



# Anthropogenic disturbance and the formation of oak savanna in central Kentucky, USA

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## ABSTRACT

**Aim** To deepen understanding of the factors that influenced the formation of oak savanna in central Kentucky, USA. Particular attention was focused on the link between historical disturbance and the formation of savanna ecosystem structure.

**Location** Central Kentucky, USA.

**Methods** We used dendrochronological analysis of tree-ring samples to understand the historical growth environment of remnant savanna stems. We used release detection and branch-establishment dates to evaluate changes in tree growth and the establishment of savanna physiognomy. We contrasted our growth chronology with reference chronologies for regional tree growth, climate and human population dynamics.

**Results** Trees growing in Kentucky Inner Bluegrass Region (IBR) savanna remnants exhibited a period of suppression, extending from the establishment date of the tree to release events that occurred *c.* 1800. This release resulted in a tripling of the annual radial growth rate from levels typical of oaks suppressed under a forest canopy ( $< 1 \text{ mm year}^{-1}$ ) to levels typical of open-grown stems ( $3 \text{ mm year}^{-1}$ ). The growth releases in savanna trees coincided with low branch establishment. Over the release period, climatic conditions remained relatively constant and growth in regional forest trees was even; however, the growth increase in savanna stems was strongly correlated with a marked increase in Euro-American population density in the region.

**Main conclusions** Our data suggest that trees growing in savanna remnants originated in the understorey of a closed canopy forest. We hypothesize that Euro-American land clearing to create pasturelands released these trees from light competition and resulted in the savanna physiognomy that is apparent in remnant stands in the IBR. Although our data suggest that savanna trees originated in a forest understorey, this system structure itself may have been a result of an unprecedented lack of Native American activity in the region due to population loss associated with pandemics brought to North America by Euro-Americans. We present a hypothetical model that links human population dynamics, land-use activities and ecosystem structure. Our model focuses on the following three land-use eras: Native American habitation/utilization; land abandonment; and Euro-American land clearance. Ecological understanding of historical dynamics in other ecosystems of eastern North America may be enhanced through recognition of these eras.

## Keywords

Cultural landscape, dendrochronology, historical ecology, land-use history, landscape dynamics, remnant vegetation, tree ring.

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## INTRODUCTION

The structure, composition and dynamics of oak-dominated ecosystems have often been related to disturbance processes. In lowland temperate Europe, for example, large herbivores (Vera, 2000) and fire (Svenning, 2002) have been implicated as factors that maintained prehistoric oak forests. In the dehesa system of southern Spain and Portugal, a long history of anthropogenic disturbance created oak savanna ecosystems that cover vast areas (> 3.1 million ha; Joffre *et al.*, 1999; Plieninger *et al.*, 2003). In deciduous forests of eastern North America, *Quercus* was a historically dominant genus, probably due to a combination of canopy-opening disturbances that included the use of fire by Native Americans (Abrams, 1992). Variation through time in disturbance frequency and intensity initiates complex long-term dynamics in oak ecosystems.

In North America, oak savannas have been significantly influenced by disturbance processes (Nuzzo, 1986). Oak savanna was often part of an ecotone from grassland to forest that was structured by the frequency and intensity of disturbance (Nuzzo, 1986; Packard & Mutel, 1997). The use of fire by Native Americans probably contributed to the maintenance of oak savanna, which was an important ecosystem type in midwestern North America and in the Central Valley of California (Nuzzo, 1986; Packard & Mutel, 1997; Standiford, 2002). During Euro-American settlement, oak savanna was largely converted to agricultural use, resulting in substantially reduced areas and altered ecosystem states (Nuzzo, 1986; Packard & Mutel, 1997; Bowles & McBride, 1998; Brewer & Vankat, 2004). Because of these losses, oak savanna is now a threatened ecosystem type in North America (Nuzzo, 1986) and is the focus of restoration efforts in a variety of settings (Anderson & Brown, 1983; Faber-Langendoen & Davis, 1995; Tester, 1998; Peterson & Reich, 2001).

Ecological restoration is often guided by reference conditions that identify target conditions for ecosystem composition and structure. Reference conditions often also include disturbance factors that contributed to the formation and maintenance of ecosystem structure (Foster, 1988; Moore *et al.*, 1999; Egan & Howell, 2001; Lunt & Spooner, 2005). Dendrochronological analysis of tree-ring samples has been particularly useful for identifying reference conditions (Brown *et al.*, 2001; Winter *et al.*, 2002; Fulé *et al.*, 2003; Guyette & Spetich, 2003; Grissino-Mayer *et al.*, 2004). In eastern North America, dendrochronological analyses have added to our understanding of forest stand development (Henry & Swan, 1974), and growth dynamics of dominant species have been elucidated (Canham, 1990). Much has also been learned about historical disturbance factors and how they relate to the formation of ecosystems (Guyette *et al.*, 2002; Soucy *et al.*, 2005). Dendrochronology enables the identification of links between disturbance and ecosystem development that can be used to design restoration activities in modern forest stands (Kipfmüller & Swetnam, 2001).

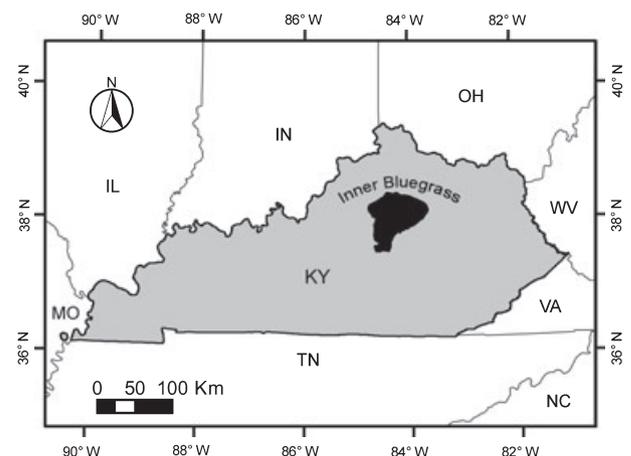
We conducted a dendrochronological analysis of oak savanna in the Inner Bluegrass Region (IBR) of central

Kentucky, USA. Due to fertile soils and abundant forage, early Euro-Americans found this region highly suitable for agriculture, and land conversion was rapid (Wharton & Barbour, 1991). Oak savanna has become rare in the region and is currently the focus of multi-organizational efforts (e.g. Kentucky State Nature Preserves Commission, Nature Conservancy, University of Kentucky) to conserve and restore some of the remaining ecosystem vestiges. To understand the processes that influenced the development of savanna vegetation, we used dendrochronology to identify establishment dates and to investigate the growth patterns of trees in savanna remnants. In particular, our work addressed the following two questions: (1) Did trees in IBR vegetation remnants grow throughout their life span in light-saturated conditions typical of oak savanna? (2) Was the growing environment of remnant savanna trees substantially altered during the establishment of Euro-American settlements in the region?

## MATERIALS AND METHODS

### Site description

The IBR (Fig. 1) is defined largely by its underlying geology (Braun, 1950; Wharton & Barbour, 1991). It is located on the Jessamine Dome of the Cincinnati Arch geological formation, and is the only extensive upland in Kentucky where Ordovician limestone is exposed (O'Brien, 1984; Wharton & Barbour, 1991). The soils of the IBR are phosphate-rich, silt loams that are deep and well drained (O'Brien, 1984; Wharton & Barbour, 1991). Because of leaching in the limestone bedrock, the IBR is characterized by rolling (karstic) topography (Braun, 1950; Wharton & Barbour, 1991). Elevation in the IBR ranges from c. 180 to 330 m a.s.l. Regional climate is continental, and mean annual temperature and precipitation are 12.8°C and 111.8 cm, respectively (Wharton & Barbour, 1991).



**Figure 1** Map depicting the Inner Bluegrass Region (IBR; shaded black) in the state of Kentucky, USA. Map design by Greg Abernathy of the Kentucky State Nature Preserves Commission.



**Figure 2** A portion of Griffith Woods, a typical remnant oak savanna in the Inner Bluegrass Region of Kentucky, USA.

Savanna vegetation in the IBR is very rare and exists as scattered remnant patches, mostly on private land. These remnants are characterized by a distinctly savanna-like structure (Dyksterhuis, 1957), with large trees that are widely separated (*c.* 15 stems  $\text{ha}^{-1}$ ; Bryant *et al.*, 1980) in grass-dominated fields (Fig. 2). To our knowledge, all of the existing remnants have been used for agriculture for at least some portion of their recent history. Dominant tree species include *Quercus macrocarpa*, *Quercus muehlenbergii* and *Fraxinus quadrangulata*. Other large trees found in remnant patches include *Quercus shumardii*, *Carya laciniosa* and *Juglans nigra* (Wharton & Barbour, 1991). Botanical nomenclature follows Jones (2005).

### Field methods

Practically the entire land area of the IBR has been developed for urban, suburban and agricultural uses, and there are only a few remaining stands of ancient trees. Because there are so few existing old trees in the region, the opportunity for sample collection was limited. Furthermore, the collection of increment cores from live trees was forbidden by the management of preserves housing two of the larger tracts of remnant vegetation. Thus sample collection was necessarily opportunistic. Samples were collected from: (1) standing dead and recently fallen stems in preserves, (2) live stems in non-protected areas, (3) large logs from fallen trees that had been accumulated by a speciality woodworking operation, and (4) archaeological samples from Euro-American settlement-era log structures. Whole-stem cross-sections of downed trees were collected whenever possible using a chainsaw; otherwise increment cores were collected following typical dendrochronological procedures (Stokes & Smiley, 1968; Grissino-Mayer, 2003). To gain an understanding of the timing of low branch establishment (initiation of savanna physiognomy), branch cross-sections were collected from fallen trees and from branches broken during wind events. Samples were collected

at the branch collar, near the main stem. Minimum, mean and maximum height from the ground of branch samples was 1.5, 5.2 and 9.0 m, respectively.

### Laboratory methods

Following collection, sample surfaces were prepared for data collection. Tree cross-sections were smoothed with a hand-held power planer then sanded with a belt sander and a series of increasingly finer grit sanding belts, ranging in roughness from 80-grit (177–210  $\mu\text{m}$ ) to 400-grit (20.6–23.6  $\mu\text{m}$ ; Orvis & Grissino-Mayer, 2002). Increment cores were glued into a slotted wooden mount (Stokes & Smiley, 1968) then sanded by hand using the same series of sandpaper grit. Surface preparation was complete when anatomical features of the tree rings were readily apparent under  $\times 40$  magnification (Stokes & Smiley, 1968; Johnson & Gutsell, 1994).

Each sample was then analysed to collect ecological information (Stokes & Smiley, 1968; Johnson & Gutsell, 1994). All the tree rings in each sample were counted, graphical 'skeleton' plots that highlight years of abnormally narrow rings (pointer years) were constructed, and these plots were then used to cross-date samples against a regional master chronology (Stokes & Smiley, 1968; Schweingruber *et al.*, 1990). Once dates were confidently assigned to each ring, annual increments were measured to the nearest 0.01 mm using an Olympus SZ40 boom dissecting microscope ( $\times 40$ ), VELMEX unislide stage, ACU-RITE linear encoder and Quick-Check digital readout device. Stem cross-sections were dated in the same fashion and were inspected for wound events that might be attributable to historical fire in these stands (McEwan *et al.*, 2007). Following wound dating, cross-sections were subsampled to create sections small enough to enable tree-ring measurement using the unislide stage.

### Analytical methods

Temporal patterns of establishment and sample size distributions were examined by plotting the establishment date (first year of growth) against each sample diameter (Mikan *et al.*, 1994). Regression analysis (Zar, 1999) was used to assess the relationship between tree establishment and stem diameter in remnant savanna trees. Regression analysis was performed using the NUMBER CRUNCHER STATISTICAL SOFTWARE (NCSS) package (Hintze, 2004).

Each tree-ring series was then analysed to detect releases indicative of events that altered stand structure, increasing resource availability. In oaks, the accepted minimum release suggesting increased light due to canopy disturbance is a 25% increase in mean growth between adjacent 10-year segments of a tree-ring series (Nowacki & Abrams, 1997). In this study, we identified release as an increase of  $\geq 100\%$  in growth between two 15-year segments. According to Lorimer & Frelich (1989), a change of this magnitude is indicative of a 'major sustained release'. We followed Rubino & McCarthy (2004) in utilizing the median (rather than the mean) as the measure of central

tendency, thus accounting for non-normal tendencies in tree-ring data.

Three reference chronologies were used to track regional conditions over the life span of IBR trees. The first was a ring-width chronology from white oak (*Quercus alba*;  $n = 29$ ) trees growing in an old-growth portion of the Lilley Cornett Woods, Appalachian Research Station (LCWARS; Cook, 2006) in south-eastern Kentucky. Because of widespread logging and land clearance, old-growth forest is very rare in Kentucky, and old-growth portions of LCWARS have been valuable for establishing reference conditions (Muller, 1982; McEwan & Muller, 2006). Tree-ring data from LCWARS were downloaded from the International Tree-Ring Data Bank (Cook, 2006) and the chronology was created by averaging the untransformed raw measurement data for each year. Tree growth in old-growth *Q. alba* from LCWARS was useful for comparison with that of remnant savanna trees in the IBR because the trees were of similar age, but had grown throughout their life span in a forest setting. This chronology was also useful in that any substantial alteration in regional climate that would influence tree growth in LCWARS would also be detected in the chronology developed from IBR savanna stems.

The second reference chronology was developed to assess more directly the potential for long-term changes in climate to have influenced tree growth in the IBR. This climate chronology was developed using the Palmer drought severity index (PDSI), which incorporates the effects of temperature and precipitation to assess moisture availability (Palmer, 1965; NOAA, 2006a). We used instrumented PDSI values from 1895–2005 that were downloaded from the National Climate Data Center CLIMVIS archive (Kentucky Climate Division 3; NOAA, 2006b). For years prior to instrumentation, we used PDSI reconstructions (grid point 228, Cook *et al.*, 2004; NOAA, 2006c). We used regression analysis (in *ncss*, Hintze, 2004) to test for trends in PDSI (thus available moisture) during the growth years of the savanna trees.

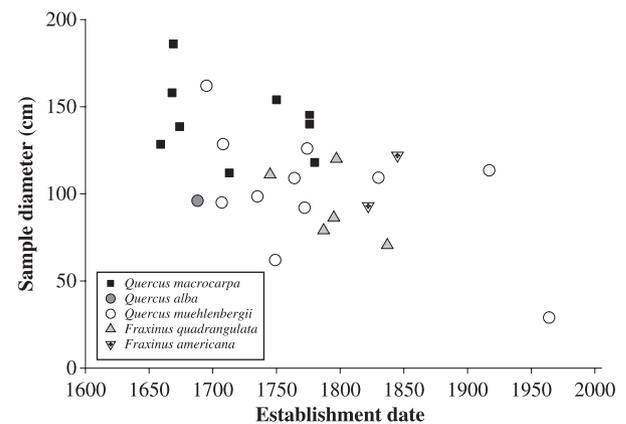
The final reference chronology was used to investigate trends in regional Euro-American population during the growth years of remnant savanna trees. This chronology was developed using population census data from four IBR counties that were downloaded from the Geospatial & Statistics Data Center at the University of Virginia Libraries (Geo-Stats, UVL, 2006). The chronology began at 1760, 30 years prior to the first census, and served as an approximate zero point in the history of Euro-American settlement in the region. Euro-American population in the years 1770 and 1780 was back-calculated from the 1790 census assuming a doubling of the population size during each 10-year period. The year 1960 was used as the end point because land clearance would be decoupled from population growth beyond that point in time, as practically all the native vegetation had been cleared well before 1950 (Braun, 1950). A correlation between the Euro-American census data and decadal mean tree-ring width was made using Spearman's rank correlation (Zar, 1999) in *ncss* (Hintze, 2004). For all

statistical tests in this study,  $P \leq 0.05$  was considered statistically significant (Zar, 1999).

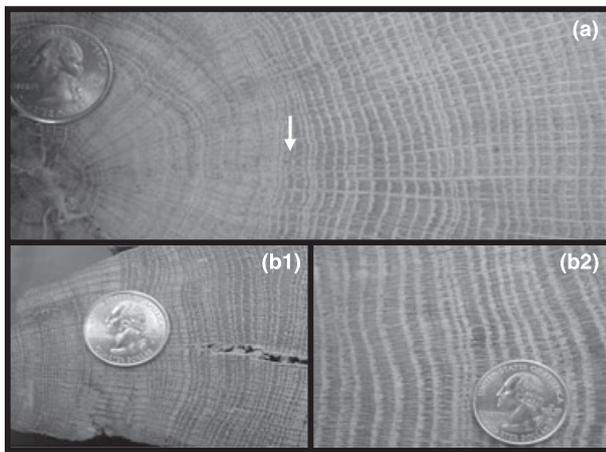
## RESULTS

Stem cross-sections ( $n = 21$ ), increment cores ( $n = 18$ ), branch sections ( $n = 16$ ) and archaeological samples ( $n = 4$ ) were collected from six species. Most samples were collected from the three characteristic dominants in remnant savannas, as follows: *Q. muehlenbergii* ( $n = 19$ ), *Q. macrocarpa* ( $n = 18$ ) and *F. quadrangulata* ( $n = 12$ ). Other samples were collected from *Fraxinus americana* ( $n = 2$ ), *C. laciniosa* ( $n = 2$ ) and *Q. alba* ( $n = 2$ ). Three stems were only identifiable to the genus *Quercus*, and two were archaeological samples too decayed for identification. Many of the sampled stems had some decay near the pith so initiation dates could not be established. In stems free of decay, the earliest initiation dates were for *Q. macrocarpa* that established *c.* 1650 (Fig. 3). *Quercus muehlenbergii* and *Q. alba* also had establishment dates prior to 1700, while the earliest *F. quadrangulata* initiation date was 1745. Trees in IBR savanna remnants exhibited sample diameters exceeding 150 cm (Fig. 3), vastly larger than is typical for regional oak forests (McEwan *et al.*, 2007). A statistically significant negative relationship existed between establishment date and diameter in these stems ( $P < 0.01$ ; regression line not shown). A great deal of variability was unexplained by this relationship ( $r^2 = 0.32$ ), and stems with sample diameters of *c.* 125 cm had initiation dates that ranged from *c.* 1650 to 1910 (Fig. 3).

Samples from IBR savanna trees exhibited a growth release that was readily apparent and substantial. Stems initiating prior to *c.* 1760 had narrow growth rings beginning at the pith and extending until *c.* 1800, when they exhibited a several-fold increase in ring width (Fig. 4a). In some stems, tree rings were more than seven times wider in the years following 1900 than in years prior to 1760 (Fig. 4b1 & b2). This contrast in growth



**Figure 3** Establishment patterns as indicated by establishment date–diameter relationships for samples collected from remnant savanna trees in the Inner Bluegrass Region of Kentucky, USA. Only samples that had sound wood to the pith (*c.* 50% of the samples collected) are depicted.

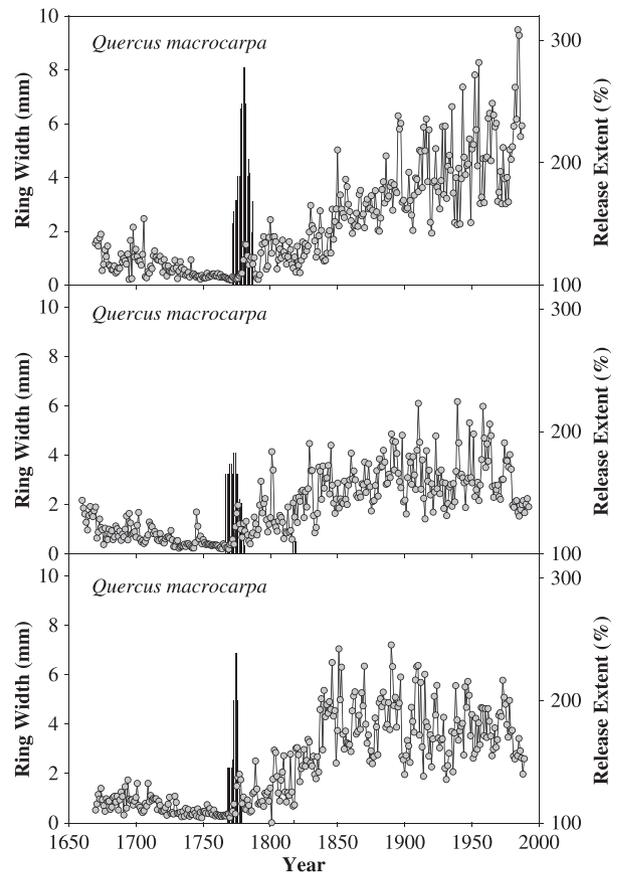


**Figure 4** Tree-ring sections from two *Quercus macrocarpa* stems collected in the Inner Bluegrass Region of Kentucky, USA. (a) The coin (diameter = 24 mm) is near the pith and the arrow indicates a several-fold increase in tree-ring width that occurred in 1820. (b1) The same coin positioned near the pith of a different sample, where it covers 46 years (1724–70). (b2) The coin is located on the sample nearer to the bark, where it covers 6 years (1915–21).

rate was present in the three oldest stems in the study (*Q. macrocarpa*) and was marked by release in the growth chronologies (Fig. 5). Each of these trees had narrow tree rings from establishment through to c. 1760, at which point release events were detected, and rapid growth was obvious beginning in the early 1800s (Fig. 5). These release events included median growth increases of > 200%, and growth rings were consistently wide throughout the 1900s (Fig. 5).

A mean annual ring-width chronology, including all stems in the study, exhibited a considerable increase beginning c. 1800 and lasting until c. 1880 (Fig. 6a). In contrast, mean annual ring width of *Q. alba* growing in an old-growth portion of LCWARS (Cook, 2006) was relatively even throughout its temporal span (Fig. 6a). The period of increasing growth rates among IBR stems coincided with the initiation of low branches (Fig. 6b). Branch sections from savanna trees exhibited a range of diameters, and initiation occurred from c. 1800 to 1900 (Fig. 6b). Release events were detected primarily from the late 1700s through to the late 1800s, and all growth releases of  $\geq 300\%$  occurred from 1800 to 1850 (Fig. 6c). Although sample density was insufficient to develop a regional fire history (McEwan *et al.*, 2007), scarring was conspicuously infrequent in the tree-ring record of IBR remnant savanna stems (Fig. 6d). The wounds that were found in IBR savanna stems did not display the morphological characteristics typical of a fire scar (McEwan *et al.*, 2007), and occurred only after 1800 (Fig. 6d).

Growth of IBR trees increased over the period 1760–1960, even though there was no apparent precipitation trend during this period. Mean tree-ring width for all samples was  $< 1 \text{ mm year}^{-1}$  in 1760 and had increased to  $3 \text{ mm year}^{-1}$  by 1960 (Fig. 7a). Over the same period, precipitation (as measured by



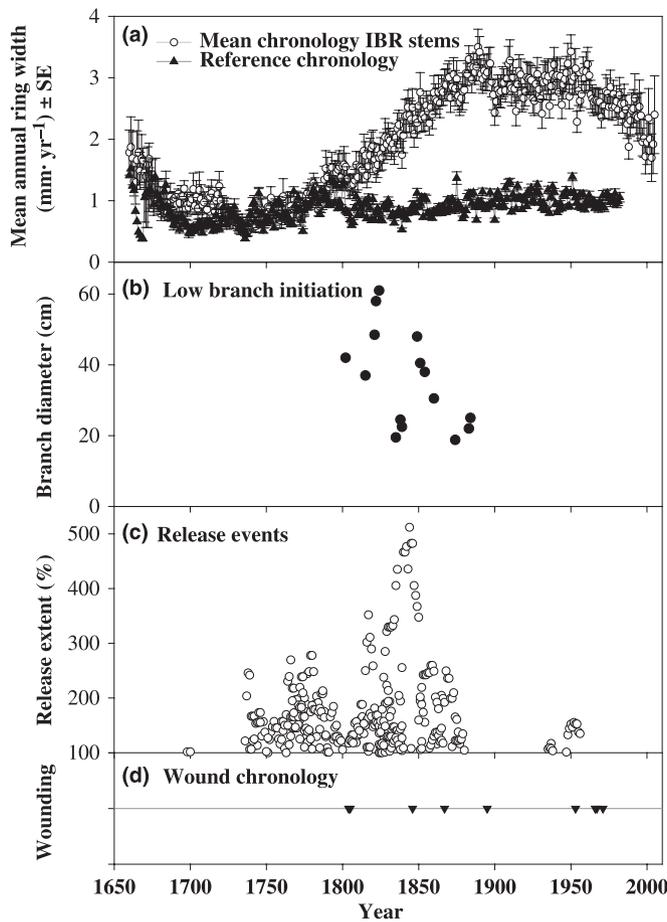
**Figure 5** Tree-ring chronologies and release events in the three oldest trees collected from remnant savannas in the Inner Bluegrass Region of Kentucky, USA. Each panel is an individual tree. Line and scatter plots represent the growth during a given year. Histogram bars represent the extent of release during a 'release year' (see text for release definition).

PDSI) exhibited high-frequency variation, but the overall trend was flat (slope = 0.002) and not statistically different from zero ( $P = 0.78$ ; Fig. 7b). In contrast, human population numbers increased in a pattern similar to mean annual ring width (Fig. 7c). The Euro-American population of the IBR is assumed to have been near zero in 1760, but increased exponentially over the period 1780–1840 (Fig. 7c). The temporally matching (1760–1860) episodes of Euro-American population expansion and increasing growth rate in savanna trees resulted in a strongly correlated ( $P < 0.0001$ ;  $r^2 = 0.78$ ) relationship between these two (biologically unrelated) variables.

## DISCUSSION

### Canopy dynamics and the historical growth environment

The growth of IBR savanna remnant trees was characterized by an increase c. 1800 that was abrupt and striking, and thus



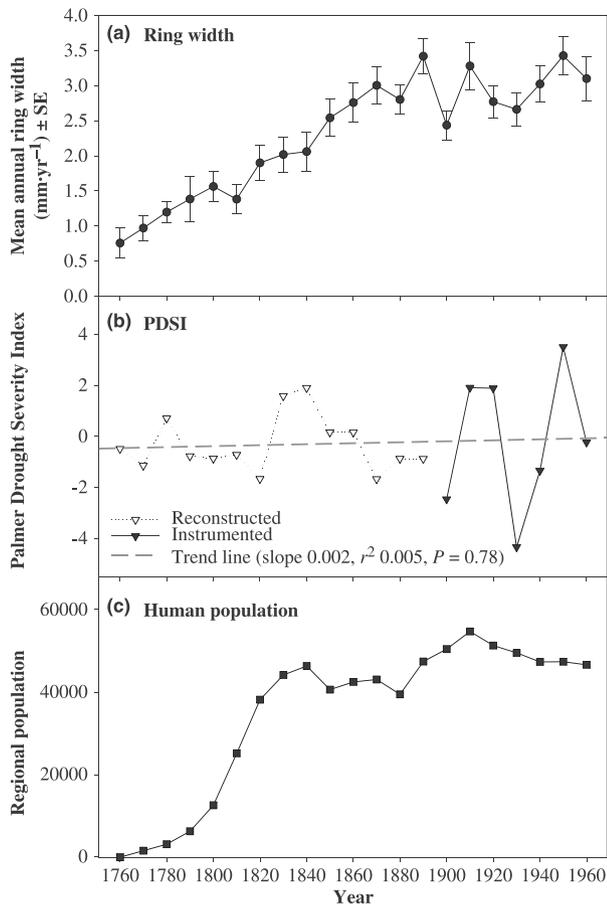
**Figure 6** Composite growth chronology and ecological features of remnant savanna trees in the Inner Bluegrass Region (IBR) of Kentucky, USA. (a) Line and scatter plots representing mean annual ring width ( $\pm 1$  SE) for all IBR samples ( $\circ$ ) and *Quercus alba* from an old-growth forest in eastern Kentucky ( $\blacktriangle$ ). (b) Pith dates and diameters of low branches collected from remnant IBR savanna trees. (c) All growth releases from all IBR samples. (d) All wounds recorded on all IBR samples are plotted as downward-pointing triangles on the same line.

indicative of an increase in light availability. Light-related release events have been documented in a variety of species (Canham, 1990; Winter *et al.*, 2002; Sheppard *et al.*, 2005). For instance, Rentch *et al.* (2003) found that the growth of oaks under a forest canopy was  $\leq 1 \text{ mm year}^{-1}$ , and when released from light competition their growth was consistently  $> 2 \text{ mm year}^{-1}$ . Trees in IBR savanna remnants exhibited a long period of growth typical for oaks under a forest canopy ( $\leq 1 \text{ mm year}^{-1}$ ), then exhibited release events that were vastly larger than can be attributed to factors other than a substantial increase in available light (Rubino & McCarthy, 2000, 2004; Rentch *et al.*, 2003). Low branch initiation in savanna remnant trees occurred during the same period as the marked growth releases, further substantiating the idea that the trees were responding to a large increase in available light. Following the release, ring widths typical for oaks growing in light-saturated conditions ( $\geq 3 \text{ mm year}^{-1}$ ; Rentch *et al.*, 2003; Rubino & McCarthy, 2004) were apparent throughout the remainder of the chronology ( $> 150$  years in some cases). These results strongly suggest that trees sampled in our study were growing in a light-limited setting (forest) prior to *c.* 1760, and were subsequently exposed to light-saturated conditions (savanna) during Euro-American settlement.

An ecosystem transformation associated with Euro-American settlement contrasts with conclusions drawn in previous

work, which suggested that savanna physiognomy was the prehistorical condition of IBR vegetation (Bryant *et al.*, 1980; Wharton & Barbour, 1991). This previous work relied on surveys of existing vegetation and quotes from explorers and early settlers who described open conditions (Bryant *et al.*, 1980; O'Brien, 1984; Wharton & Barbour, 1991). In particular, some early explorers noted large areas dominated by native cane (*Arundinaria gigantea*), which is a shade-intolerant species (Wharton & Barbour, 1991). The recorded statements of explorers, however, are contradictory in some instances, and some early descriptions refer to the IBR as being forested (Wharton & Barbour, 1991). Land-deed records that were created during Euro-American settlement indicate that shade-tolerant forest trees such as *Acer saccharum* and mesic forest understorey species such as *Asimina triloba* and *Carpinus caroliniana* were frequently encountered in the IBR (Campbell, 1989). Areas exhibiting dominance by *Q. macrocarpa*, *Q. muehlenbergii* and *F. quadrangulata* were noted in the mid-1800s (Campbell, 1989), well after agricultural development of the IBR landscape (Wharton & Barbour, 1991).

More surveys of early records are needed to clarify the composition of the IBR at the time of Euro-American contact, and more collection of ancient wood is needed to bolster our limited sample size. Even so, our data support the hypothesis that just before the arrival of Euro-Americans, the IBR was a



**Figure 7** Trends over 200 years in tree growth, drought and human population in the Inner Bluegrass Region of Kentucky, USA. (a) Mean annual ring width ( $\pm 1$  SE) for all trees sampled. (b) The long-term trend in moisture availability as measured by the Palmer drought severity index. Reconstructed data, open triangles; measured data, closed triangles; trend line for the period, grey long dashes. (c) Regional human population (census data) where each point represents the mean value for the given year.

predominantly forested landscape. The accounts of early settlers are consistent enough to substantiate the idea of some open areas in the IBR, but these were probably part of a broader forest mosaic. This forested ecosystem was disrupted as Euro-Americans cleared the landscape for settlements and created pasturelands. Agricultural development was well under way by 1800, and pastureland has been a consistently dominant land use in the IBR since that time (O'Brien, 1984; Wharton & Barbour, 1991), providing remnant trees with open growing conditions.

**Anthropogenic disturbance and ecosystem structure**

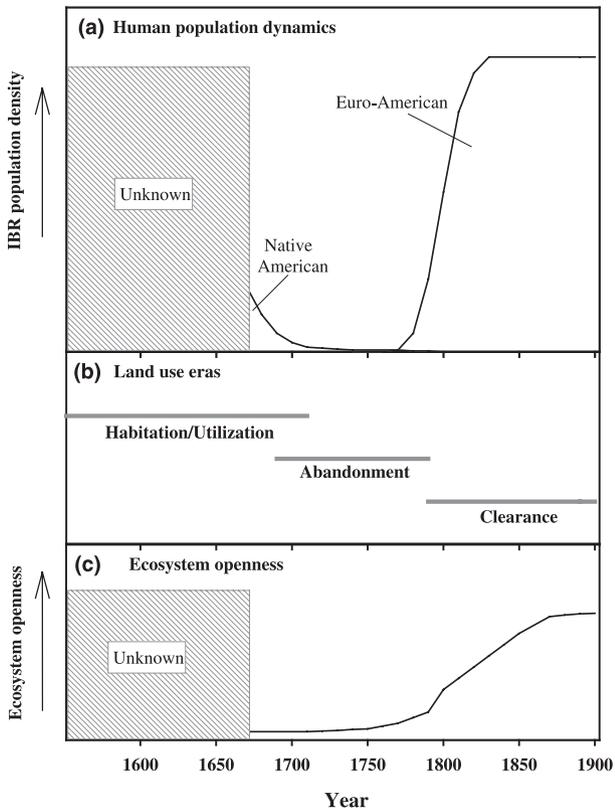
A clear relationship between anthropogenic disturbance and ecosystem structure has been demonstrated in many locations (Foster *et al.*, 2002; Guyette *et al.*, 2002; Keeley, 2002). For instance, oak savanna has been actively managed in quasi-

silvopastoral systems on the Iberian Peninsula, and anthropogenic disturbance was probably a contributing factor to the formation of oak savanna in California and midwestern North America (Abrams, 1992; Standiford, 2002; Plieninger *et al.*, 2003). In forests of the Missouri Ozarks, several phases of human settlement have been identified. These included a period of Native American habitation, then depopulation (c. 1650–1750), then phases of Euro-American settlement – each phase of human history had specific ecosystem consequences (Guyette *et al.*, 2002).

Our data suggest that the ecological history of vegetation in the IBR was strongly influenced by human affairs (Fig. 8). Euro-American settlement of the region began c. 1780 and population numbers increased exponentially thereafter (McBride & McBride, 1996; O'Malley, 1999; Fig. 8a). This population increase was accompanied by an era of land clearance associated with agricultural and economic development (Friend, 1999; Fig. 8b). Land clearance associated with Euro-American settlement resulted in rapid transformation of the native vegetation to agricultural uses (particularly pastureland; Wharton & Barbour, 1991). Because of these land-clearance activities, ecosystem openness increased concomitantly with increases in Euro-American population size (Fig. 8c).

The era immediately preceding Euro-American settlement may have been characterized by an atypically low population density of Native Americans (Fig. 8). Archaeological evidence suggests that Native American population density plummeted c. 1670 (Henderson, 1992; Kelton, 2002; Fig. 8a). This population decline was related to the arrival of infectious European diseases, particularly smallpox, which killed up to 95% of a region's inhabitants (Ramenofsky, 1987). The indigenous people who survived, joined by eastern peoples who were moving west to escape the colonial sphere, apparently lived mainly along the Ohio River, creating multi-ethnic villages (Henderson, 1999). A few villages may have remained in the IBR, but the number of regional inhabitants, and therefore the human impact on the landscape, would have been greatly diminished. Period records indicate that native inhabitants abandoned the river settlements c. 1758, but apparently continued to use the region for hunting (Henderson, 1992, 1999; McBride & McBride, 1996). When the earliest Euro-American settlers arrived in the late 1760s, the regional population had been markedly reduced, and the Native Americans who remained were probably having a minimal impact on the landscape (Henderson, 1992; Fig. 8a). Thus a period of low Native American population density, and accompanying land abandonment, immediately preceded the arrival of Euro-American settlers (Fig. 8b). This era of land abandonment coincided with extremely slow growth in regional trees, suggesting light limitation associated with growth in a closed-canopy forest (Fig. 8c).

Prior to the catastrophic decline in population due to European plagues, Native Americans may have had a substantial influence on the IBR landscape, including creating and maintaining some degree of canopy openness (Lewis, 1996). While population numbers remain unknown (Fig. 8a),



**Figure 8** A hypothetical model linking human populations, land-use eras and ecosystem openness in the Inner Bluegrass Region of Kentucky, USA. (a) The Euro-American population curve is generalized and based on census data; the declining Native American population curve is hypothetical, based on archaeological data (see text). (b) Land-use eras are conceptual, based on general patterns of population number and land-use activities during the given time frame. (c) The ecosystem openness curve is hypothetical and derived from tree-ring data.

Native Americans inhabited the IBR for at least several thousand years prior to Euro-American contact (Railey, 1996; Sharp, 1996). By AD 1400, Native Americans were clearing land for home sites and utilizing at least some portions of the IBR for gardens (Sharp, 1996; Fig. 8b). This agrarian lifestyle was typical of Native American practices in other North American ecosystems (Doolittle, 1992) and on some areas of the nearby Cumberland Plateau (Delcourt *et al.*, 1998). Prehistoric Native American land use would have required some extent of land clearing, although the effect on overall ecosystem openness is unknown (Fig. 8c).

## CONCLUSIONS

Human history is an important driver of ecological dynamics in many forests of eastern North America. Native Americans undoubtedly influenced some North American ecosystems prior to *c.* 1600 (Cronon, 1983; Williams, 1989; Denevan, 1992). Native American populations then precipitously declined due to European plagues, which probably resulted

in altered disturbance regimes in these ecosystems (Williams, 1989; Whitney, 1994). Finally, Euro-American activities resulted in clearing of vast areas and substantial alteration of the landscape (Williams, 1989; Russell, 1997). The ecological history of remnant savanna in the IBR highlights these three phases of human history and reinforces the notion that anthropogenic disturbance regimes have been dynamic over the past 400 years. Sustained focus on long-term ecosystem response to human cultural changes may enhance our ecological understanding of dynamics in other forests of eastern North America.

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