2006). Kay (2007) concluded that lightning-caused fires were largely irrelevant and that the dominant ecological force was Aboriginal burning.

Archaeological and anthropological evidence

Native settlement and land-use patterns differed according to the environment, cultural preferences and period. Settlement patterns ranged from (1) highly mobile, semi-nomadic, hunter-gatherers that set up temporary encampments through (2) seasonally moving tribes that reused sites associated with specific resources (eg, shellfish and nut collection, hunting grounds) to (3) highly sedentary, agricultural- or aquatic-based societies residing in long-term villages. Territory size differed according to resource needs and distribution, with highly mobile groups (#1) requiring the largest tracts and sedentary tribes (#3) the smallest. Indian-ignited fires probably varied accordingly, with highly mobile groups burning large tracts of land for game management and mast resources and sedentary tribes burning local tracts near villages.

The importance of environmental settings on settlement and land-use patterns across four physiographic provinces was studied by Pagoulatos (1992). Archaeological sites were categorized as long-term 'base' locations (eg, villages) or temporary 'target' locations (eg, encampments) based on the diversity of artefacts associated with different occupation types. The Highlands and Piedmont Lowlands physiographic provinces, having primarily target locations, were used on a seasonal basis for game procurement. A mix of base and target locations in the Ridge and Valley Physiographic Province indicated long-term Native residency along major rivers with temporary resource gathering in the surrounding uplands (also see Cunningham, 1983). This is typical of a collecting society (collectors) whereby resources are moved to people at permanent residences. The Coastal Plain Physiographic Province contained a mix of base and target locations representative of collecting and foraging societies (seasonal movements of people to resources) with primary residencies along major rivers and tributaries and the coastline. Interior locations were used and reused for hunting and gathering (Pagoulatos, 1992). The Great Maryland Barrens spans thousands of acres northwest of Chesapeake Bay and was the deliberate result of Indian burns for game management (Marye, 1955). Upon removal of local Indian tribes and cessation of fires, this so-called 'barrens' converted to closed-canopy oak forests at a rapid pace. Upon European settlement, the barrens proved to be quite fertile for agriculture, thus further substantiating its fire basis versus poor soil conditions.

The cultural complexity was highly variable along the Eastern Seaboard at the time of European contact, ranging from simple bands to large tribal organizations to chiefdoms (Custer, 1994). Native sustenance graded from hunting and gathering lifestyles in the north (Maine) to agriculture in the south (Massachusetts southward) (Patterson and Sassaman, 1988). The cultural maps of Driver and Massey (1957) showed increases in cultivated plants, long-term occupation, Native populations and use of fire from north to south. Burning seemed to be intrinsically linked to agriculture, as southern tribes burned often and northern tribes (mainly aquatic-based) did not. Apparently, landscape burning did not convey the same advantages in the north as in the south (Patterson and Sassaman, 1988). Further north, fish and aquatic resources were abundant during the various seasons when the benefits of broadcast burning could be realized. Since canoes provided the chief mode of transportation, the advantages of open forests were unimportant. Tribes from the northern Great Lakes did not practice much agriculture and they were less dependent on fixed locations (more mobile); thus less apt to alter their environment out of economic necessity. Overall, fire was most common where Indian populations were greatest and their land-use practices most intensive (Patterson and Sassaman, 1988). The same can be said for possible tree horticulture. It is interesting to note that the northern limits of oak and hickory roughly correspond with the northern limits of Native agriculture (Raup, 1937).

Palaeo-archaeological data record long-term and generally increasing nut, fruit and berry consumption by eastern Natives during the Holocene. At Meadowcroft Rockshelter (PA), charred and uncharred hackberry (*Celtis*) seeds and charred and uncharred nutshells of walnut and hickory were common throughout the deposits along with *Chenopodium*, *Vaccinium* and *Rubus* seeds (Adovasio *et al*., 1978). Some nutshells and *Chenopodium* seeds dated to the Palaeo-Indian Cultural Period (>10 000 yr BP). A shift from boreal evergreen to temperate oak-dominated systems fostered a dramatic increase in the number of areas suitable for human habitation and resource procurement (Custer, 1994). This transition occurred earlier in the south (eg, *c*. 12 500 yr BP in central Tennessee (Delcourt, 1980)) closer to glacial refugia and later in the Northeast and Middle Atlantic regions (*c*. 5000 yr BP; Custer, 1994). The mast generated by these hardwood forests apparently maximized food sources for humans, both directly (acorn and nut consumption) and indirectly (game animal forage; Ritchie, 1985). In the southern Midwest, a shift from mesic, closed-canopy to open oak-hickory forest increased the abundance of deer and mast, which led to a change in Indian behaviour from hunter-gatherer foraging to collector-settlement strategy (Stafford *et al*., 2000). As such, Native populations flourished during the Late Archaic period. Over time there was a general trend toward (1) sedentism/decreased mobility, (2) smaller territories, (3) more permanent villages, (4) selective and specialized resource procurement, and (5) increased reliance on cultigens (Chapman *et al*., 1982; Pagoulatos, 1992; Delcourt *et al*., 1998).

Did Native Americans remain in an area long enough to benefit from the planting and/or tending of fruit and mast trees? Various lines of evidence and reason indicate so. Amongst cultivators there was a big difference between the southeastern Mississippian farmers that lived in permanent villages (from 50 to several hundred years of occupation) and farmed on alluvial (riparian) soils versus upland swidden cultivators (Snow, 1995). Upland swidden farmers moved their villages every decade or two and probably did not concentrate their efforts in tree tending. However, some hunter-gatherers returned to the same places on a seasonal basis and may have invested time in tending key tree species (Snow, 1978). Reoccupation was not uncommon, and often people moved only very short distances. Native American tribes were also highly territorial, and territories were maintained through constant surveillance and usage. This might have actually provided an incentive for tribes to plant and tend trees. Plantations would have served as distinct, long-term markers, helping establish 'turf' while providing a readily accessible food source for Natives and their game. Native mobility ensured efficient acquisition of these food stuffs, either through direct transport or seasonal moves to food sources. Around AD 1000, the subsistence techniques changed dramatically when intensive planting (mostly corn) resulted in longer occupation throughout much of the eastern USA. Surely, as Natives became increasingly sedentary and agriculturally astute over time, the benefits of planting local fruit and mast trees would have been realized.

More recent works question the prevalence of slash-and-burn shifting agriculture in pre-Columbian North America (Mann, 2005). Clearing fields from forests was an incredibly labour-intensive task with only stone implements and fire. Instead of small, stump-ridden fields indicative of transitory slash-and-burning techniques, early European accounts suggest that Native fields were often large, stump-free tracts (Doolittle, 1992). Moreover, the existence of raised fields, constructed by piling earth into hills, platforms or ridges, denotes intents of permanency. Contrary to popular belief, fields once created were probably kept in production for long periods and only briefly fallowed (Doolittle, 1992). If left fallow over extended periods, Natives probably burned areas to prevent woody plant invasion to maintain open grassy habitats for game (especially deer) and ease the future return to agriculture. Mann (2005: 298–300) purports that slash-and-burn shifting agriculture was mainly a product of European's metal axe (Mann, 2005: 298–300).

Dietary mast and fruit trees

Balanocultures (cultures that lived on nuts) existed throughout the world, producing some of the most stable and affluent cultures throughout human history (Logan, 2005). The high nutritional value and ability to satiate made acorns a staple food for many; its abundance and desirability might have even keyed the transition to sedentary life in the ancient world (Bainbridge, 1985; Logan, 2005)). Acorns were easy to procure and transport and could be stored for later use. Indeed, the only laborious step was in their preparation (leaching, shelling and grinding) or drying (parching) for preventing mould during storage. Within North America, balanocultures were most highly developed in California with well over 100 acorn-based tribes (Logan, 2005). During high mast years (years when trees produced an abundance of nuts or acorns, eg, every 4–7 years), Native Americans may have collected enough mast in a few weeks to last for several years. In the eighteenth century, William Bartram (reprinted in 1998) observed that one family of Creek Indians stored up to 100 bushels of hickory nuts. In the eastern USA, a diverse array of mast species was used in Indian diets, including acorns, hickory, pecans (*Carya illinoensis*), chestnuts, chinquapins (*Castanea* spp.), walnuts, butternuts (*Juglans cinerea*) and beechnuts (Neumann, 1989). Acorns were sometimes buried at river edges where they would both stay fresh and be leached of their tannins by passing water (Logan, 2005). Early European settlers reported uncovering large acorn caches while plowing along old stream courses.

Mast was a critical resource for carbohydrates and fat calories, and at least 30 tree species or genera produced dietary nuts and acorns used by Native Americans prior to European contact (Table 1; Yanovsky, 1936; Trigger, 1978; Reidhead, 1984; Gremillion, 1995; DeMallie, 2001; Fogelson, 2004). Of the approximately 30 oak species in the eastern USA (Elias, 1980), at least 17 were widely distributed and commonly used in the Native American diet (Table 2). These included white oak (*Q. alba*), bur oak (*Q. macrocarpa*), chestnut oak (*Q. prinus*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), southern red oak (*Q. falcata* var. *falcata*), scarlet oak (*Q. coccinea*) and post oak (*Q. stellata*), to name a few. Oaks are divided into two taxonomic groups – white oaks (*Leucobalanus*) and red oaks (*Erythrobalanus*). Acorns of the white oak group are sometimes sweet enough to eat raw (Kavasch, 1977); otherwise they were boiled in a wood ash lye solution to draw out oils, which were then made into butter and added to meat or corn (Bennett, 1955). The acorns of red oaks are typically more bitter than those of white oaks because of their high tannin content and may actually be toxic to humans if eaten raw. As such, red oak acorns were prepared by shelling and boiling in several changes of water, which may have included wood ash lye to help leach out tannins (Kavasch, 1977). Buckeye (*Aesculus*) nuts are also potentially toxic, and Native Americans pounded and repeatedly leached the powder, producing flour used in breadstuffs (Reidhead, 1984). Acorns and other nuts not eaten or processed immediately could be parched and stored (Bennett, 1955; Trigger, 1978). The acorns were often cached in hollow trees or on pole structures to protect them from rodents (Trigger, 1978). The acorns were processed when needed, typically during the winter months when other resources were scarce. Owing to the insipid taste of certain acorns, they were often mixed with other foods. For instance, Great Lakes tribes (Ojibwa, Menominee and Iroquois) ate acorns flavoured with maple syrup, blackberries, meats and bear oil well into the nineteenth century (Anonymous, 1924; Logan, 2005).

The nuts of five hickory species were commonly eaten by Native Americans (Table 1). As with acorns, Native Americans pounded hickory nuts into flour to make cakes (Trigger, 1978;

Table 1 List of dietary mast (nut) and fruit trees used by Native Americans in the eastern USA prior to European settlement

Common name	Scientific name
A. Mast trees	
Buckeye	*Aesculus* spp.
Pignut hickory	*Carya glabra*
Pecan	*C. illinoensis*
Shellbark hickory	*C. lacinosa*
Shagbark hickory	*C. ovata*
Mockernut hickory	*C. tomentosa*
American chestnut	*Castanea dentata*
Allegheny chinkapin	*C. pumila*
Redbud	*Cercis canadensis*[a]
Hazelnut	*Corylus americana*
American beech	*Fagus grandofolia*
Honey locust	*Gleditsia triacanthos*[a]
Kentucky Coffee Tree	*Gymnocladus dioicus*[a]
Butternut	*Juglans cinerea*
Black walnut	*J. nigra*
Oaks	*Quercus* spp.[b]
B. Fruit trees	
Serviceberry	*Amelanchier laevis*
Black chokecherry	*Aronia melanocarpa*
Pawpaw	*Asimina triloba*
Wild papaya	*Carica papaya*
Sugarberry	*Celtis laevigata*
Hackberry	*C. occidentalis*
Flowering dogwood	*Cornus florida*
Persimmon	*Diospyros virginiana*
Hawthorn	*Crataegus* spp.
Mulberry	*Morus rubra*
Blackgum	*Nyssa sylvatica*
Ogeechee lime tree	*Nyssa ogeechee*
American plum	*Prunus americana*
Chickasaw plum	*P. angustifolia*
Black cherry	*P. serotina*
Chokecherry	*P. virginiana*
Sweet crabapple	*Pyrus coronaria*
Elderberry	*Sambucus canadensis*
Sassafras	*Sassafras albidum*
Buffaloberry	*Shepherdia argentea*
Blackhaw	*Viburnum prunifolium*

Compiled from Yanovsky (1936), Trigger (1978), Reidhead (1984), Gremillion (1995), DeMallie (2001), Fogelson (2004).
[a] Inner pod pulp used as sweetener or seed eaten.
[b] Approximately 30 oak species occur in the eastern USA and the acorns of almost all of them could have been used for food.

Table 2 Distribution of important oak (*Quercus*) species used for their mast in the Native American diet in various regions of eastern North America

Species	Northeast	Great Lakes	Midwest and Central plains	South and Southeast	Mid-Atlantic
Q. alba	+	+	+	+	+
Q. bicolor	+	+	+		+
Q. coccinea	+	+		+	+
Q. ellipsoidalis		+			
Q. falcata var. *falcata*				+	+
Q. imbricaria			+		
Q. laevis				+	
Q. macrocarpa		+	+		
Q. marilandica		+	+		
Q. muehlenbergii		+	+		
Q. prinus	+			+	+
Q. prinoides		+	+	+	+
Q. rubra	+	+	+	+	+
Q. shumardii			+	+	
Q. stellata			+	+	+
Q. velutina	+	+	+	+	+
Q. virginiana				+	

Fogelson, 2004). They were also boiled to extract oils used to make butter. Where multiple mast tree species were present, Natives seemed to prefer hickory nuts, based on archaeological evidence (Delcourt *et al*., 1986). The nuts of walnut, chinkapin and chestnut were also popular and used for flour or reduced to oil (butter) (DeMallie, 2001). For the Cherokee Indians, acorns were a starvation food; they preferred chestnut, walnut, hickory and butternut (Fogelson, 2004: 342). They also ate hazelnut (*Corylus americana*), beechnuts and pecans. The Chickasaw Indians routinely used pecans, acorns, walnuts, chestnuts and hickory nuts. A thick liquid made from hickory nuts was used as a condiment for bread and other foods (Fogelson, 2004). Native Americans also used the seeds and/or pods of three legume trees: honey locust (*Gleditsia triacanthos*), Kentucky coffee tree (*Gymnocladus dioicus*) and redbud (*Cercis canadensis*). The fleshy, inner seed pod of these species was scraped and used as a sweetener (Reidhead, 1984). In addition, the sap of maple and birch (*Betula*) was collected and used as a sweetener by Native Americans (Bennett, 1955).

Fleshy tree fruits were used for complex carbohydrates, vitamins and minerals and at least 20 fruit- and berry-producing trees native to the eastern USA were commonly consumed by Native Americans (Table 1). In the southeast USA, persimmon (*Diospyros virginiana*), elderberry (*Sambucus*), hackberry and sugarberry (*Celtis*), hawthorne (*Crataegus*) and paw paw (*Asimina triloba*) were most accessible (Fogelson, 2004: 62). They eliminated the astringent taste of persimmon by leaving the fruit on the tree until after the first frost (Briand, 2005). Fruits and berries could be eaten in season or dried and used throughout the year (Lieberman, 1984). Cherokees girdled trees and used fire to clear areas to stimulate production of woody shrub and vines important to their diet, such as raspberry, elderberry, blackberry, blueberry, huckleberry and grapes. They ate wild cherries (*Prunus*), pawpaw, mulberry (*Morus*), serviceberry (*Amelanchier*) and persimmon. Creek Indians ate fruits of plum (*Prunus*), mulberry, persimmon and honey locust pods (Fogelson, 2004: 375–76). Seminole Indians in northern Florida were reported to have large groves of wild sour orange (*Citrus aurantium*; introduced by the Spanish) near their villages, and their diet also included native fruits of wild plum, wild cherry, pawpaw and the berries of many shrubs (Fogelson, 2004: 342, 431, 456). The Catawban people in the Carolinas ate mulberry, persimmon and plums (Fogelson, 2004: 304). Plains Indians ate wild plum, chokecherry, buffaloberry (*Shepherdia canadensis*), hackberry, serviceberry, hawthorne, sand cherry and gooseberry (*Ribes*) (DeMallie, 2001: 53, 371). By the eighteenth century, fruit-tree orchards (including peach, pear and apple) were commonly associated with Native American villages in the east, but many of these species were introduced by Europeans.

The calorie content of hickory nuts (mean = 7.10) for the two species listed in Table 3 is similar to that of black walnut (6.73 calories), and much higher than that of northern red oak (3.87 calories) and white oak (4.44). The calorie content of acorns for Shumard oak and black oak is slightly higher at 5.22 and 5.36, respectively (Table 3). Hazelnut has a high calorie content of 6.83, whereas that of chestnut is only 3.69. A similar trend also exists with the lipid content of nuts being highest in hickories (mean = 61.3%), black walnut and butternut (54.7%) and hazelnut (67.4%) and lower in oak species (13.1%) and chestnut (6.0%; Table 3). Protein content is highest in black walnut and butternut (mean = 26.4%), intermediate in hickories (14.4%) and hazelnut (12%), and lowest in oak (6.3%) and chestnut (6.0%; Table 3). Seeds of *Liriodendron tulipifera* (not a mast species) have low calorie, lipid and protein content (Table 3). On the basis of these data, it is not surprising that widely distributed hickory was one of the most important nuts used by Native Americans in the eastern USA (Trigger, 1978; Gremillion, 1995; DeMallie, 2001; Fogelson, 2004). Walnut was also important, but its distribution is much more restricted than hickory and oak, preferring wet-mesic areas along major river systems (Burns and Honkala, 1990). Despite the fact that they were not the most favoured, oaks were essential to the Indian diet and undoubtedly contributed the greatest quantity of mast of any eastern tree genera based on its vast distribution and abundance in the pre-European forest (Bennett, 1955; Gremillion, 1995).

Native American impacts on mast trees from the witness tree record

Early land surveys in the eastern USA used witness (or bearing) trees to identify property corners and other boundaries (Whitney, 1994; Black and Abrams, 2001). For many areas, witness trees are the only quantitative information on presettlement forest composition. They represent an invaluable historical resource, despite some potential biases in tree selection by early surveyors. This

Table 3 Calorie, lipid and protein content of nuts used by Native Americans

Species	Calorie (perg)	Lipids (%)	Proteins (%)	References
Black walnut	7.47	63.7	28.6	Ivan and Swihart (2000)
	6.23	23.1		Smith and Follmer (1972)
	7.04			Havera and Smith (1979)
	6.54	62.8	18.8	Talalay *et al*. (1984)
	6.35	60.0	29.0	Gremillion (1998)
Butternut	7.09	64.1	29.2	Talalay *et al*. (1984)
Shagbark hickory	7.56	72.0	16.4	Ivan and Swihart (2000)
	6.57	29.3		Smith and Follmer (1972)
	7.56			Havera and Smith (1979)
	7.04	70.0	13.7	Talalay *et al*. (1984)
	6.75	74.0	13.0	Gremillion (1998)
Mockernut hickory	7.39			Havera and Smith (1979)
Pecan	6.91	70.0	9.0	Havera and Smith (1979)
Northern red oak	5.12	32.4	5.8	Ivan and Swihart (2000)
	4.92			Havera and Smith (1979)
	3.28	22.5	6.1	Petruso and Wickens
(1984)				
White oak	4.17	4.6		Smith and Follmer (1972)
	4.46			Havera and Smith (1979)
	2.55	6.8	6.3	Petruso and Wickens
(1984)				
	3.69	6.0	6.0	Gremillion (1998)
	4.49	16.4	3.7	Ivan and Swihart (2000)
Bur oak	4.34	9.8		Smith and Follmer (1972)
	5.05			Havera and Smith (1979)
		7.9	8.0	Petruso and Wickens
(1984)				
Shumard oak	5.22	20.3		Smith and Follmer (1972)
Black oak	5.36			Havera and Smith (1979)
Chestnut oak		4.6	8.5	Petruso and Wickens
(1984)				
Chestnut	3.69	6.0	6.0	Gremillion (1998)
Hazelnut	6.83	67.4	12.0	Talalay *et al*. (1984)
Tulip poplar	4.56	4.4	8.2	Ivan and Swihart (2000)

section will focus on mast tree distribution because fruit trees rarely dominate forests in the eastern USA. They are only occasionally mentioned in the witness tree records and always at low levels. This has been attributed, at least in part, to the fact that the seeds of fruit trees are primarily bird-dispersed, often resulting in low-density populations (Abrams, 2007).

In southern New England and eastern New York, white oak and black oak were typically the first- and second-rank species, with witness tree counts for each ranging from about 15 to 36% (Table 4). Other dominant tree species in this region included white pine (*Pinus strobus*), hickory and chestnut. This contrasts with northern New England and western New York where presettlement forests were dominated by sugar maple, beech, spruce, basswood and hemlock. In the southern and central regions of the Lake States, oak represented 19–26% of presettlement forests in southern and central Michigan and Wisconsin, including bur oak savannas (Cottam, 1949; Kilburn, 1960; Nowacki *et al*., 1990). The peak distribution for mast tree species in the presettlement forest was in the oak-hickory, oak-pine and former oak-chestnut regions of the Mid-Atlantic, central Appalachians and Piedmont, Midwest, and Central States (Table 4). In the Mid-Atlantic region, white oak was the dominant species with 21–49% frequency. In central Pennsylvania, white oak dominated valley floor forests, but was less important than pine species and chestnut oak on ridges (Nowacki and Abrams, 1992; Abrams and Ruffner, 1995). In the Midwest and central regions, white oak and black oak were the dominant species (Table 4). In the South and Southeast region, oak and beech had frequencies of 5–18% in forests with *Magnolia*, maple and pine (Table 4). In the Piedmont and central and southern Appalachians, oaks were dominant in the original forest (Braun, 1950).

Witness-tree data also indicate that Native Americans provided the necessary inroads for mast species (especially oak) to exist in regions dominated by fire-sensitive northern hardwoods (Black and Abrams, 2001). Old clearings and oak-hickory-pine forests growing in areas previously inhabited by Native American were reported in land survey records for central New York State (Marks and Gardescu, 1992). Surveys for the Holland Land Company in western New York reported that oak communities were concentrated along the Allegheny River and its tributaries that were inhabited by the Seneca people (Seischab, 1990). Whitney and Decant (2003) reported an association between Iroquois settlements and oak-chestnut forests in the witness tree record across northwestern Pennsylvania. Black *et al*. (2006) linked Native Americans with forest composition on the Allegheny Plateau of northwestern Pennsylvania, where Native peoples lived almost continuously for the past 10 000 years. The study area had a relatively high concentration of witness trees, revealing forests dominated by beech (30%) and hemlock (27%), with lesser amounts of sugar maple, birch, white pine and chestnut (Lutz, 1930; Whitney, 1990). In this environment Native American land clearing and burning could be expected to negatively impact sugar maple and hemlock and increase oak, hickory and chestnut. Geospatial analysis indicated that beech, hemlock and maple dominated areas of low Native American activity, whereas a diverse mix of oak, beech, hemlock, chestnut, pine and maple occurred in areas of high Native American activity. Collectively, mast-based witness trees (oak, hickory and chestnut) composed 1.4% of the low and 34.3% of the high Native American activity zone. Native populations apparently reduced competing northern hardwood species by girdling and fire, thereby favouring mast trees. Indian tribes are thought to have fostered mast in this fashion, even to the extent of creating highly productive orchards (Munson, 1986).

Table 4 Percent composition of witness tree species in pre-European settlement forests for various locations and States in the eastern USA

Region, location	Presettlement forest composition	Reference
Northeast		
northern VT	beech (32%), spruce (14%), maple (12%), hemlock (12%), oak (5%)	Cogbill *et al.* (2002)
northern NH	beech (25%), hemlock (15%), pine (12%), oak (12%), spruce (10%)	Cogbill *et al.* (2002)
western NY	beech (32%), sugar maple (18%), basswood (12%), white oak (11%)	Seischab (1990)
eastern NY	white oak (36%), black oak (15%), hickory (10%), elm (6%)	Glitzenstein *et al.* (1990)
central MA	white oak (27%), black oak (26%), pine (18%), hickory (9%)	Whitney and Davis (1986)
central MA	white oak (20%), pine (20%), hemlock (10%), chestnut (8%)	Foster *et al.* (1998)
CT and RI	white oak (33%), hickory (10%), chestnut (9%)	Cogbill *et al.* (2002)
MA	white oak (25%), pine (16%), maple (6%), hemlock (6%)	Cogbill *et al.* (2002)
eastern NY	white oak (17%), beech (16%), hemlock (10%), pine (9%)	Cogbill *et al.* (2002)
Lake States		
central MI	jack pine (20%), red pine (19%), white pine (11%), white oak (2%)	Whitney (1994)
central MI	red pine (40%), white oak (19%), white pine (15%), aspen (12%)	Kilburn (1960)
southern WI	bur oak (60%), white oak (26%), black oak (13%)	Cottam (1949)
central WI	sugar maple (37%), white oak (25%), red oak (16%), elm (12%)	Curtis (1959)
central WI	pine (28%), aspen (17%), larch (12%), white oak (10%)	Nowacki *et al.* (1990)
Mid-Atlantic		
northern NJ	white oak (34%), black oak (18%), hickory (15%), red oak (9%)	Russell (1981)
northern NJ	white oak (31%), hickory (25%), black oak (19%), chestnut (12%)	Ehrenfeld (1982)
northwest PA	white oak (21%), beech (13%), maple (17%), black oak (6%)	Whitney and Decant (2003)
northwest PA	beech (49%), hemlock (20%), maple (9%), birch (8%)	Black *et al.* (2002)
southeast PA	black oak (33%), white oak (17%), chestnut (15%), hickory(15%)	Mikan *et al.* (1994)
southeast PA	black oak (33%), white oak (30%), hickory (28%)	Black and Abrams (2001)
southwest PA	white oak (40%), black oak (9%), hickory (9%), dogwood (8%)	Abrams and Downs (1990)
central PA		
Allegheny Mts		
plateaus	white oak (26%), chestnut (19%), pine (19%), maple (10%)	Abrams and Ruffner (1995)
stream valleys	hemlock (24%), maple (21%), white pine (15%), birch (15%)	Abrams and Ruffner (1995)
Ridge and Valley		
ridges	chestnut oak (14%), white oak (12%), pine (19%), chestnut (11%)	Abrams and Ruffner (1995)
valleys	white oak (30%), pine (25%), hickory (17), black oak (10%)	Abrams and Ruffner (1995)
ridges	pine (27%), chestnut oak (18%), white oak (11%), chestnut (13%)	Nowacki and Abrams (1992)
valley	white oak (41%), white pine (12%), hickory (12%), black oak (9%)	Nowacki and Abrams (1992)
eastern WV		
ridges	white oak (35%), chestnut (15%), chestnut oak (13%), black oak (12%)	Abrams and McCay (1996)
valleys	white oak (23%), maple (22%), pine (15%), basswood (10%)	Abrams and McCay (1996)
southern WV	white oak (24%), chestnut (12%), hickory (9%), chestnut oak (6%)	Abrams *et al.* (1995)
northern VA	white oak (49%), red oak (26%), hickory (7%)	Orwig and Abrams (1994)
southwest VA	red oak (25%), white oak (18%), chestnut (9%)	McCormick and Platt (1980)
western Virginia	white oak (26%), pine (13%), chestnut oak (9%), hickory (9%)	Stephenson *et al.* (1992)
Midwest and central region		
central MO	white oak (32%), black oak (11%), sugar maple (9%), elm (8%),	Wuenscher and Valienas (1967)
eastern IL	white oak (27%), black oak (18%), hickory (6%), elm (10%)	Roders and Anderson (1979)
southern IL		
south slopes	white oak (81%)	Fralish *et al.* (1991)
ridge tops	white oak (45%), black oak (33%),	Fralish *et al.* (1991)
northeast OH		
fine till	beech (36%), sugar maple (17%), white oak (14%)	Whitney (1994)
coarse till	white oak (37%), hickory (13%), black oak (6%)	Whitney (1994)
north-central OH	hickory (34%), white oak (30%), bur oak (11%), black oak (11%)	Whitney (1994)
southeast OH	white oak (40%), hickory (14%), black oak (12%), beech (8%)	Dyer (2001)
South and southeast		
north FL	magnolia (21%), beech (14%), maple (7%), white oak (5%)	Delcourt and Delcourt (1977)
central GA	pine (27%), black and red oak (21%), post oak (18%), white oak (7%)	Cowell (1995)
southeast TX	pine (25%), white oak (18%), pin oak (10%), red oak (9%)	Schafale and Harcombe
(1983)		
east-central AL	white oak (13%), beech (9%), pine (9%), maple (5%)	Black *et al.* (2002)
east-central Al	pine (79%), blackjack oak (7%), post oak (4%)	Black *et al.* (2002)
east-central AL	post oak (25%), hickory (20%), red oak (14%), black oak (13%)	Black *et al.* (2002)

A study of witness-tree distribution in southeastern Pennsylvania revealed that Native American village sites had increased density of hickory, walnut and black locust but decreased density of white oak (Black and Abrams, 2001). Black oak and scarlet oak did not vary between high and low Native American activity sites. Northern hardwood forests surrounding Crawford Lake in southern Ontario were dominated by beech, sugar maple and birch and were transformed to oak and pine forests as a result of Indian fires after AD 1400 (Clark and Royall, 1995). Pine nuts were not an important food for Native Americans in the east as they were in the west, but open fire-maintained pine woodlands would attract and provide ample feed for game and otherwise facilitate hunting, gathering and travel (Foster *et al*., 2004). Prior to 1830, an unusually large oak savannah of white oak, red oak and black oak existed near Indian agricultural villages in northeastern Wisconsin, a region that was otherwise dominated by northern hardwoods and conifers (Dorney and Dorney, 1989). It is thought that frequent Indian-set fires created and maintained this oak savanna prior to European settlement. Indian fires were also recorded in the 1820–1830s surveyor notes from southeastern Wisconsin (Dorney, 1981). In that study region, however, Native Americans showed little preference for different vegetation types for some villages were in sugar maple-basswood-oak forests while others were in oak savannas.

Native Americans as active promoters of mast and fruit trees

In addition to increasing mast tree distribution through the passive or indirect means discussed above, evidence suggests that Native Americans purposely promoted mast and fruit trees through planting and cultivation (Davies, 1994). MacDougal (2003) reviewed 67 texts related to pre-European land management and plant use and reported that 21 mast and fruit trees and 16 berry-producing shrub species were potentially cultivated by Native Americans in the eastern USA. Indians actively manipulated oak-hickory-chestnut forests with fire to provide more abundant food resources (Caldwell, 1958). This included (1) increased browse quality and quantity for deer and for concentrating the herd in managed areas, (2) increased mast quality and quantity for winter-spring subsistence, and (3) a reduction of forest-floor litter to facilitate mobility and mast collection. Day (1953) concluded that Native Americans favoured nut trees and other food plants and were probably responsible for increasing them in the pre-European forest. This included the planting of chestnut, Canada plum (*Prunus nigra*) and Kentucky coffee tree near Indian villages. Thinning forests, clearing underbrush, removing competing tree species and periodic understory burning by Native Americans resulted in more-open forests, with presumably less competition, trees with larger crowns, more rapid recycling of nutrients and higher soil nutrient levels (Nixon *et al*., 1980; Leibermann, 1984; Whitney, 1994). This would in turn have favoured light-demanding trees and stimulated mast and fruit production in a wide variety of species (Sharp and Sprague, 1967; Lassoie *et al*., 1980; Garrett and Kurtz, 1982).

Hammett (1992a, b) reviewed literature on the aboriginal landscapes of the southeast USA and concluded that through managed burning, clearing and planting, Native Americans created and maintained a mosaic landscape that yielded high food output. She listed 18 trees by genus or species mentioned by early explorers or identified from archaeological sites as important to Native Americans, and seven anthropogenic-created or utilized patches, including hunting camps, field/gardens, edge areas/meadows, old-fields, parkland/orchards, wetlands/swamps/marshes and waterways. Nut and fruit trees, particularly cherry, plum, chestnut, hazelnut, hickory, oak, persimmon and walnut were an important part of the diet for southeastern Indians. Native American practiced some level of agroforestry (from minimal to significant) throughout much of eastern North America, with the possible exception of northern New England and the northern Lake States regions, outside the range of oak- and hickory-dominated forests (Raup, 1937; Trigger, 1978; Fogelson, 2004).

Mast and fruit trees are often mentioned in the immediate vicinity of Native American villages (Liebermann, 1984). During the Sullivan campaign in 1779, thousands of fruit trees (possibly non-native species introduced by Europeans) were destroyed near Iroquois villages in western New York (Fischer, 1997). In 1773, William Bartram (reprinted 1998) observed evidence of orchards and other forms of tree-crop management in old Indian settlements in Georgia with accompanying fields containing persimmon, honey locust, Chickasaw plum (*Prunus angustifolia*), mulberry, black walnut and a plantation of shellbark hickory (*C. lacinosa*). He concluded that these native forest species thrive better and are more fruitful in cultivated plantations. During the early 1700s, honey locust and live oak (*Q. virginiana*) were intentionally established by Native Americans in the Carolinas (Lawson, 1967). In a study of Native American impacts on witness-tree distribution in east-central Alabama, Foster *et al*. (2004) concluded that Native Americans directly and indirectly impacted the distribution of certain useful tree species. For example, yaupon (*Ilex vomitoria*) was apparently planted because it was important for religious and social purposes (Bartram, 1998). Yaupon was used to make a strong ‘black drink’ that was imbibed daily for purification and social reasons. Hackberry also had higher density near Indian villages (Foster *et al*., 2004). Indians practiced management of nut trees by removing competing vegetation and concentrating stands on productive areas (Gremillion, 1998, 2004; Hammett, 1992a). Creek Indians in Georgia cultivated pecan trees, as well as collected its nuts from the wild (Fogelson, 2004: 397). However, MacDougall (2003) concludes that care must be taken when interpreting some accounts of early explorers owing to the possibility that fruit and mast trees and berry-producing shrubs may have established *after* abandonment of an Indian village and may not be a direct result of Indian cultivation. For instance, vast expanses of shade-intolerant sweetgum (*Liquidambar styraciflua*) and cane (*Arundinaria gigantean*) found growing on fertile Southern floodplains by European settlers were thought to be the product of old-field succession after the collapse of Native populations (Hamel and Buckner, 1998).

Black walnut populations in the northern mid-Atlantic region are often associated with pre-European Native American villages (Wykoff, 1991). This author opines that walnut and pawpaw as well as some hickories and oaks were planted by Native Americans prior to European settlement. Black *et al*. (2006) found black walnut restricted to areas immediately adjacent to villages in Pennsylvania and that it possessed the highest Native American Index score, suggesting some type of cultivation or selection. Munson (1986) reviewed literature on the importance of hickory nuts in the Native American diet. He concluded that large quantities of hickory nuts were collected nearly every year and that this would only be possible if hickory was grown in plantations or orchards with high nut yields. In natural forests, yields are typically much lower, except during mast years, and that almost all the nuts would be collected by squirrels while they were still on the tree. This may also explain why Indians would forage nuts and acorns from caches created by small mammals (Bonnickson, 2000). In the southeast, Native people cleared forest gaps to cultivate plants and used fire and girdling in upland forests to increase the proportion of oak, hickory, chestnut and walnut (Delcourt *et al*., 1998). In this respect, they created groves or orchards of mast trees (Delcourt and Delcourt, 2004). Bonnickson (2000) argues that Mississippi people cut shade-tolerant trees to prevent them from replacing oak, hickory and chestnut trees important to their diet.

Algonquians in Virginia produced orchards of fruit trees after 1660 (Trigger, 1978: 258). In the 1620s, Morton (1883) reported an exchange of chestnuts from interior to coastal peoples in Massachusetts. Such accounts suggest that valued dietary tree species were actively propagated and managed and occasionally transported outside their ranges where climate and site conditions allowed. Indeed, MacDougall (2003) reviewed 24 accounts that directly describe the trade, transport or cultivation of indigenous plants by Native Americans of eastern North America. The northern migration of pawpaw to Ohio and New York was thought to have been facilitated by Iroquois transport and planting (Keener and Kuhns, 1997), but it was later argued that the distribution of the species could be explained by mammal dispersal (Murphy, 2001).

Native American impacts on vegetation – localized or ubiquitous?

The preponderance of evidence suggests that Native American's land-use practices promoted the distribution and importance of mast and fruit trees prior to European settlement. This occurred through direct and indirect means, such as land clearing for agriculture, broadcast burning of vegetation, the abandonment of villages and agricultural fields, and the planting, transport and cultivation of favoured tree species. Native Americans lived throughout the eastern biome at reasonable high population levels, and it is difficult to discern any large tracts of land that were not directly or indirectly impacted by them (Trigger, 1978; Demallie, 2001; Fogelson, 2004). We believe that Native Americans directly promoted mast and fruit trees by cultivation and planting, although the scarcity of conclusive evidence is due to the low number of European explorers and settlers in North America at the time of first contact. Because of the multipurpose nature of prescribed fire, then and now, it is sometimes difficult to say whether Indian burning and the subsequent increase in mast trees was a direct or indirect result. Nonetheless, we believe that Native Americans actively used fire as a management tool and that this skill level is consistent with what they used in cultivating numerous agricultural crop species. Many fires burned into the surrounding forests and beyond, and there exists a direct link between Indian burning and the widespread distribution of mast species and grasslands prior to European settlement. Once started, Native Americans did not possess the means to put out landscape fires, which would have burned until a precipitation event or a natural firebreak was incurred (Stewart, 2002).

Some argue that fire and fire-adapted vegetation may be more a function of climate rather than active burning by Native Americans (Parshall and Foster, 2002; Shuman *et al*., 2004). We certainly do not dismiss the importance of climate in controlling vegetation. The change in dominance from northern (boreal) conifers to oak and hickory in the early Holocene was undoubtedly driven by a warming climate following glacial retreat (Watts, 1979; Webb, 1988). However, increasing Indian populations and corresponding use of fire at that time probably contributed to this change in dominance. We believe that climate does *not* stand alone as the primary factor for the long-term perpetuation of mast trees in the eastern forest during the middle to late Holocene. One irrefutable fact is that the vast majority of oak, hickory and pine forests in the eastern USA will be replaced within one generation by later successional species, most notably maples and beech, in the absence of fire (Nowacki *et al*., 1990; Abrams, 1992, 1998, 2003; Lorimer, 2001). Similarly, tallgrass prairies and oak savannas in the Midwest and Central Plains regions existed for thousands of years with frequent fire. These vegetation types quickly converted to closed canopy forests, including non-oak species, when fire suppression started in the early 1900s (Gleason, 1913; Abrams, 1986; Nuzzo, 1986).

How did all these fires start? In most of the eastern USA (outside of the extreme south and southeast), lightning-caused fires are rare. If we accept that this condition has not changed much in the last several millennia, than we must conclude that Native Americans were responsible for the vast majority of fires throughout the eastern forest and prairie biomes. We believe that forests dominated by mast species were initially formed mainly as a result of postglacial climatic warming but were perpetuated primarily as a result of Indian burning. These forests persisted through several periods of dramatic climate change, more recently including the 'Mediaeval Warming' (AD 800–1300) and 'Little Ice Age' (AD 1400–1700). The palaeocharcoal record indicates that warmer and drier climate promoted the extent of Indian burning (and to a lesser extent lightning fires), whereas cooler and moisture periods retarded it (Pederson *et al*., 2005). Despite these significant climatic shifts, oak, hickory and chestnut forests (with low levels of red maple) in the east and oak savannas and tallgrass prairies in Central Plains persisted during the middle and later Holocene.

The long-term persistence of mast-dominated forests, savannas and tallgrass prairie in the eastern USA only makes sense in the context of persistent and extensive Indian burning through periods of both warming and cooling climate during the middle and later Holocene. Each of these vegetation types were apparently fostered and maintained by Native Americans through a variety of management strategies that included periodic fire. A lack of management would have led to a dramatic decline or conversion in each of the vegetation types (Abrams, 1992). There was a strong incentive for Native Americans to manage mast forests and savannas and tallgrass prairie – that is to meet their gastronomic needs. Open mast forests and savannas produced an abundance of nuts and acorns in addition to having grass- and herb-rich understories that supported large game populations. The latter would also have occurred in frequently burned pine forests in northern and southern forests. Tallgrass prairie sustained huge populations of large ungulates vital to the Indian diet. The loss of these vegetation types in the absence of periodic fire would have meant starvation for many Indian tribes.

Much of the original prairie vegetation throughout the Midwest and Central Plains was maintained by very frequent Native American burning in lieu of mast forests (Anderson, 2006). Therefore, we conclude that large game animals were more important than nuts and acorns to the Indian diet in that region. Further east, Native Americans also created and maintained grassland inclusions in the vast matrix of oak, hickory, and chestnut forests for the purpose of attracting game, but their extent was often limited (Marye, 1955; Marks and Gardescu, 1992). The decreasing precipitation gradient that exists from the eastern seaboard to the Central Plains is an important controlling factor relegating vast grasslands to the west and mast forests to the east even within the context of Native American burning. Once again, lightning strikes and climate cannot fully explain the large amount of burning that occurred prior to European settlement. Curtis (1959) when describing the influence of Indians on vegetation stated that:

> With this one tool [fire], the Indians changed a very large portion of the entire vegetational complex of Wisconsin…the oak openings, sand, oak, and pine barrens, bracken-grasslands, true prairies, brush prairies, fens, sedge meadows, shrub communities, and pine forests all owe their origin or maintenance to the repeated presence of fire. To a limited extent, the results could have been obtained by lightning fires, but the known incidence of dry lightning in Wisconsin is totally incapable of explaining the huge areas influenced by fire…the

presence of nomadic hunting tribes throughout the state in the entire postglacial period means that man-made fires were an important if not the sole cause of the fires.

In this respect, we believe that the vast majority of vegetation in the eastern USA was managed directly or indirectly by Native Americans, especially through the use of fire.

The dramatic changes in vegetation structure and composition as a result of fire suppression following the collapse of Native American populations (1600s–1800s) associated with European diseases and settlement, followed by government policies (the Smokey Bear campaign) during the last 70–100 years are unparalleled during the last 5000 years (Nowacki and Abrams, 2008). We conclude that Native Americans profoundly impacted the distribution and importance of mast and fruit trees and tallgrass prairie as a primary food source through both active and passive means, and that they *ubiquitously* impacted these vegetation types at the regional and biome levels (not only at the local level). Without their extensive influences prior to European settlement, the Eastern deciduous forest and prairie biomes would have been dramatically different, thus altering our perception of the natural vegetation of the eastern USA.

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