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Influence of river channelization and the invasive shrub, *Ligustrum sinense*, on oak (*Quercus* spp.) growth rates in bottomland hardwood forests

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Keywords

Bottomland hardwood forests; Channelization; Chinese privet; Dendrochronology; Flood pulses; Forested wetlands; Hydrology; *Ligustrum sinense*; Riparian forests; Tree ring dating; Woody invasive species

Abbreviations

BACI = before-after/control-impact; BAI = basal area increments; BLHF = bottomland hardwood forest; CWD = coarse woody debris; HR = hydrology removed; INV = invaded and channelized site/impact; NON = non-invaded and channelized site/control; PDSI = Palmer Drought Severity Index; REF = non-invaded and non-channelized reference site/control; RW = raw ring width; SFS = signal-free standardization of basal area increment chronologies.

Nomenclature

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Abstract

Question: Do river channelization and a common invasive shrub, *Ligustrum sinense* Lour. (Chinese privet), affect tree growth rates in forested riverine wetlands?

Location: Three sites along the Wolf River, in and near Memphis, Tennessee, USA.

Methods: We cored and analysed 83 oak trees within three study sites. Correlations of river channelization and climatic variables with basal area increments (BAI) and detrended BAI (SFS) were analysed to investigate channelization effects. Significant correlations were removed from BAI chronologies (BAI-HR) to isolate the effect of *L. sinense*. We investigated effects of *L. sinense* on tree growth using a before–after/control–impact (BACI) experimental design with one location impacted by invasion (INV), two control locations that were not invaded (NON and REF) and covariates of tree age and size. We conducted a two-factor mixed effects ANCOVA to determine if there was a significant interaction (BACI) effect.

Results: Channelization promoted faster canopy oak growth in all sites, spring drought significantly slowed growth in NON, while summer precipitation promoted wood production in NON. Investigation of *L. sinense* impact on tree growth revealed a significant BACI effect, such that trees in INV grew slower after invasion than trees in the non-invaded control sites (NON and REF).

Conclusions: We suggest that faster growth after channelization may be a consequence of increased aerobic conditions, by enabling higher oxygen availability to tree roots. However, many of the obligate bottomland tree species struggle to regenerate in drier, post-channelized conditions. Thus, native drought-tolerant species may have an advantage in the sub-canopy and regeneration layers of these altered forests. Instead, *L. sinense*, an invasive and drought-tolerant species, has invaded most locations adjacent to the channelized portion of the Wolf River. *L. sinense* presence reduces the channelization advantage by slowing growth of canopy oaks and possibly contributing to accelerated mortality. These results suggest an emerging shift to a commonly held paradigm with respect to invasive shrub species. Not only do invasive shrubs crowd out other small woody species and herbaceous plants, but they also have the ability to impact the structure of the forest canopy.

Introduction

Bottomland hardwood forests (BLHFs) perform valuable ecosystem functions. They sequester nutrients and sediments, filter groundwater and create habitats for diverse species (Johnston et al. 1990; Richardson et al. 2007). Plant species that thrive in these forested wetlands are often specialists, requiring restricted physical conditions to survive and reproduce (Shankman 1996). These species are relatively non-competitive and rely on seasonal inundation, or flood pulses, to remain prolific. They have many adaptations that give them advantages in riverine dynamics. Physical adaptations to anaerobic conditions resulting from frequent long-term inundation include: shallow roots, buttressing, lenticels and aerial roots (Middleton 2002). Vegetative reproduction is an adaptation to high flow events that break limbs (Planty-Tabacchi et al. 1996; Naiman & Décamps 1997; Hood & Naiman 2000). Seed germination of many native BLHF species is significantly higher in hydric conditions than xeric conditions (Middleton 2002). Riparian species also take advantage of flood pulses as a means of seed dispersal – hydrochory (Schneider & Sharitz 1986; Guo et al. 1998; Capon 2003; Richardson et al. 2007). Because of their dependency upon seasonal flood pulses, BLHFs are fragile ecosystems. Unfortunately, over 50% of all BLHFs in the United States were destroyed by 1980 resulting from deforestation linked directly to agriculture (Gosselink et al. 1990) and indirectly to urbanization (DeFries et al. 2010). Furthermore, the remaining BLHFs are threatened by invasive species and altered hydrologic regimes (Vitousek et al. 1996; Richardson et al. 2007).

Ligustrum sinense is a broad-leaved, semi-evergreen invasive shrub native to southeast China. Invasion of *L. sinense* frequently occurs in disturbed riverine areas in Australia, New Zealand and the US (Ward 2002; Grove & Clarkson 2005; Pokswinski 2008). Invasion results from viable offspring (seeds and vegetation) being dispersed long distances and decreased biodiversity in areas of established colonies (Richardson et al. 2000; CBD 2006). *L. sinense* was brought to the US as an ornamental hedgerow and is now among the top invaders of the southeastern US, where it occupies land in nearly every county in the region and is expanding its range to the north and west. Dense *L. sinense* invasions occur along riparian zones, in ditches, lowlands and disturbed wetlands (Brown & Pezeshki 2000; Panetta 2000; Merriam 2003; Grove & Clarkson 2005; Brantley 2008; Osland et al. 2009; Hudson 2013). *L. sinense* has many life-history traits that make it perfectly adapted to the dynamics of riparian floodplains and promote successful invasion. It has high phenotypic plasticity and when grown in hydric conditions it produces lenticels and aerial roots (Brown & Pezeshki 2000), it reproduces

asexually through broken limbs or runners (Morris et al. 2002) and the viable *L. sinense* seeds are highly buoyant and are dispersed by water, as well as birds and mammals, into BLHFs (Ward 2002; Foard 2014).

Globally, many BLHF rivers and streams are hydrologically altered to control flooding and reduce flood risks to humans. These alterations include damming, rerouting and/or channelizing waterways (Middleton 2002). In the 1920s, the U.S. Army Corps of Engineers began a large-scale project to channelize the Wolf River, a major tributary of the Mississippi River in southwestern Tennessee, US. Within 35 yrs the lower 35.2 km were channelized. Although channelization ceased in 1964, the ecology of the Wolf River BLHF was permanently altered, and the water table lowered substantially (Weins & Roberts 2003). Following channelization, the natural flooding regime changed and the surrounding regions no longer retained the necessary hydrology to maintain ‘wetland’ classification (Weins & Roberts 2003). Since the land surrounding the river became drier (i.e. decreased flood frequency and duration), new, competitive woody species from surrounding upland populations would be expected to occupy the area (Shankman 1996). However, *L. sinense* is one of the few species to establish, thrive and reproduce (Houston et al. 2010). Years after invasion, the established bottomland hardwood species exhibited severe canopy loss and above average tree mortality (Houston et al. 2010), which is evident by the increased abundance of dead wood littering the forest floor (Foard 2014).

In this study we characterized stand features and utilized dendrochronology to make inferences about the biotic and abiotic conditions influencing the growth of bottomland hardwood oak trees (Stokes & Smiley 1968; Speer 2008). Dendrochronology is the study of annual rings produced by trees. Tree rings often indicate favourability of conditions present throughout the life of the trees. If conditions are favourable trees grow fast – reflected by wider than average annual rings.

This study aims to answer two questions: (1) what roles do climate and river channelization play in oak tree growth in BLHFs; and (2) do oak trees in *L. sinense*-invaded sites grow slower after invasion than in non-invaded sites? We hypothesized that the woody wetland species that once thrived in historical flood pulses began to struggle in less suitable, drier conditions following channelization, and that *L. sinense* invasion exacerbated tree mortality in these stands.

Methods

Site and tree selection

Tree cores were collected from sites located along the Wolf River, Tennessee, US. To investigate *L. sinense* impact on

oak growth a before–after/control–impact (BACI) design was used (Smith 2002). Three sites were selected – one impacted site, INV, located in invaded/channelized portions of the river; and two reference sites, NON and REF, located in non-invaded/channelized and non-invaded/non-channelized locations, respectively (Fig. 1). Logging records are not available for all sites, but based on knowledge of historical logging practices, stand structures and known logging history nearby, it is probable that all sites were clear-cut in the early 1900s, and forests regenerated naturally after logging (Lorimer 1980; Houston et al. 2010).

Oak trees were cored because they produce consistent annual rings (D. W. Stahle 2012 pers. comm.) and because they are common in BLHFs. We cored and analysed 13–18 *Quercus nigra* L. (water oak), six to eight *Q. pagoda* Raf. (cherrybark oak), five *Q. michauxii* Nutt. (cow oak) and two *Q. lyrata* Walter (overcup oak) per site. Trees >25 cm DBH, with matched DBH and within 300 m of the original Wolf River channel were selected to minimize variability in the response to channelization while maximizing river gauge height responses, and to ensure that stand level conditions were similar and consistent among sites (Copenheaver et al. 2007; Speer 2008). Cores were analysed from 25 to 30 trees per site (INV, NON, REF), for a total of 83 trees (Fig. 1). The chosen species are adapted to BLHF conditions and theoretically represent typical BLHF responses (Burke & Chambers 2003).

One GPS coordinate per location (INV, NON and REF) was selected using a true randomized number generator

from the website <http://www.random.org>. Coordinates were located and transects were established parallel to the original (meandering) Wolf River channel. Every healthy-looking oak tree (solid trunk, with few dead limbs and no rotten material) along the transect that matched our selected criteria was sampled until we cored the target number of trees. We selected trees in INV first because there was a scarcity of healthy-looking trees, and we wanted to ensure trees in all sites were physically comparable (Fig. 1). Following methods from Speer (2008) we extracted two perpendicular cores from each tree (north and east, if possible). Then we stored and prepared the cores for analysis. For each cored tree, DBH and tree height were recorded, common tree health variables were assessed and surrounding species compositions were surveyed. Additionally, coarse woody debris (CWD) was quantified in INV and NON.

Tree, site and stand characteristics

To investigate tree health characteristics, we estimated percentage dieback, live crown ratio and percentage canopy missing for each tree (Nowak et al. 2005). ANOVAs were conducted in Minitab (v 16; Minitab Inc., State College, PA, US) comparing tree size, health and age variables to determine if there were significant differences among sites.

We incorporated quadrat and vegetation sampling techniques from Krebs (1999) and the U.S. Environmental Protection Agency (2011) to gather species and site composition data. We randomly selected a 100-m² quadrat

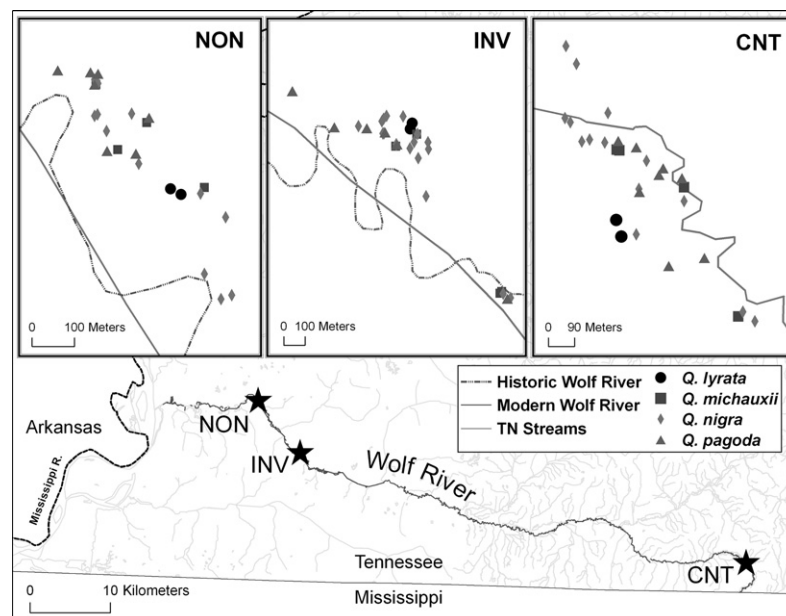


Fig. 1. Map of dendrochronology sites (INV = invaded/channelized, NON = noninvaded/channelized, REF = non-invaded/non-channelized) and trees located along the Wolf River, TN, USA, including the locations of the Wolf River before and after channelization.

adjacent to each sampled tree and identified all woody species and estimated percentage cover, average diameter and average height of all stems in the quadrat. Sørensen's index of similarity (Wolda 1981), wetland prevalence (Weins & Roberts 2003) and Simpson's diversity indices (Smith & Smith 2001; Burton et al. 2005) were compared for all pair-wise comparisons of sites. Wetland prevalence is a value (1–5) that shows the degree to which established species require wetland conditions to proliferate (1 = most and 5 = least). One-way ANOVAs were used to test for significant differences among sites.

To determine if the amount of fallen trees and broken limbs was higher when *L. sinense* was present (Bragg & Heitzman 2009), the following CWD variables were measured and recorded for three 300-m² transects in INV and NON: wood type, debris type, large and small end diameters (cm), length (m), evidence of cutting (yes or no) and decay class (Vose et al. 1999). CWD volume was calculated using Smallian's formula (Bragg & Heitzman 2009). Mass for the woody debris was calculated by multiplying the volume by the specific gravity. Specific gravity is based on Bragg (2013) decay classification.

Timing of *L. sinense* invasion

We established the timing of *L. sinense* arrival first so we could determine appropriate dendrochronology methods for this study. *L. sinense* does not produce annual rings because it is an evergreen shrub and has multiple annual growth spurts. Therefore, aging *L. sinense* required alternative methods to dendrochronology. To determine when

L. sinense became abundant we used three methods. First, we utilized historical winter aerial photographs and visually identified *L. sinense* – the only colonial, broad-leaved evergreen shrub in the BLHFs along the Wolf River (Houston et al. 2010; Fig. 2). Second, two documented first-hand accounts from long-term residents of the region who were frequent visitors of the Wolf River throughout their lives – Chapman (1977) and Larry Smith (pers. comm., 4 Dec 2013). Finally, statistical inferences were derived from site-level chronologies *via* non-parametric Superposed Epoch Analyses in Dendro Tools (v 1.0; <http://www.djburnette.com/programs/dendrotools/index.html>). All methods indicated the same approximate time interval for *L. sinense* dominance – between 1970 and 1980.

Dendrochronology and statistical methodology

Cores were visually cross-dated using the list method, and temporal overviews of annual growth were established in each location (Speer 2008). Next, annual radial growth (i.e. raw ring width or RW) of each tree core was measured to an accuracy of 1 µm. The measures were transferred to quality control software, COFECHA (Holmes 1983; Table 1). After ensuring quality, the data were transferred to ARSTAN (Cook 1985), and chronologies were constructed.

Our goal was to isolate the effects of river flow and invasive species; thus, we needed to remove other detectable influences first. We examined the radial growth to see if there were any obvious trends, and we noted that growth for all sites declined in a typical negative exponential trend

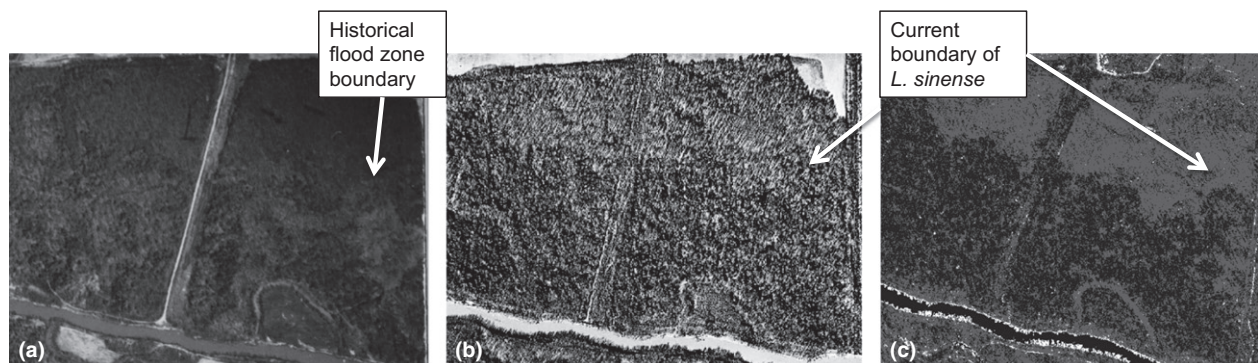


Fig. 2. Comparison of winter aerial photographs and a remotely sensed image of an *L. sinense*-invaded forest adjacent to The Wolf River near Memphis, Tennessee. (a) The flood zone immediately surrounding the meandering remnant of the Wolf River after channelization in 1954. Visible are lighter-colored large gaps between trees, representing the absence of *L. sinense*. (b) An aerial photograph of the same location from February 1981 after *L. sinense* invasion. Because *L. sinense* is the only evergreen species in this location today, the presence is clearly indicated by the dark “popcorn” appearance of the area overlapping the historical Wolf River flood zone. The range of *L. sinense* in the flood zone was verified by remote sensing techniques. (c) Reflectivity of *L. sinense* in Shelby Farms along the Wolf River. *Ligustrum sinense* is accurately identified with a two-meter spectral resolution using Digital Globe's Worldview-2 platform. Aerial photographs (a and b) retrieved from Shelby County Archives (<http://register.shelby.tn.us>) and reflectivity image (c) is modified from Quarles (2012), with permission.

Table 1. Tree size, age, wetland prevalence and diversity, and raw ring width (RW) intercorrelation, sensitivity and dating information for sampled trees from each site (INV = invaded/channelized, NON = non-invaded/channelized, REF = non-invaded/non-channelized). Tree size, age, wetland prevalence and diversity displayed with 95% Tukey confidence intervals calculated in Minitab. Tree dating information is from COFECHA using 32-yr cubic smoothing splines. Variables and locations with significant differences from both other sites are highlighted in grey. Asterisks represent sites that were significantly different from each other but not different from the third site.

Tree and Site Characteristic	INV	NON	REF
Trees Assessed per Site	30	25	28
Mean DBH	65.69 ± 6.40	67.34 ± 6.59	67.28 ± 6.96
Mean Height	32.47 ± 2.05	37.56 ± 1.41	37.86 ± 1.61
% Dieback	8.93 ± 3.26	7.28 ± 3.07	8.21 ± 3.17
Live Crown Ratio	27.86 ± 5.96	26.77 ± 4.98	28.34 ± 6.01
% Canopy Missing	39.0 ± 8.1	19.3 ± 7.3	15.0 ± 5.9
Mean Age ($F_{(2,80)}$)	67.07 ± 5.12*	64.60 ± 5.53	58.29 ± 3.76*
Mean Wetland Prevalence Index	2.869 ± 0.09	2.632 ± 0.08	2.643 ± 0.10
Mean Diversity (D-1)	0.16 ± 0.039	0.74 ± 0.047	0.72 ± 0.063
Richness	47	50	37
Dating Information			
# Dated Cores	58	47	59
RW Series Inter-correlation	0.454	0.499	0.491
RW Mean Sensitivity	0.235	0.206	0.201

after 1980. Therefore, we removed the negative exponential age-related growth factor by transforming RW to basal area increments (BAI, measured in cm^2) using the formula from Biondi (1999), which assumes concentric circles of annual growth. To investigate the influence of hydrology (river gauge height) on tree growth, while accounting for the increase in basal area due to age, we detrended BAI chronologies using signal-free standardization (SFS). We used BAI and SFS chronologies for analyses because we wanted to emphasize site- and stand-level signals (i.e. river gauge height and *L. sinense*) that might be removed through typical detrending methods (Cook & Kairiukstis 1990; Melvin & Briffa 2008; Fig. 3).

We investigated variability in growth among-species (*Q. lyrata*, *Q. michauxii*, *Q. nigra* and *Q. pagoda*) and species-within-site chronologies (four species chronologies per site, totalling 12 chronologies). We determined that all species showed the same general growth trend in all locations for RW and BAI chronologies (Foard 2014), and thus we grouped them together by site for analyses. We also sampled similar proportions of species in all sites.

The BAI and SFS chronologies were assessed for significant climatic signatures before river gauge height. The climatic variables PDSI, precipitation and temperature were obtained from National Climatic Data Center (<http://www.ncdc.noaa.gov>, TN Zone 4). Using Dendro Tools, correlation function analyses were conducted between mean monthly climate (PDSI, precipitation, temperature) and site chronologies (INV, NON, REF; Appendices S1–S3). We considered the correlation to be significant if statistical results met the following criteria: Pearson correlation coefficient $>|\pm 0.45|$ and $P < 0.001$ for all chronologies and monthly combinations of climate data. Only one SFS

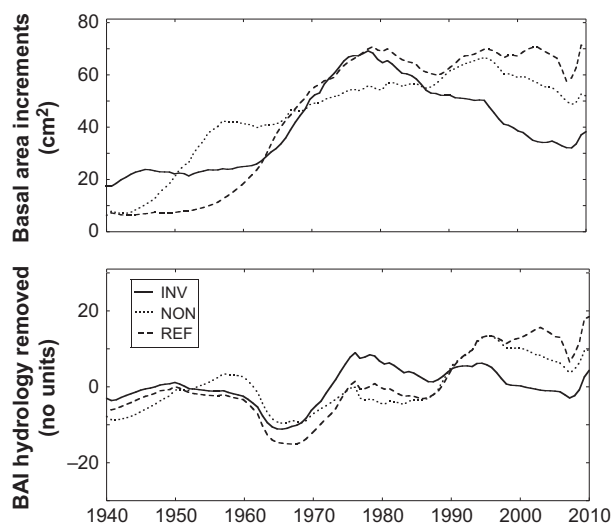


Fig. 3. Master chronologies for each site (INV = invaded/channelized, NON = noninvaded/channelized, REF = non-invaded/non-channelized) in basal area increments (BAI, top) and BAI-hydrology removed (BAI-HR, bottom) from 1940 to 2010. BAI-HR values were calculated by regressing BAI to significant river gauge height and then solving for the residuals. Chronologies made with KaleidaGraph (4.1.1 Synergy Software Inc., Reading, PA, USA), curved fits set at 100 fit points.

chronology was correlated with climate, NON-SFS. None of the BAI chronologies showed significant correlations with climate variables. Thus, BAI chronologies were used to test for an *L. sinense* effect.

Wolf River gauge height data were acquired from the U.S. Army Corps of Engineers (<http://www.rivergages.com>, Wolf River Gauge WF111). We used one river gauge for all analyses because it was the only Wolf River gauge

Table 2. Months and variables with most significant correlations to site-level basal area increments (BAI) and signal-free standardized detrended BAI chronologies (SFS) from 1936 to 2011, plus the resulting Spearman and Pearson correlation coefficients; n = number of years used in regression analyses (limited by available river gauge data and chronology length). All correlations in this table are statistically significant ($P < 0.01$ and Pearson correlation coefficient $>|\pm 0.45|$).

	Highest correlated Month/s	Pearson's Correlation	Spearman's Correlation	n
INV-BAI	Aug Gauge Height	-0.834	-0.745	57
NON-BAI	Aug Gauge Height	-0.821	-0.646	57
REF-BAI	Aug Gauge Height	-0.777	-0.618	54
INV-SFS	Jul Gauge Height	-0.493	-0.460	57
NON-SFS	Jan Gauge Height	-0.447	-0.367	57
	Jun–Aug mean PDSI	0.484	0.467	75
	May–Jul mean precip.	0.455	0.309	75
	Jun temperature	-0.447	-0.441	75
REF-SFS	Jul Gauge Height	-0.775	-0.674	54

with temporal depth >30 yrs. Using BAI and SFS chronologies, significant hydrologic signatures were identified and correlation function analyses were conducted using Dendro Tools. Correlation matrices were conducted between all available monthly climate and river gauge height data, as well as select combined monthly averages vs each site (INV, NON, REF; Appendix S4). There were strong correlations of BAI and SFS with river gauge height (i.e. Pearson's correlation coefficient $>|\pm 0.45|$ and $P < 0.001$ for all three sites). However, there is a natural growth bias produced by converting to BAI that emphasizes fast growth later in life, and may be responsible for the significant correlations of BAI to river gauge height (Fig. 3; Bowman et al. 2014; Stephenson et al. 2014). Thus, regression models were conducted on SFS chronologies to describe river gauge height relationship with tree growth for each site (Table 2).

The BAI chronologies showed the strongest correlations with mean Aug gauge height for all sites, thus promoting analogous statistical approaches among sites. Mean river gauge height for Aug was missing for 18 observations, so we estimated nine observations with mean Nov and Mar gauge height via multiple regression analysis ($F_{(2, 48)}, P < 0.001, R^2 = 0.925$). The river gauge height responses were removed from the BAI chronologies for each site by regressing BAI to mean Aug river gauge height and then solving for the residual. Therefore, the resulting chronologies, BAI hydrology removed (BAI-HR), isolated stand-level (*L. sinense*) growth influences (Fig. 3).

We used Minitab to conduct a two-factor mixed effect ANCOVA with interaction (BACI) on all BAI-HR chronologies to determine if there was a significant effect of *L. sinense* after invasion while controlling for tree size and age. The dependent variables were tree growth mea-

surements BAI-HR, the fixed independent variable was before/after *L. sinense*, the random independent variable was site (NON, INV, REF) and the covariates were DBH and age. Given that the independent terms (before/after and site) were not significant, the output from the interaction term in the model revealed whether there was a BACI effect. We removed the 10 yrs when *L. sinense* was establishing and compared 30 yrs before (1940–1969) vs 31 yrs after (1980–2010) because we wanted to account for the variability of tree response time and maintain a sample depth more than five trees per site. Additional details about all methods can be found in Foard (2014).

Results

Tree, site and stand characteristics

Tree, site and stand characteristics support that sites are appropriate for comparative analyses. ANOVA and 95% Tukey confidence intervals revealed that there was no significant difference in tree DBH among sites ($F_{(2, 80)} = 0.09, P = 0.92$; Table 1). Trees in INV were shorter than trees in NON and REF combined ($F_{(2, 80)} = 13.14, P < 0.001$) by between 3.2 and 7.2 m on average. There was no significant difference in tree heights between NON and REF. There were no significant differences among sites for percentage dieback ($F_{(2, 80)} = 0.28, P = 0.76$) and live crown ratio ($F_{(2, 80)} = 0.08, P = 0.93$). Trees in INV had increased percentage canopy missing than trees in NON and REF ($F_{(2, 80)} = 15.2, P < 0.001$) of between 14.3% and 30.8% on average. Trees in NON and REF were not significantly different from each other (Table 1). Trees in REF were significantly younger than trees in INV ($F_{(2, 81)} = 3.3, P = 0.04$) by 8.7 yrs on average; however, age was accounted for in our final BACI analysis on BAI-HR. Trees in NON were not significantly different than INV or REF (Table 1).

Sørensen's index of similarity among all pair-wise comparisons of sites revealed that 67–70% of all woody species were common among all sites, supplying more evidence that sites were highly comparable. The mean wetland prevalence for INV (2.869) was significantly higher than NON (2.627) and REF (2.643), indicating that the species present in INV have slightly higher tolerances to xeric conditions than the other two sites ($F_{(2, 87)} = 16.55, P < 0.001$). Wetland prevalence in NON and REF were not significantly different. Species in INV are likely to be found in uplands 1.14–6.43% more often than species in NON and REF (Table 1). Species richness values for INV, NON and REF were 47, 50 and 37, respectively. Simpson's diversity index values for INV, NON and REF were 0.16, 0.74 and 0.72, respectively, and were significantly lower in INV than in NON and REF ($F_{(2, 87)} = 185.15, P < 0.001$; Table 1).

Overall there were higher numbers of pieces, larger volumes and increased masses of CWD in INV than in NON – there were 15.67 pieces of CWD 100 m^{-2} in INV, and 4.78 pieces of CWD 100 m^{-2} in NON, on average. CWD mass and volume were higher in INV than NON by 2431 kg 100 m^{-2} , and 6.08 $\text{m}^3\text{ }100\text{ m}^{-2}$, on average, respectively. In INV there were 13.44 logs 100 m^{-2} (logs = fallen branches or tree trunks), which was more than NON by 8.77 logs 100 m^{-2} , on average. There was a mean of 1.33 stumps 100 m^{-2} in NON, which was more than INV by 1.22 stumps. There were no snags in NON; however, there was a mean of 0.89 snags 100 m^{-2} in INV. In INV and NON, decay class 3 (highest decomposition; most wood not intact) and decay class 2 (wood intact with some bark loss) were most common, respectively. Pieces of CWD in decay class 1 were three times more in INV than NON (Appendix S5).

Dendrochronology results

The COFECHA output revealed that all RW chronologies had series intercorrelation values >0.45 and mean sensitivity values between 0.201 and 0.235; therefore, they were accurately dated and appropriate for dendrochronological analysis (Table 1). Raw ring widths for all series can be found in Appendices S6–S8.

There were no significant correlations among the climatic variables, precipitation, temperature and PDSI vs RW and BAI chronologies. INV-SFS and REF-SFS chronologies were not significantly correlated with climate variables, which is supported by other studies that found some BLHF tree species are not sensitive to climatic variables (Copenheaver et al. 2007). However, NON-SFS was positively correlated with mean Jun–Aug PDSI and mean May–Jul precipitation while correlating negatively with Jun temperature (Table 2, Appendices S1–S3). Thus, the trees in NON tend to grow faster when conditions are cool and wet from late spring into the summer. The most statistically significant multiple regression model ($P < 0.01$ and VIF = 1.0 for all variables) for NON-SFS showed that Jan gauge height, May–Jul precipitation and Jun temperature explained 41.2% of the variability in growth ($F_{(3, 57)} = 13.30, P < 0.001$).

All site chronologies (BAI and SFS) were significantly correlated with river gauge height (Table 2). Contrary to our hypothesis that trees slowed in growth as a result of channelization, all chronologies revealed significant negative correlations with river gauge height – as river height decreased, tree growth increased (Table 2). The coefficients of determination for BAI revealed that river gauge height explains 56%, 54% and 76% of the variability in tree growth in INV, NON and REF, respectively. For SFS, the coefficients of determination revealed that river gauge

height explains 24%, 20% and 60% of the variability in tree growth in INV, NON and REF, respectively.

To determine the effect of *L. sinense* on tree growth, we chose to use BAI-HR chronologies because all chronologies underwent the same detrending techniques (removal of Aug gauge height) thereby reducing model complexity while isolating unidentified signals. Two-factor mixed effects ANCOVA (BACI-ANCOVA), with REF and NON combined (REF/NON) as control sites in the BACI model and INV as the impacted site, revealed that there was a significant BACI effect (interaction) in response to *L. sinense* ($F_{(1,182)} = 4.8, P < 0.05$). BAI was a significant co-variate ($P < 0.001$) and age was not ($P > 0.1$), but both were left in the model to ensure statistical integrity. There were no significant main effects for site or before/after variables ($P > 0.1$).

All BAI site chronologies increased in growth over time, which can be attributed to strong inverse correlations with concurrent changes in hydrology (Table 2). When river gauge height effects were removed from the chronologies (BAI-HR), the impacted site (INV) showed a smaller increase in growth after invasion when compared to the non-invaded sites. Thus, BAI-HR chronologies revealed that after accounting for size, age, climate and river height, trees in *L. sinense*-invaded habitats grew slower than trees in non-invaded habitats after invasion (1980–2010) than they did before invasion (1940–1969). Without invasion, the forest is not expected to be in decline since tree age and size is not that of senescing trees (Pederson et al. 2005). Given that the majority of all other contributing factors were constant (size, similarity, wetland prevalence and richness) we attribute this slowing of growth to an impact caused by *L. sinense* invasion.

Discussion and conclusions

Tree, site and stand characteristics

The similarities in tree, site and stand characteristics are a result of the selection methods. Thus, the differences that were present can be explained by the invasion of *L. sinense*. Our selection methods for choosing trees to analyse for growth were so stringent (e.g. we selected healthy-looking trees) that we may have inadvertently selected individuals that were least impacted by *L. sinense* invasion and underestimated the true effect. It is possible that the reduction of canopy tree growth is even more at the stand level than our data show.

Tree health and CWD data indicate that trees in INV may be self-thinning in response to competition with *L. sinense*. Trees in INV had low mean percentage dieback (9%), which indicates that there were few visible dead limbs. However, percentage canopy missing was higher in INV than the other two sites (Table 1), which may also be

an explanation for significantly shorter trees in INV. Another possible explanation for shorter tree heights in INV could be a result of the lack of competition with canopy trees. Nonetheless, these results suggest that trees in INV are concentrating resources toward the remaining living canopy branches, and that dead or dying branches are shed from the tree quickly. This 'self-thinning' postulation is further supported by the CWD data. Trees in INV shed large quantities of limbs, as is evident by three times more pieces of CWD in INV than in NON, nearly all of which (99%) were limbs (expressed as logs). Moreover, the amount of CWD from each decay class was evenly distributed in INV, which indicates that trees have been losing limbs at a steady rate. Thus, the data support that trees in INV are likely responding to *L. sinense* by self-thinning, which may eventually lead to accelerated tree mortality.

Reduced diversity in INV is undoubtedly a result of the mass amounts of densely packed *L. sinense* stems that reduce evenness in the diversity measurements. These lowered diversity values are supported by the findings of many other *L. sinense* investigations, which all noted low diversity in *L. sinense*-invaded sites compared to non-invaded sites (Merriam & Feil 2002; Grove & Clarkson 2005; Pokswinski 2008; Hanula et al. 2009; Klock 2009; Osland et al. 2009; Ulyshen et al. 2010; Hanula & Horn 2011a,b; Greene & Blossey 2012).

Effects of climate and river gauge height

Only one site chronology, NON-SFS, correlated significantly with climate. Trees in NON were sensitive to late spring and summer drought characteristics (i.e. they tended to grow better during cool and wet conditions). Sensitivity to climate indicates that trees are less responsive to site and stand level dynamics (Bartens et al. 2012). However, conclusions related to these associations are outside the scope of this manuscript. We suggest that further research be conducted to describe mechanisms of variability in climatic sensitivity of urban BLHF trees.

Trees in the BLHFs along the Wolf River used in this study showed a significant response to river gauge height (see similar results in Copenheaver et al. 2007; Smith et al. 2013). These findings support that these species are more receptive to groundwater, river water and microsite characteristics than they are to climatic variables. Moreover, the responses of BLHF oak trees to river gauge height and channelization are similar to those observed by Weins & Roberts (2003), who looked at the effect of river head-cutting on the rates of *Quercus phellos* L. (willow oak) growth. They cored trees in an impacted site where the water table was observed to have dropped as a result of channelization and head-cutting. They investigated decadal growth of BAI from 1940 to 2000 and, like us, they observed that all trees

increased in growth after channelization. However, trees in their reference site did not continue to increase in growth as much as trees in their head-cut (altered) site for the 10 yrs between 1990 and 1999. The differing results may be because Weins & Roberts (2003) had less temporal data to analyse (i.e. we collected trees later and had ten more years of growth data), and it is possible that the trees in their reference site may have grown much faster after 1999. Another possible reason for different results between our studies could be a result of the species analysed; they cored *Q. phellos*, which might respond differently to hydrology than the four oak species in our study.

We offer one possible explanation for inverse relationships to flow. We suggest that historic, seasonal flood pulses maintained anoxic conditions in BLHFs and were a limiting factor on tree growth. Thus, as a result of channelization, soils supplied more oxygen to the roots and allowed the trees to grow more rapidly (Shankman 1996). The adaptations to anaerobic conditions allow BLHF species to thrive where upland species cannot (Middleton 2002); yet, similar to upland species, these BLHF-adapted species grow more when they have more access to oxygen in their roots. These results also support that BLHF species are vulnerable in altered hydrologic conditions because they are specialists, adapted to flood pulsing (Middleton 2002; Richardson et al. 2007).

An interesting observation about response to river height is that trees in REF showed stronger correlations to river gauge height than INV and NON (Table 2). The trees in REF are approximately 25 km upstream from the channelized river, while trees in INV and NON are located directly adjacent to the channelized river. This response is possibly due to changes in the water table. Trees in BLHFs obtain the majority of their water from the water table (Naiman & Décamps 1997; Copenheaver et al. 2007), which is correlated with stream gauge height (Weins & Roberts 2003). The water table dropped significantly in channelized and head-cut portions of the river after channelization, but did not drop in the reference reach (Weins & Roberts 2003). Trees in REF may be influenced by the water table, and thus contribute to the strong river height correlations. Trees in INV and NON may access less water from the lowered water table, explaining less correlation with river gauge height.

Effects of *L. sinense*

Bottomland hardwood forests with altered flood regimes are highly vulnerable to invasion by woody shrubs (Middleton 2002; Richardson et al. 2007; Foard 2014). Once established, invasive shrubs like *L. sinense* significantly reduce native regeneration (Grove & Clarkson 2005; Brantley 2008; Smith et al. 2008; Boyce 2009; Osland

et al. 2009; [Greene & Blossey 2012](#)) and suppress canopy tree growth ([Hartman & McCarthy 2007](#); this study). Thus, invasive shrubs, like *L. sinense*, pose major threats to native forest dynamics and diversity ([Boyce 2009](#)).

The dendrochronology data supply evidence that *L. sinense* is most likely responsible for reduced oak tree growth in BLHFs of the Wolf River, Tennessee, US. After a thorough literature search only one other study determined that an invasive shrub slows canopy tree growth – [Hartman & McCarthy \(2007\)](#). Similar to [Hartman & McCarthy's \(2007\)](#) observations of forests invaded by the shrub *Lonicera maackii* (Rupr.) Maxim. (amur honeysuckle), we discovered that *L. sinense* is likely responsible for reduction in growth of native trees, despite at least three important differences in the approaches between the two studies that could have resulted in different outcomes: (1) we matched tree species and diameters among sites, (2) we investigated growth–climate relationships and (3) we removed significant hydrological signals to isolate the effects of *L. sinense*. Nonetheless, our studies show the same qualitative results that invasive shrubs are detrimental to established canopy trees ([Hartman & McCarthy 2007](#)). Combined, these two studies help broaden our understanding of the impacts of invasive shrubs; not only do invasive shrubs crowd out other small woody species and herbaceous plants resulting in reduced biodiversity, but they also have the ability to impact the structure of the forest canopy.

We suggest the mechanisms by which *L. sinense* reduces tree growth are competition for water or nutrients, different growth habits (evergreen vs deciduous and/or colonial vs individual), lack of herbivory and possible allelopathy. Many studies have supplied evidence of direct competition between *L. sinense* and native plants. When *L. sinense* seedlings compete against native plants, *L. sinense* makes up the largest proportion of survivors in the next growing season ([Merriam & Feil 2002](#); [Greene & Blossey 2012](#)). Dissimilar plants, such as vines, are common within dense *L. sinense* stands, indicating that *L. sinense* has out-competed similar species ([Tilman et al. 1997](#); [Merriam & Feil 2002](#); [Wilcox & Beck 2007](#); [Klock 2009](#)). [Greene & Blossey \(2012\)](#) found evidence that after long-term invasion, *L. sinense* drives mortality of native seedlings. *L. sinense* has lower levels of herbivory than a native shrub in the same family (Oleaceae), *Forestiera ligustrina* ([Morris et al 2002](#)). Also, evidence for allelopathy has been discovered in leaf extract and in leaf-and-root extract ([Grove & Clarkson 2005](#); [Pokswinski 2008](#), respectively). More research should be done to quantify allelopathy of *L. sinense in situ*.

In conclusion, invasive shrubs like *L. sinense* pose major threats to longevity of native BLHFs. Forest integrity, the measure of a forest's ability to support diverse communities and produce timber ([Seymour & Hunter 1999](#)), is

greatly reduced in shrub-invaded forests ([Houston et al. 2010](#)). Many researchers have also shown that regeneration of native woody species is nearly non-existent in invaded forests ([Grove & Clarkson 2005](#); [Brantley 2008](#); [Smith et al. 2008](#); [Boyce 2009](#); [Osland et al. 2009](#); [Greene & Blossey 2012](#)). Furthermore, hydrologic alteration, resulting in dry conditions, greatly reduces native BLHF germination ([Middleton 2002](#)). Thus, invaded forests can become shrub monocultures that support very little biodiversity ([Merriam & Feil 2002](#); [Greene & Blossey 2012](#)).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Correlation matrices for PDSI.

Appendix S2. Correlation matrices for precipitation.

Appendix S3. Correlation matrices for Temperature.

Appendix S4. Correlation matrices for river gage height.

Appendix S5. Table of coarse woody debris for invaded vs. non-invaded sites.

Appendix S6. Raw ring widths for the invaded/channelized site (INV).

Appendix S7. Raw ring widths for the non-invaded/channelized site (NON).

Appendix S8. Raw ring widths for the non-invaded/non-channelized site (REF).