HYDROLOGIC EFFECTS ON DIAMETER GROWTH PHENOLOGY FOR *CELTIS LAEVIGATA* AND *QUERCUS LYRATA* IN THE FLOODPLAIN OF THE LOWER WHITE RIVER, ARKANSAS

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Abstract—Bottomland hardwood (BLH) forests represent an extensive wetland system in the Mississippi Alluvial Valley and southeastern USA, and it is currently undergoing widespread transition in species composition. One such transition involves increased establishment of sugarberry (*Celtis laevigata*), and decreased establishment of overcup oak (*Quercus lyrata*). The ecological mechanisms that control this transition are not well understood. We measured monthly diameter growth with dendrometer bands on 86 sugarberry and 42 overcup oak trees at eight sites in the floodplain of the White River (AR, USA) with differing hydrologic regimes. For both species, growth attenuated earlier at drier sites compared to wetter sites. Overcup oak grew slightly longer through late August, suggesting its growth period extends across both wet and dry periods. In contrast, sugarberry growth rate decreased substantially by mid-July. While these results did not necessarily indicate a mechanism for increased prominence of sugarberry, they suggest sugarberry growing season does not as much coincide with the typically drier period of late summer and may be less affected by these conditions. Overcup oak grows later into the dry season and water table conditions during this period may determine if overcup oak benefits from this relatively extended growth period.

INTRODUCTION

Floodplain forests are valued highly for their ecological functions, which depend upon hydrologic conditions (Sparks 1995). Bottomland hardwood forests (BLH) of the southeast are commonly wetlands, defined by often having hypoxic soil conditions driven by frequently saturated or flooded soils (Patrick 1981). Connectivity to rivers and river flow rates largely control the timing of flooding and soil saturation in many BLH floodplain wetlands. Given the seasonality of river flows and climate, floodplain BLH forests typically transition between wet to dry states. In the BLH forests of the Lower Mississippi Alluvial Valley (LMAV) flooding usually occurs in winter and the early growing season, and soils become drier throughout the summer (Dewey and others 2006). This results in a complex stress regime typical of many non-tidal forested floodplains (Parolin and others 2010), in which saturated conditions transition to water limited conditions through the growing season.

Superimposed upon the natural hydrologic regime, anthropogenic developments have altered the hydrologic cycle leading to changes in BLH forests (King and others 2012). Few large rivers in the United States have natural flow regimes because levees, dams, and other engineering structures affect river flows and exchange with associated floodplains (Merritt and others 2010); these alterations affect tree growth. Studies have demonstrated relationships between BLH tree growth and hydrology (Anderson and Mitsch 2008, Megonigal and others 1997, Mitsch and others 1991), so large alterations in hydrology often affect growth patterns (Gee and others 2014, Reily and Johnson 1982).

Parallel to these changes, species composition has also changed in BLH, tending towards species associated with drier or wetter conditions (Gee and others 2014, Hanberry and others 2012). Multiple mechanisms may be responsible for this change in species composition. One likely mechanism is a reduced disturbance regime, whether from reduced flooding or reduced disturbance from other sources, such as fire and timber harvesting (Oliver and others 2005). Shade tolerant species are generally less flood tolerant (Battaglia and Sharitz 2006), and reduced flooding enables establishment of trees that would otherwise die from flooding (e.g.,

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sugarberry, *Celtis laevigata*; Conner and others 2002). Another possible mechanism is that the shift towards drier conditions creates more favorable growing conditions for some species compared to others. In this study, we investigate this latter hypothesis.

We examined timing of intra-annual diameter growth of wetter-association and drier-association BLH species (overcup oak, *Quercus lyrata* and sugarberry, respectively) with regard to floodplain hydrology. Dendrometer bands are useful for measuring fine-scale growth increments throughout the growing season to examine timing of growth and how growth responds to intra-annual variation in environmental conditions (Keeland and Sharitz 1993). This method was used to determine how growth varied throughout the growing season and how timing of growth was related to site hydrology and species.

METHODS

Study Site

The study was conducted at eight plots in the Dale Bumpers White River National Wildlife Refuge on the White River floodplain in southeastern Arkansas, USA. The White River is 1162 km long and drains a 7.2×10^4 km^2 area of northern Arkansas and southern Missouri. Within the refuge, the active floodplain ranges from 8-14 km wide. The floodplain is often highly connected to the river and becomes inundated seasonally. Flooding is generally extensive from December through June, peaking between March and early June. Conditions generally became dry July-November. The southern portion of the refuge experiences deeper flooding in spring because of backwater flooding from the Mississippi River, but channel incision and entrenchment (i.e., gradual deepening of the main channel with respect to floodplain) of the southern floodplain (Schumm and Spitz 1996) has led to greater depth to water table during the summer (fig. 1). The northern reach of the White River floodplain is less incised and more affected by river flows and headwater events during the summer (fig. 1). This study was conducted in 2014 when conditions were atypically wet in the northern section of the refuge and typical for the southern section of the refuge.

We established eight study plots with contrasting hydrology on these two reaches of the floodplain. Four sites were located in the northern section of the refuge, classified as 'Riverine Backwater' (Klimas and others 2009). Four plots were established in southern zone, also classified as 'Riverine Backwater,' although with a slightly drier vegetation composition (Klimas and others 2009).

Study Species

Overcup oak is a relatively slow growing oak species with shallow roots (often due to association with clayey soils in alluvial wetlands) that generally have later leaf-out than co-occurring species (Solomon 1990). Sugarberry is a shade-tolerant species that is also shallow rooted on wet sites (Kennedy 1990). In a review of species tolerances to water logging, Hook (1984) classified overcup oak as 'highly tolerant' and sugarberry as 'weakly tolerant.'

Measurements

In each plot, four subplots (0.04 ha) were established for assessing stand characteristics and selecting measurement trees. Species and diameter (DBH) were recorded for every tree with DBH > 5.0 cm.

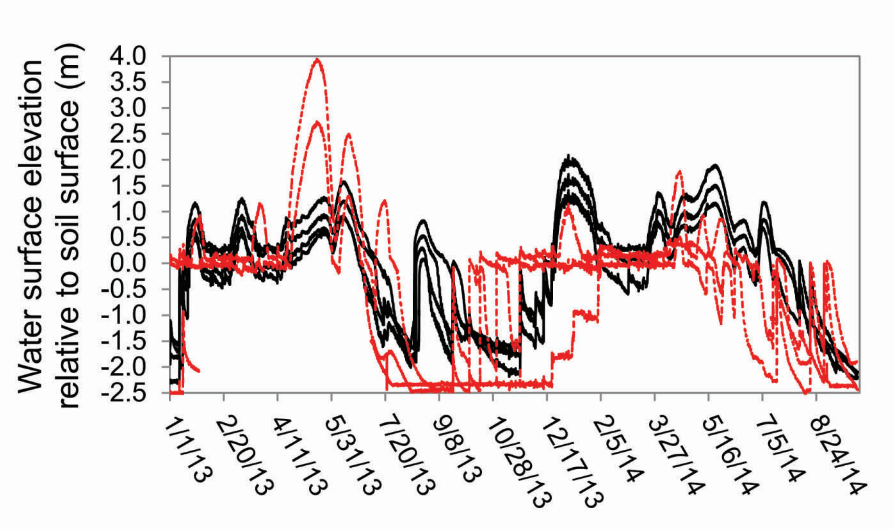

Figure 1—Water levels in plots on the White River floodplain for 2013 and 2014 (study year). The four black lines are for plots on the northern zone of the floodplain and the three red lines are wells in plots in the southern zone.

Stainless steel dendrometer bands (Hall 1944) were installed at 1.4 m height on 216 trees (70 overcup oak and 140 sugarberry). Sizes of banded trees varied considerably (table 1) to represent the range of trees found within the stands. Bands were installed in the summer of 2012 and allowed to settle for a year for accurate measurements (Bower and Blocker 1966, Keeland and Sharitz 1993). Bands were measured with vernier calipers to the nearest 0.1 mm in 2013 and 2014. Measurements were zeroed at the beginning of the 2014 growing season, and we report data from five increments throughout the 2014 growing season (June 25, July 13, August 6, August 23, October 1).

At each plot, a ~2.5 m deep well was installed for monitoring depth to water table with water level recorders (Hobo; Onset Computer Corp., Cape Cod MA, USA), logged at hourly intervals. Relative surface elevation among trees was surveyed with an autolevel (Robert Bosch LLC, Farmington Hills, MI), zeroed with respect to the ground level at the co-located monitoring well.

Analyses

Trees that did not show substantial growth (minimum 0.25 cm in circumference) were excluded because of poor data resolution, which left 42 overcup oak and 86 sugarberry trees remaining. Excluded trees were mostly small and suppressed. Tree diameter increment was compared between species by t-test and compared to diameter for each species by simple correlation. For each tree, data from the dendrometer bands were converted to cumulative fractional growth through the season to examine seasonal diameter growth curves; curve shape indicates timing but not magnitude of differences among trees (i.e., high values do not indicate more growth). Trees were partitioned by size as ‘small’ (< 20 cm for sugarberry, < 35 cm for overcup oak) versus ‘large’ (> 20 cm for sugarberry, > 35 cm for overcup oak) to determine size effects on growth curves. Different criteria were used for each species because of different size distributions. Location within plots was separated based on microtopography. The highest 50 percent of trees were classified as ‘Higher’ and the lower 50 percent as ‘Lower’ with the exception of one site that was classified entirely as ‘Higher’ because it had minimal microtopography and was the least flooded site. These stratifications of the data were used as treatments, with differences tested for each measurement date by 2-sample t-tests ($\alpha = 0.05$). We estimated the growing season started with day of year (DOY) 100, corresponding with the approximate leaf out date estimated from satellite imagery (MODIS phenology products, http://phenology.cr.usgs.gov/), although the actual leaf out date was likely later for overcup oak (Solomon 1990). All analyses were conducted in MATLAB (Mathworks Inc., Natick, MA).

RESULTS

Stand Characteristics

Despite different hydrogeomorphic settings, stand structure was similar across all study areas. All plots had multi-cohort, closed canopy forests (basal area of 30.4 ± 10.2 m^2 ha^{-1}; mean ± SD). Dominant species were *Celtis laevigata, Quercus lyrata, Carya aquatica, Liquidambar styraciflua, Fraxinus* spp.*, Quercus texana,* and *Ulmus americana.* The study species, sugarberry and overcup oak, accounted for 17 and 27 percent of basal area, and 20 and 13 percent of all stems (605 ± 215 stems ha^{-1} for trees with DBH > 5 cm), respectively, together accounting for 16 to 92 percent of all stems per plot.

Table 1—Sample sizes (N) and tree sizes (diameter at breast height; DBH) and growth (diameter increment; DI) for *C. laevigata* and *Q. lyrata* trees with dendrometer measurements from the North (wetter) and South (drier) zones of the White River floodplain. Small, Med[ium] and Large refers to trees with DBH < 20 cm, 20-35 cm, and > 35 cm, respectively

		Celtis laevigata			*Quercus lyrata*		
Site	*Size*	*N*	*DBH (cm)*	*DI (cm yr^{-1})*	*N*	*DBH (cm)*	*DI (cm yr^{-1})*
North	Small	14	16.0 ± 1.0	0.6 ± 0.4	0	No Data	
North	Med	18	27.0 ± 0.9	0.6 ± 0.4	3	31.6 ± 5.2	0.7 ± 0.4
North	Large	5	43.3 ± 3.4	0.8 ± 0.5	12	54.3 ± 14.0	2.2 ± 1.3
South	Small	29	3.9 ± 4.2	0.6 ± 0.3	9	20.9 ± 2.4	1.1 ± 0.3
South	Med	14	26.1 ± 4.8	0.8 ± 0.5	3	28.2 ± 4.2	1.3 ± 0.7
South	Large	7	44.3 ± 5.7	0.8 ± 0.5	15	59.7 ± 12.9	1.5 ± 0.5

Annual Growth Increments

The magnitude of annual diameter increment and its relationship with size differed between species. The 2014 diameter increment for overcup oak exceeded sugarberry ($p < 0.0001$). For sugarberry, diameter increment was not related to tree diameter ($r = 0.11$, $p = 0.33$), but for overcup oak, diameter increment was positively correlated to tree size ($r = 0.36$, $p = 0.024$). These relationships held across both northern and southern plots (table 1).

Intra-annual Growth Trends

Dendrometer data indicated differences in growth trends between species and hydrogeomoprhic setting. Upon the first dendrometer measurements (DOY 176), 75 ± 17 percent (mean ± SD) of annual growth had occurred in sugarberry trees (fig. 2). In contrast, only 56 ± 18 percent of overcup oak growth had occurred by this time. Accordingly, a lower proportion of late-season growth occurred in sugarberry compared to overcup oak. Growth increments in overcup oak remained steady until DOY 235. Neither species had substantial growth in the last measurement period (DOY 235 to DOY 273). Growth trends were not size dependent for either species (fig. 2A), and showed minor, statistically insignificant effects of microtopographic position (fig. 2B). Stratifying the data by river reaches (north versus south) resulted in separation among means (fig. 2C). For multiple periods, t-tests indicated significant differences in cumulative fractional growth between the northern and southern sites for overcup oak (DOY 176, $p = 0.0082$; DOY 217, $p = 0.0027$) and sugarberry (DOY 176, $p = 0.03$; DOY 194, $p = 0.01$, DOY 217, $p = 0.01$). While our results may suggest that the northern site has a longer growing season, lack of precise north/south leaf-out dates prevents inferring total length.

DISCUSSION

Growth phenology varied by species and by site conditions. For both species, a greater proportion of growth occurred early in the season for the drier, southern sites (fig. 2C). In contrast, the wetter, northern sites (fig. 1) sustained growth later into the season. Phenological differences between sites appear to have been related to differences in hydrology. Greater connectivity between floodplain and river allows for flood waters to replenish soil water and maintain a higher water table. In contrast, the southern reach of the river lost connectivity with the floodplain and the water table lowered with summer recession. A study using sapflow probes to examine functioning of these two species within the same study plots in the refuge found agreement with this study; trees in one of the southern sites had signs of reduced function or early senescence that were not apparent in a northern site (Allen and others 2014).

Species differences in growth timing suggest differences in their response to environmental conditions, which may affect species interactions and community changes. While sugarberry has been classified as ‘weakly flood tolerant’ and overcup oak as ‘highly flood tolerant’, based on their typical zonation (Hook 1984), our results suggest that these classifications oversimplify their habits. Further testing is needed, but because the majority of sugarberry growth occurred in the early portion of the season, they showed tolerance to deep flooding in our study year. However, sugarberry grew less in late summer, coincident with drier conditions. Dormancy or a partial state of dormancy is a common means of avoiding water deficits but differs from tolerance because tolerance is generally associated with morphologic adaptations that allow function to be less affected during stressful conditions but otherwise would limit maximum photosynthesis (Lambers and others 2006). In contrast to sugarberry, overcup oak grew during both the early (flooded) and late portion of the growing season. This shift toward later season growth can be considered an adaptation of overcup oak to flooding in spring, and its flood tolerance may be viewed more appropriately as flood avoidance, which has been shown also for overcup oak rooting habits (Burke and Chambers 2003). For overcup oak, later season growth may lead to increased sensitivity to seasonal dynamics of water tables and a need for adaptation to multiple stressors (wet and dry), which is uncommon (Niinemets 2010). Confounding inferences on tolerance and avoidance inferences, there may be inherent differences in carbohydrate usage or storage, and growth does not necessarily reflect tree function or photosynthetic activity.

Similar to reduction in other disturbances (Oliver and others 2005), elimination of, or reduction in, flooding has been shown to favor sugarberry (Gee and others 2014, Hanberry and others 2012). This may be related to shade tolerance of sugarberry (Battaglia and Sharitz 2006), which also allows recruitment in the absence of flood disturbance (i.e., extended flooding kills sugarberry trees; Broadfoot and Williston 1973). Further, presence and success of saplings are not just limited by site conditions, but are also limited by seed production, dispersal, and fecundity (Clark and others 1999, Streng and others 1989). Our results suggest the greater shade tolerance of sugarberry (versus overcup oak) by the lack of size differences in diameter growth increment for sugarberry. For overcup oak trees, larger trees likely receive more sunlight and had greater diameter growth. While recruitment and disturbance regimes are certainly relevant to changing species composition, phenological avoidance of stress can be important for defining species interactions (Lovell and Menges 2013) and could be an additional mechanism that is advantageous to sugarberry in many settings, including novel

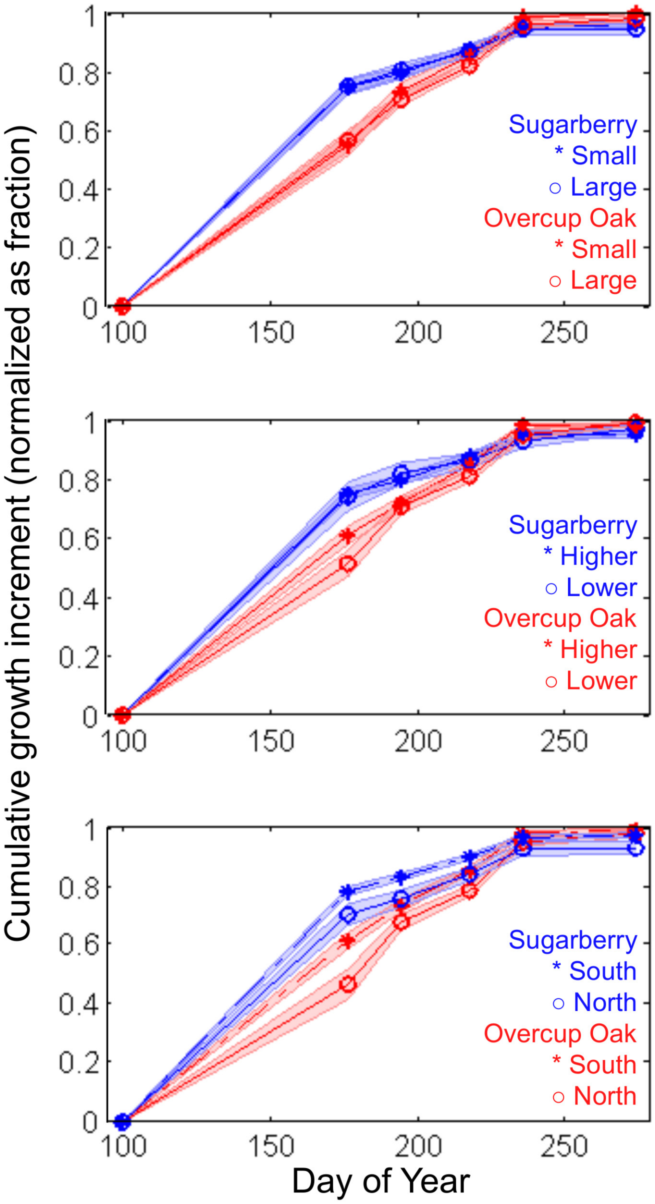

Figure 2—Cumulative fractionational growth curves derived from dendrometer band measurements of sugarberry *(Celtis laevigata)* **and overcup oak (***Quercus lyrata***) trees on the White River floodplain from the 2014 growing season. Comparisons are of (a) tree diameters, (b) tree relative elevations within plots, and (c) plot location on the wetter, northern plots or drier, southern plots.**

hydrogeomorphic conditions of BLH systems. Because sugarberry grew little during the late season in 2014, thereby demonstrating avoidance of the dry conditions, while overcup oak did not, this may be a relative benefit to sugarberry with respect to hydrologically altered BLH forests with drier conditions in late growing season. Inter-annual variations in sub-annual growth trends must be investigated to develop a fuller understanding of how phenotypic plasticity interacts with hydrologic variability at various time scales in these forests to control species composition.

CONCLUSIONS

Dendrometer data from 128 trees on the White River floodplain suggest that sugarberry grows rapidly in the early growing season while overcup oak grows more steadily and later into the growing season. For both, growth decreases earlier in drier sites. These phenological differences between species indicate potential differences in mechanism for response to stresses associated with transitioning from wet to dry conditions.

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