

EFFECT OF FLOOD REGIME ON TREE GROWTH IN THE FLOODPLAIN AND SURROUNDING UPLANDS OF THE WISCONSIN RIVER

KATHARINE I. PREDICK,^{a*} SARAH E. GERGEL^b and MONICA G. TURNER^a

^a *Department of Zoology, University of Wisconsin, Madison, WI 53706, USA*

^b *Department of Forest Sciences, University of British Columbia, Vancouver, BC, V6T 1Z4 Canada*

ABSTRACT

Flood regime and vegetation flood tolerance interact to influence tree growth in riverine landscapes. We studied tree growth in floodplain and upland forests of the Wisconsin River. About a century ago, levees set back from the river were constructed on this floodplain. The levee restricts some floodplain area from overbank flood events, but leaves a portion of active floodplain still inundated by floods. We addressed two questions: (1) how do growth rates of flood-tolerant and flood-intolerant tree species in the floodplain differ with flood regime? (2) At the stand level, how does growth rate differ with flood regime and between floodplain and upland areas? Annual tree growth rates from 1991 to 2000 were determined from tree increment cores for both individual species and stands. Tree growth rates of individual species varied between flood regimes. The most flood-tolerant species (*Betula nigra* and *Fraxinus pennsylvanica*) grew faster in areas with active flooding, while the growth of less flood-tolerant species (*Quercus velutina* and *Q. ellipsoidalis*) was depressed in swales and active floodplain. However, stand-level tree growth did not differ between the floodplain and upland, or between flood regimes within the floodplain. Therefore, variation in the growth of individual species may not scale up to create differences in stand-level tree growth because forest community composition varies spatially with flood regime. We suggest that growth rates are similar among sites because each community comprises of species adapted to their current flood regime. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: basal area increment; flood tolerance; tree production; levee; microtopography; restricted flooding; radial growth; riparian forest

Received 31 October 2007; Revised 11 March 2008; Accepted 17 March 2008

INTRODUCTION

Flood regime is an important driver of species composition and ecosystem processes in floodplain forests. Productivity and vegetation growth vary among species and are influenced by the frequency and severity of floods in active floodplains (Brinson, 1990). Floodplains can be highly productive and are typically assumed to have higher productivities than upland forests (Brinson, 1990; Naiman and Décamps, 1997). However, few studies directly compare floodplain and upland productivity between stands in the same river system (but see Johnson and Bell, 1976).

The role of flooding is more frequently investigated by measuring productivity or growth before and after a change to the hydrologic regime. Both river regulation and dam construction have been shown to decrease floodplain tree growth and productivity (Reily and Johnson, 1982; Bakhiev and Treshkin, 1994; Middleton and McKee, 2005), and hydrologic restoration can increase productivity (Anderson and Mitsch, 2006). A review of temperate, southern bottomland forests suggests that floodplain productivity often declines due to changes in the hydrologic regime, typically because the vegetation community is not in equilibrium with the altered hydrology (Meronigal *et al.*, 1997). Anthropogenic modifications to flood regime are common; 98% of North American rivers are influenced by human modifications (Vitousek *et al.*, 1997) and 65% of large rivers worldwide are influenced by dams (Nilsson *et al.*, 2005). When flood regimes are altered by dams or levees, patterns of vegetation, sediment deposition and nutrient processing are altered (Naiman and Décamps, 1997).

*Correspondence to: Katharine I. Predick, School of Natural Resources, University of Arizona, Biological Sciences East, 1311 E. 4th St., Tucson, AZ 85721-0043, USA. E-mail: kipredick@arizona.edu

Patterns of growth and productivity within floodplains are typically attributed to the spatial distribution of floods. Floods may decrease productivity by causing root damage, or augment it by increasing nutrient availability (Brinson, 1990). Flooding negatively impacts vegetation growth when stagnant water creates anoxic conditions around roots (Odum *et al.*, 1979; Mitsch and Rust, 1984; Megonigal *et al.*, 1997). However, sediment deposited by floods can increase growth by providing nutrient subsidies (Mitsch *et al.*, 1979; Brown and Peterson, 1983; Krauss *et al.*, 2006), particularly in rivers that drain agricultural areas. Flood events can also enhance soil fertility by increasing decomposition rates (Baker *et al.*, 2001) and phosphorous availability in floodplain soil (Wright *et al.*, 2001).

Indeed, flood events have been demonstrated to both increase (Conner and Day, 1976; Taylor *et al.*, 1990; Robertson, 1992; Burke *et al.*, 1999) and decrease (Brown and Peterson, 1983; Mitsch *et al.*, 1991; Megonigal *et al.*, 1997; Dudek *et al.*, 1998) floodplain vegetation growth. When viewed within an entire growing season, these subsidies and stresses may offset one another and eliminate any relationship between flood characteristics and productivity or tree growth (Mitsch and Rust, 1984; Dudek *et al.*, 1998). Individual trees may change growth rates or the allocation of resources to roots versus shoots in response to flooding and, in time, permanent physiological changes can occur after flood regimes are altered (Kozłowski and Pallardy, 1996; Kozłowski, 2002). Furthermore, the influence of flooding on vegetation growth varies among species with different flood tolerances. Flood-tolerant tree species have adaptations, such as adventitious roots, stem buttressing, root flexibility and root and stem aerenchyma, which allow them to withstand root anoxia, both as seedlings and adults. These species can establish and grow on floodplain sites which are too inhospitable for flood-intolerant vegetation (Kozłowski, 1984; Kozłowski, 2002).

In this study, we used the highly modified Wisconsin River floodplain to address several questions about the interaction between tree growth and flood patterns. About a century ago, levees were constructed on this floodplain set back from the river. The levee restricts some of the floodplain from overbank flood events, but leaves a portion of active floodplain still inundated by floods. Comparing floodplain stands on both sides of the levee provides an excellent opportunity to examine the long-term impact of flood alterations on tree growth.

First, we examine the growth rates of three species which exhibit a range of flood tolerance, to address the question: (1) How do growth rates of individual trees of the flood-tolerant and flood-intolerant tree species in the floodplain differ with flood regime? *B. nigra* is a species with high flood tolerance that can withstand flood events as seedlings and adults (Grelen, 1990; McIninch *et al.*, 1994). The moderately flood-tolerant *F. pennsylvanica* can withstand flooding as an adult (Kennedy, 1990), whereas seedlings survive only limited flooding (Hosner, 1958). Lastly, *Q. velutina* and *Q. ellipsoidalis* are representative flood intolerant species, both as seedlings and adults (Sander, 1990). We hypothesized that flood-tolerant species would grow most rapidly in active floodplain, whereas flood-intolerant species would grow faster in restricted floodplain and upland locations. Second, we focused on differences in growth between upland and floodplain forest stands and the effect of anthropogenically restricted flood regime on stand-level growth. We ask: (2) At the stand-level, how does growth rate differ with flood regime and between floodplain and upland areas? We hypothesized that stand growth rates would be highest in active floodplain.

METHODS

Study sites

This study was conducted in the upland and floodplain of the Wisconsin River (Figure 1). In this region, precipitation averages 81 cm and the mean annual temperature is 7°C (Martin, 1965). Alluvial deposits from the Cambrian (500 million years b.p.) as well as 12 000 yr old glacial lake deposits cover the region (Curtis, 1959). Upland soils are clay, silt and sand loams or simply sand. Floodplain soils are predominantly sand, with a small amount silt and clay loam (Curtis, 1959). *F. pennsylvanica*, *Ulmus americana* and *Acer saccharinum* are the most common tree species on the floodplain (Turner *et al.*, 2004), whereas *A. saccharum*, *Q. alba*, *Q. rubra* and *Q. velutina* dominate in upland stands.

River flow in this reach averages $360 \text{ m}^3 \text{ s}^{-1}$ during the spring and $120 \text{ m}^3 \text{ s}^{-1}$ in the fall. Annual flow is highly regulated by upstream dams, which reduce flood peaks and increase base flow relative to undammed conditions

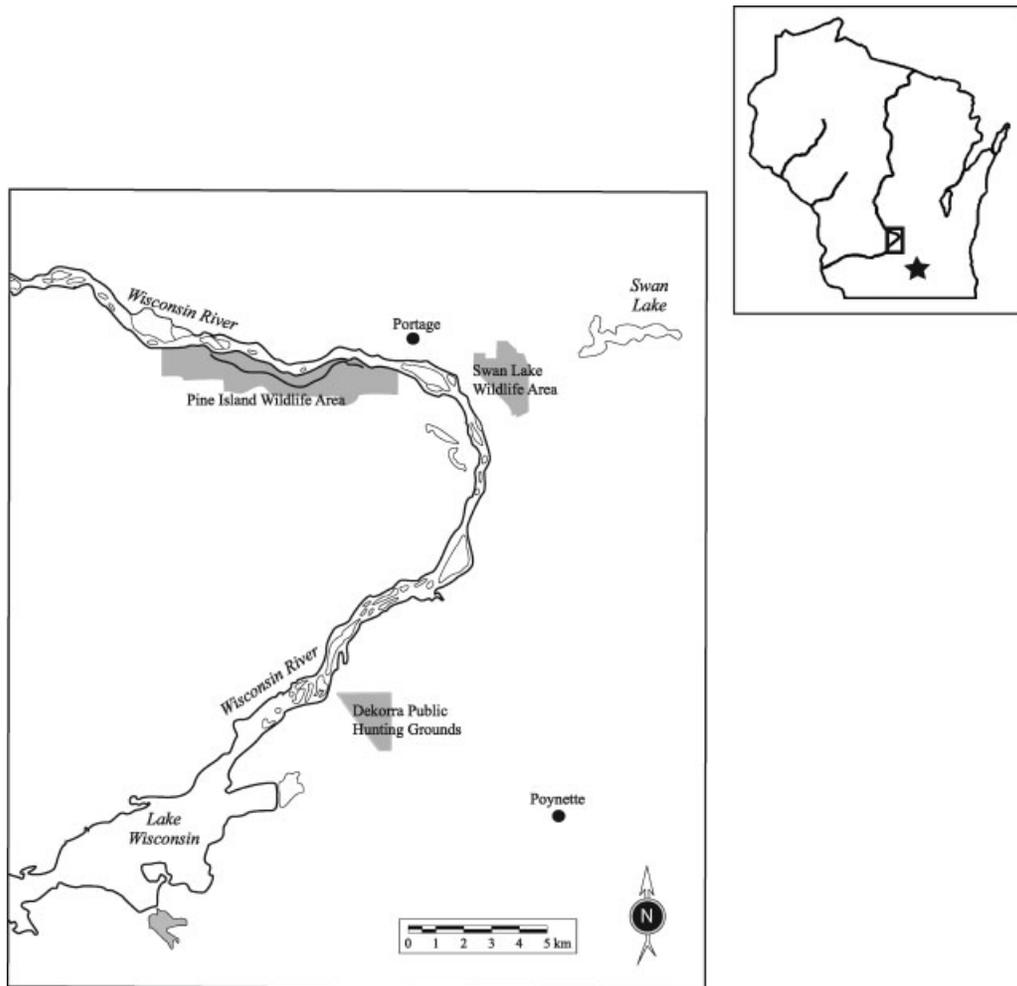


Figure 1. Map of study sites along the Wisconsin River in south-central Wisconsin. All floodplain plots and one upland plot were all located in the Pine Island Wildlife area, where the levee is indicated by dark line. The remaining upland plots were located in the Swan Lake Wildlife area and Dekorra Public Hunting Grounds

(Dixon and Turner, 2006). Large patches of floodplain forest border over 75% of the river bank in this reach, resulting in high hydrologic connectivity between the floodplain and river (Freeman *et al.*, 2003). Undulating ridge and swale topography characterizes the floodplain, which influences flood frequency and creates a mosaic of vegetation communities (Liegel, 1988).

A setback levee constructed approximately 100 years ago completely eliminated overbank flooding, excepting one breach in 1938, on a portion of the floodplain (Gergel *et al.*, 2002). Ponds can develop outside the levee due to high groundwater tables (Pfeiffer, 2001), but long-term flooding is uncommon. Gergel *et al.* (2002) used HEC-RAS modelling software to estimate the flood stage, power and extent on both sides of the flood control levee and on floodplain with no levee present. They found the number of flooding events and flood durations were similar between active floodplain sites inside the flood control levee and those without levees present, but sites in restricted floodplain (outside the flood control levee) experienced no flooding in most years. Flood shear stress was $1.2 \text{ N m}^{-2} \pm 0.1 \text{ SE}$ on active floodplain sites with a levee present and $3.2 \text{ N m}^{-2} \pm 0.3 \text{ SE}$ active floodplain sites without a levee, suggesting that sediment deposition onto leveed active floodplain sites due to flooding is limited (Gergel *et al.*, 2002).

A difference in tree species composition was also observed between active and restricted floodplain sites by Gergel *et al.* (2002). They assessed vegetation composition using a modified importance value, or the sum of the

relative basal area and relative abundance of each species. All sites were subjected to an active flood regime before the levee was built. They assume that species composition was similar among sites before levee construction and differences observed a century later are due to differences in flood regime. Importance values of *F. pennsylvanica* were 0.44 ± 0.09 SE in the active floodplain and 0.04 ± 0.02 SE in the restricted flood regime. Conversely, the importance values of *Q. velutina* and *Q. ellipsoidalis* were 0.49 ± 0.1 in the active floodplain and 0.87 ± 0.1 in the restricted floodplain. Importance values of *B. nigra* did not differ between active and restricted flood regimes (0.2 ± 0.08 SE and 0.2 ± 0.6 SE, respectively), and no species differed between leveed and unleveed active floodplain sites. This suggests that tree composition shifted towards more flood intolerant species in restricted floodplain after levee construction (Gergel *et al.*, 2002).

The differences in vegetation composition between active and restricted floodplain suggest that many individuals established after the levee was installed. However, *F. pennsylvanica* and *B. nigra* often live 100 years (Grelen, 1990; Kennedy, 1990), and *Q. velutina* and *Q. ellipsoidalis* can live up to 200 years (Sander, 1990). Therefore, this study likely includes individuals that established both before and after the levee was constructed. We expect that individuals present before levee construction altered their growth rates or root:shoot allocation in response to altered flooding conditions (Kozlowski and Pallardy, 1996; Kozlowski, 2002). Furthermore, we expect the tree species that established after levee construction and their growth rates also reflect the restricted flood regime.

Environmental variables

Daily maximum and minimum temperatures from January 1, 1991 to December 31, 2000 were obtained from the Midwestern Regional Climate Center. Temperature was used to determine the approximate dates of the growing season in each year. The growing season was defined to be between the last frost in the spring (defined as the last day when the average temperature was 0°C) and the first frost date in the fall. Calculations of the Palmer drought severity index (PDSI) for the south central region of the state were obtained from the Wisconsin State Climatology Office. The PDSI provides an indicator of moisture availability over time based on precipitation and temperature, positive values indicate moisture excess while negative values indicate drought (Heim, 2002).

Growing season and flow data were used to determine the number of days each plot was inundated during the growing season each year. Daily flow rates of the Wisconsin River from 1991 to 2000 were obtained from United States Geological Survey gaging station 05404000 at Wisconsin Dells. This gage is just upstream from the Pine Island State Wildlife Area. The largest flood in the 10 years examined was a 20-year flood event, which occurred in 1993. On floodplain plots, the number of days of flood inundation for each year was calculated using the United States Geological Survey HEC-RAS model by Gergel *et al.* (2002) and mean elevation and distance from the river were also calculated (Table I).

Table I. Sample size and average characteristics of active floodplain, restricted floodplain and upland plots. Error values represent one standard error.

	Active floodplain	Restricted floodplain	Upland
Number of plots sampled	14	15	14
Number of trees sampled	111	178	119
Average distance from river (m)*	224 ± 61	565 ± 62	—
Median distance from the river (m)*	154	517	—
Mean elevation (m)*	244.2 ± 0.85	244.1 ± 0.53	—
Stem density (stems ha^{-1})	746.5 ± 137.3	821.7 ± 82.8	718.5 ± 87.9
Basal area ($\text{m}^2 \text{ha}^{-1}$)	24.2 ± 3.82	31.8 ± 5.1	42.0 ± 6.4
Plot BAI ($\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$)	0.88 ± 0.086	0.90 ± 0.11	0.89 ± 0.13
Tree species richness	2.6 ± 0.2	3.2 ± 0.2	2.6 ± 0.3
Average percent of each plot comprised of:			
<i>B. nigra</i>	$14 \pm 6\%$	$3 \pm 1\%$	$2 \pm 2\%$
<i>F. pennsylvanica</i>	$24 \pm 6\%$	0%	0%
<i>Q. velutina</i> and <i>Q. ellipsoidalis</i>	$6 \pm 6\%$	$25 \pm 4\%$	$36 \pm 9\%$

*Data from Gergel *et al.* (2002).

Species-level sampling

Floodplain sites of the Wisconsin River were located just west of Portage, WI in the Pine Island State Wildlife Area. Between 29 and 34 individuals of each of three tree species, *F. pennsylvanica*, *B. nigra* and *Q. velutina*, were sampled in both the active and restricted floodplain. However, as *Q. velutina* often hybridizes with *Q. ellipsoidalis*, making them difficult to separate in the field, we considered these samples a composite of both species.

Sampling was done along four of the random transects running perpendicular to the river established by Gergel *et al.* (2002). Only trees larger than 5 cm diameter at breast height (dbh) were sampled. Individuals were chosen at random intervals along the transects, but outside of plots used for stand-level sampling. All individual trees of each species sampled were located at least 20 m apart, except for *F. pennsylvanica*; because it was so scarce in the restricted floodplain, every tree encountered was sampled. The microtopographic position (i.e. ridge, swale, or flat) of each tree was recorded. Ridges were defined as a relative increase in elevation compared to surrounding areas, while swales were a relative decrease. Areas were classified as flat when no discernable difference was observed compared to surrounding areas or when a tree was located on a slope adjacent to a ridge or swale.

Stand-level sampling

Plots were sampled in active and restricted floodplain in 2001, along the same transects used for species-level sampling. All plots were at least 40 m apart and have been continuously forested since the 1930s (Freeman *et al.*, 2003). Upland plots were established outside the 100-year floodplain, as indicated by US Federal Emergency Management Agency (FEMA) maps. One plot was located near the Pine Island Wildlife Area, upland of the leveed sites. Three plots were located in Swan Lake Wildlife Area just east of Portage, WI and ten plots were located in the Dekorra Public Hunting Grounds, located 8 miles northwest of Poynette, WI. Upland stands were all sampled in 2002. Upland plots were also arranged along random transects and spaced at least 40 m apart.

A total of 43 plots were sampled, 15 in restricted floodplain and 14 each in active floodplain and upland. All plots were at least 25 m from roads and located in areas that appeared undisturbed, with no apparent signs of agriculture or logging. Plots were circular, with a 10 m diameter and an area of 78.5 m². Plot sizes were slightly smaller than 100 m², an often recommended minimum size (Mueller-Dombois and Ellenberg, 1974), but the circular plot shape reduces edge effects (Sala and Austin, 2000). Additionally, our observations are similar to those obtained from larger plots in the same stand (Turner *et al.*, 2004). Within each plot, each tree was identified to species and its dbh recorded. The microtopography of each plot was recorded (i.e. ridge, swale or flat). Stem density and total basal area were calculated for each plot.

Basal area increment (BAI)

Two perpendicular increment cores were obtained using an increment borer from each tree sampled. Trees with multiple stems emerging from the same root structure were considered to have multiple boles, and for trees with multiple boles below breast height, two perpendicular cores were taken from each bole, and individually recorded. Three bark width measurements were made on each cored tree using a bark gage.

Each core ($n = 906$) was mounted in a wood block and sanded. Cores were then scanned and imported into the WinDENDRO program (Regent Instruments, 1998) where the annual growth increment was measured for each of 10 years (2000–1991). The annual increments from paired cores from the same individual were averaged. The dbh was corrected by subtracting the average bark width from each tree. The total basal area (BA_t) of each tree was calculated using the equation

$$BA_t = \pi \left(\frac{\text{corrected dbh}}{2} \right)^2 \quad (1)$$

The annual BAI for each individual (from 1991 to 2000) was calculated using the equation

$$BAI = \pi (r^{2n} - r^{2n-1}) \quad (2)$$

where r is the tree radius and n is the year of ring formation (Duschesne *et al.*, 2002). When a tree had multiple boles, the annual BAIs for each bole were summed to produce a BAI for the entire tree. For stand-level comparisons, total plot BAI was calculated by summing the BAIs of all trees in the plot.

Relative BAI

Relative BAI (RBAI) was calculated using the equation

$$\text{RBAI}_y = \frac{\text{BAI}_y}{\text{BA}_{y-1}} \quad (3)$$

where RBAI_y is the RBAI of a tree in a given year, BAI_y the BAI of a tree in a given year and BA_{y-1} is the total basal area of a tree in the previous year.

BAI provides a more useful measure of tree growth rates than radial growth (Visser, 1995), although BAI can be influenced by differences in tree size. RBAI standardizes growth by size for all individuals, correcting for the influence of tree diameter (Disalvo and Hart, 2002). Increases in BAI indicate a tree is accumulating more biomass than in previous time periods, while increases in RBAI indicate biomass accumulation in relation to the biomass present.

Statistical analyses

Statistical analyses were done using the SAS program (SAS Institute, 1996). BAI values were normalized using a natural log transformation and RBAI values were normalized using an arcsine square root transformation. Repeated measures ANOVAs were used to compare differences in individual tree growth (BAI and RBAI) between floodplain sites with active and restricted flood regime. The response of individual species to flood intensity was assessed in a repeated measures ANOVA comparing tree growth to microtopographic position. At the stand level, differences in growth between active floodplain, restricted floodplain and upland sites were compared using repeated measures ANOVA. Additionally, the role of flood intensity was examined in active and restricted floodplain stands using distance from the river, plot elevation, microtopography and annual number of days inundated in the current and previous year (as determined by HEC-RAS modelling) as indicators. Tukey's test was used to compare the means among treatments. We considered differences significant when $\alpha \leq 0.05$.

RESULTS

The abundance of tree species varied among upland, active floodplain and restricted floodplain stands. The most abundant tree species located in active floodplain stands were *B. nigra* and *F. pennsylvanica*, which comprised 23% and 18% of our observations, respectively. In floodplain stands with restricted flood regimes, 52% of the trees observed were *A. rubrum* and *Q. bicolor* comprised 15% of the observations. In upland stands, *Q. alba* comprised 29% of our observations, while 23% were *Q. velutina* and *Q. ellipsoidalis*. Plot stem density averaged 762 ± 0.79 SE (stems ha^{-1}) across all sites, and did not significantly differ among stand locations, $F(2, 40) = 0.29$, $p = 0.75$ (Table I). The total tree basal area averaged 32.7 ± 4.1 SE ($\text{m}^2 \text{ha}^{-1}$) and also did not differ significantly among stand locations in an ANOVA, $F(2, 40) = 3.03$, $p = 0.06$; however, a Tukey's test showed significantly lower basal area in active floodplain than in the upland (Table I). Seven of the 10 years examined in this study were considered unusually moist by the PDSI. The PDSI averaged 1.97 ± 0.9 SE (year^{-1}) during this study, and no droughts occurred.

Growth rates of flood-tolerant and flood-intolerant tree species

The 10 year (1991–2000) average BAIs of *F. pennsylvanica*, *B. nigra* and *Q. velutina* and *ellipsoidalis* ranged between 1145 and 2528 ($\text{mm}^2 \text{tree}^{-1} \text{year}^{-1}$), while the average RBAIs ranged between 0.042 and 0.088 ($\text{mm}^2 \text{mm}^{-2} \text{tree}^{-1} \text{year}^{-1}$) over the same time period. Repeated measures ANOVAs showed that species was a significant predictor of both BAI, $F(2, 166) = 18.38$, $p < 0.0001$ and RBAI $F(2, 166) = 5.68$, $p < 0.0001$. A Tukey's

test indicated that BAIs differed among all species, with *Q. velutina* and *ellipsoidalis* growing the fastest and *F. pennsylvanica* growing the slowest (Figure 2A). A Tukey's test among species RBAI indicated a difference between the fast-growing *B. nigra*, and the slower growing *Q. velutina* and *ellipsoidalis*; however, neither of these species had growth rates significantly different than *F. pennsylvanica* (Figure 2B).

A repeated measures ANOVA showed that the BAI of *B. nigra* was higher when subjected to active flood regimes than restricted flood regimes, $F(1, 52) = 4.06$, $p = 0.0490$ (Figure 3A). A significant interaction was also found between flood regime and microtopography, $F(2, 48) = 4.76$, $p = 0.0130$. This interaction was due to rapid tree growth on ridges in floodplain with an active flood regime and depressed growth on ridges subjected to a restricted flood regime. In this species, microtopography was a significant predictor of RBAI, $F(2, 51) = 5.35$, $p = 0.0078$, with growth rates greater in swales than on ridges; trees on flat positions had intermediate growth (Figure 3B).

In *F. pennsylvanica*, a repeated measures ANOVA of RBAI with flood regime and microtopography indicated faster tree growth in floodplain with a restricted flood regime, $F(1, 57) = 4.11$, $p = 0.0474$. Additionally, there was an interaction between flood regime and microtopography, $F(2, 57) = 3.59$, $p = 0.0341$ (Figure 4), due to suppressed growth in swales subjected to an active flood regime. The same analysis of RBAI in *Q. velutina* and *Q. ellipsoidalis* also indicated an interaction between flood regime and microtopography, $F(2, 46) = 3.43$,

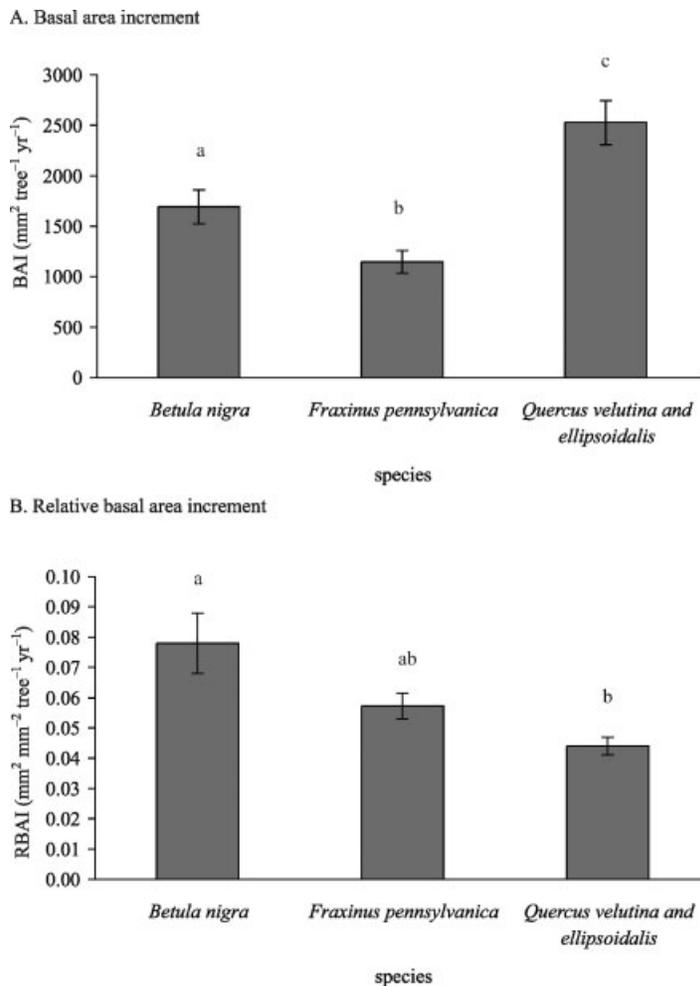
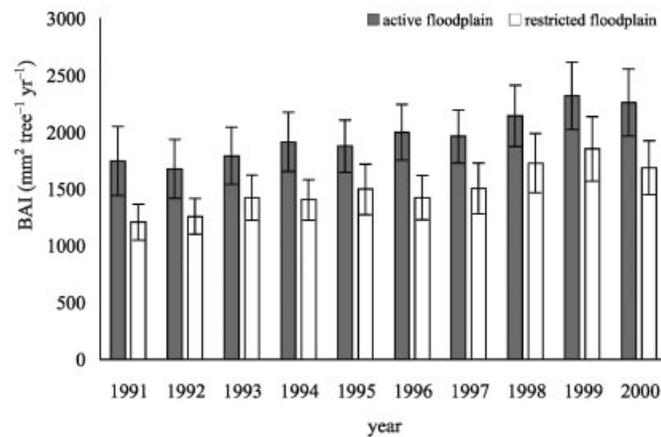


Figure 2. Annual BAI (A) and annual RBAI (B) averaged for 10 years (1991–2000) in active and restricted floodplain along the Wisconsin River for *B. nigra*, *F. pennsylvanica* and *Q. velutina* and *ellipsoidalis*. Error values represent one standard error.

A. Basal area increment



B. Relative basal area increment

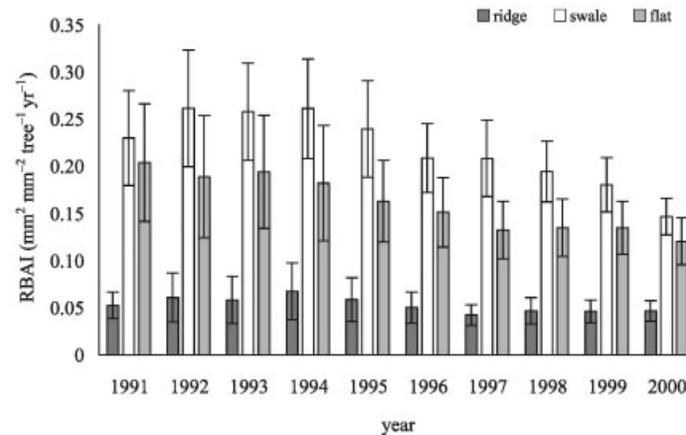


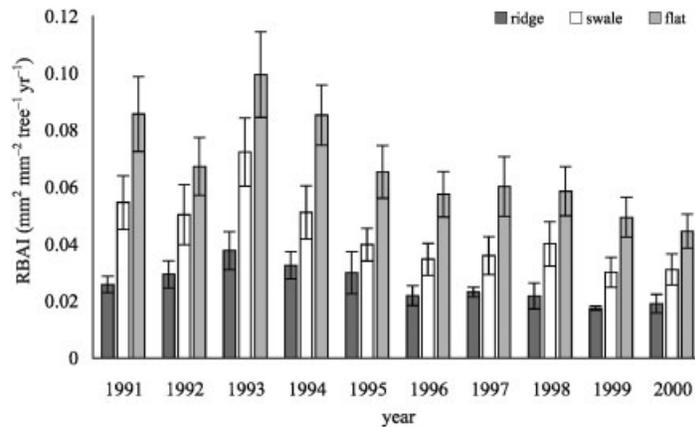
Figure 3. Annual average growth rates of *B. nigra* for 10 years (1991–2000) represented as (A) the BAI between active and restricted floodplains and (B) the RBAI located on three microtopographies. Error bars represent one standard error

$p = 0.0409$ (Figure 5). The significance of this interaction is driven by slow growth on ridges in floodplain with active flooding (Figure 5A) and average growth on ridges in floodplain where flooding is restricted (Figure 5B).

Stand-level tree growth rates

The average plot BAI of upland stands was 0.885 ± 0.13 SE ($\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$). The plot BAI of floodplain stands subjected to an active flood regime averaged 0.884 ± 0.09 SE ($\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$) while those of floodplain stands with a restricted flood regime averaged 0.895 ± 0.11 SE ($\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$). A repeated measures ANOVA indicated no significant difference in the plot BAI among stands in these three locations, $F(2, 40) = 0.06$, $p = 0.9382$ (Figure 6). No significant difference in tree growth, measured as plot-level BAI, were observed between stands subjected to active and restricted flood regimes, $F(1, 27) = 0$, $p = 0.9699$ (Figure 6). Furthermore, no predictors related to flood intensity were significant predictors of plot BAI, including: the plot distance from the river, $F(1, 20) = 0.54$, $p = 0.4720$, mean elevation, $F(1, 20) = 1.45$, $p = 0.2430$, microtopography, $F(3, 20) = 1.61$, $p = 0.2191$ and annual number of days inundated in the current $F(1, 20) = 0.01$, $p = 0.9250$ and previous year $F(1, 20) = 0.01$, $p = 0.8722$.

A. Active floodplain



B. Restricted floodplain

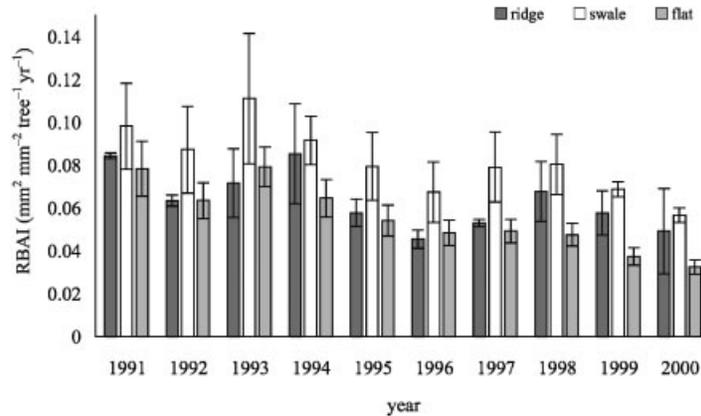


Figure 4. The annual average RBAI of *F. pennsylvanica* located on three microtopographies, within the (A) active floodplain and the (B) restricted floodplain. Error bars represent one standard error

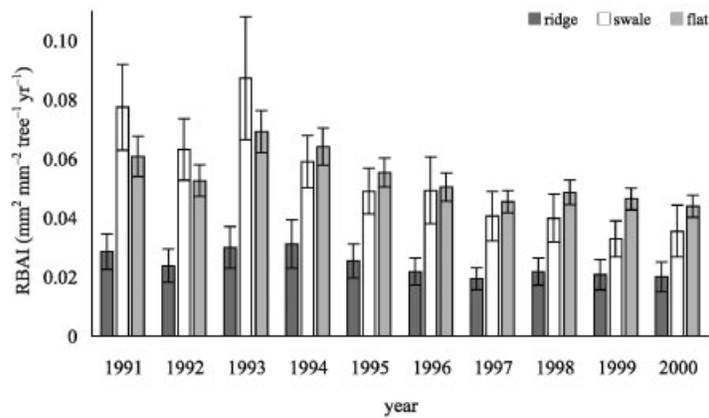
DISCUSSION

Growth rates of flood-tolerant and flood-intolerant tree species

We found growth differences among species with different flood tolerances. The different responses of *B. nigra*, *F. pennsylvanica* and *Q. velutina* and *Q. ellipsoidalis* are likely related to the interaction between flood regime and the flood tolerance of each species. The influence of fine-scale variations in flood frequency on these species is suggested by the importance of microtopography in explaining tree growth. Elevation differences across the Wisconsin River floodplain are quite small (Gergel *et al.*, 2002), so differences between a ridge and a swale are likely sufficient to transition between significantly different flood frequencies. The importance of fine scale topography (<1 m differences) was also noted in the growth of *F. nigra* (Tardif and Bergeron, 1993).

B. nigra was the only species where we observed higher growth rates with exposure to flooding. In this species, BAI was greater in active floodplain than restricted floodplain, and RBAI was greater in swales than ridges. The increased growth exhibited by *B. nigra* in active floodplain and swales may indicate that soil nutrients mobilized by soil anoxia are stimulating its growth. This species could also be growing faster in areas that experience severe flooding due to decreased competition from other species, which are unable to tolerate flooded conditions. Conversely, *F. pennsylvanica* had higher growth rates in restricted floodplain than in active floodplain, particularly in swales. This species is only flood-tolerant as an adult, but drought periods may allow flood-sensitive

A. Active floodplain



B. Restricted floodplain

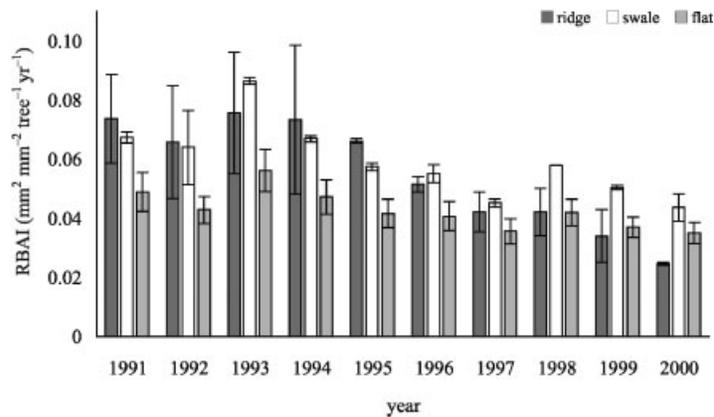


Figure 5. The annual average RBAI of *Q. velutina* and *Q. ellipsoidalis* located on three microtopographies, within the (A) active floodplain and the (B) restricted floodplain. Error bars represent one standard error

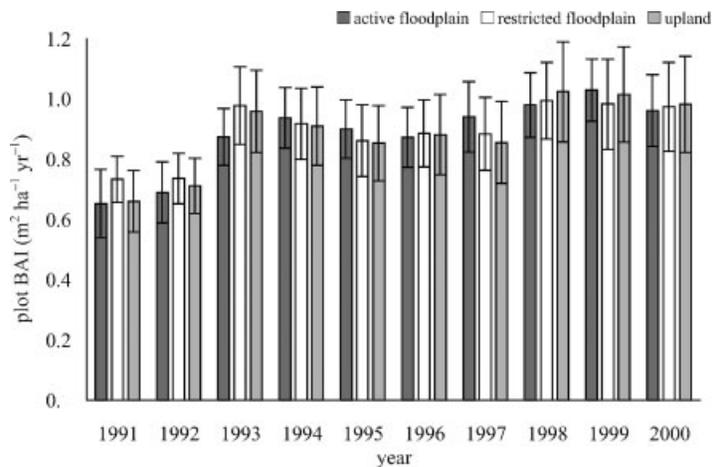


Figure 6. Annual BAI averaged for 10 years (1991–2000) for forested plots in active and restricted floodplain along the Wisconsin River and in the uplands. Error bars represent one standard error

F. pennsylvanica seedlings to establish in swales. Flood tolerance likely gives this species a competitive advantage in active floodplain, where it is more abundant than in former floodplain (Gergel *et al.*, 2002), although flooding suppresses its growth.

Both *F. pennsylvanica* and *Q. velutina* and *Q. ellipsoidalis* experienced higher growth on restricted floodplain ridges than on active floodplain ridges. There is no clear explanation for this pattern, but we hypothesize that ridges in active floodplain provide refuge from flood disturbances for many flood-intolerant species. So, active floodplain ridges may have more vegetation, and that increased density could restrict growth. However, in restricted floodplain, more areas are conducive to the growth of flood-intolerant species, so vegetation on ridges is sparser, allowing higher growth rates.

Stand-level tree growth rates

Stem density, basal area and species richness measured in the floodplain and uplands are within the range reported for other temperate floodplain and upland forests (Brinson, 1990), but lower than values reported for southern floodplain forest (Megonigal *et al.*, 1997) and temperate rainforest (Balien and Naiman, 2005). Stand-level tree growth rates did not differ among active floodplain, restricted floodplain or upland sites. This result is surprising, as both tree growth and aboveground productivity are often expected to be higher in active floodplain sites than upland sites (Johnson and Bell, 1976; Brinson, 1990; Naiman and Décamps, 1997), and anthropogenically restricted flood regimes typically decrease tree growth (Megonigal *et al.*, 1997). We expected the highest tree growth rates in active floodplain sites because of higher soil nutrient content (Megonigal *et al.*, 1997; Krauss *et al.*, 2006), and greater water availability (Reily and Johnson, 1982; Dudek *et al.*, 1998).

The similar stand-level growth rates we observed in the floodplain and uplands may be due to high water availability. The PDSI indicates that moisture was above average across all sites during this study. Therefore, water provided in flood events probably did not provide an advantage to active floodplain tree growth. Within the floodplain, low rates of sediment deposition during flood events and high ground water tables may have contributed to similarities in stand-level observed with flood regime. Deposition of sediment is uncommon in the active floodplain, because flood velocities are typically low (Gergel *et al.*, 2002). So the effect of nutrient rich sediment deposits on growth rates was probably minimal. However, the high groundwater table can create soil anoxia, resulting in nutrient mobilization (Ponnampereuma, 1984; Gosselink and Lee, 1989; Mitsch and Gosselink, 2000) in swales and low-lying areas across the entire floodplain. So, soil anoxia could create similar soil conditions in active and restricted floodplain sites, resulting in similar rates of tree growth.

Declines in tree growth often follow in the first two or three decade after a change to flood regime, and are typically attributed to decreased water availability (e.g. Johnson *et al.*, 1976; Reily and Johnson, 1982; Bakhiev and Treshkin, 1994). Furthermore, growth declines are pronounced when the community is not in equilibrium with the new hydrologic regime (Megonigal *et al.*, 1997). However, a century after the flood regime was altered we found no difference in stand-level growth between sites with active and restricted flooding. We know that many tree species are capable of altering resource allocation when exposed to an altered flood regime (Kozlowski and Pallardy, 1996; Kozlowski, 2002). Furthermore, flood-intolerant species are more prevalent in restricted floodplain than in the active floodplain, suggesting a shift in species composition has occurred (Gergel *et al.*, 2002). It is possible that changes in tree growth allocation and species composition mitigated any changes in growth that occurred immediately after the levee was constructed.

Differences in growth observed in this study likely reflect both the physiological responses of individual trees and changes in species composition that occurred after levee construction. We consider differences in growth observed between the active and restricted flood regime an interesting contrast, even though the relative contribution of physiological response and altered species composition is unknown. However, growth rates of older trees are typically slow (Kozlowski *et al.*, 1991), so we expect that the contributions of older trees (present before the levee was constructed) to stand growth rates are small. Therefore, we suggest that similarities among stand growth rates is more related to changes in species composition than the physiological responses of older trees.

The patterns we observed in tree growth may differ from patterns of total aboveground productivity in these trees. Trees with similar rates of radial growth may have different productivities due to differences in basal area, height, respiration demands, age or competition for nutrients or light (Kozlowski and Pallardy, 1996). We acknowledge that

differences among our stands might result in different patterns of tree growth allocation, creating similar radial growth rates while productivity differs. However, we know that the species composition differs greatly among sites and we consider any differences in growth due to morphological differences among species both relevant and interesting to this study. For example, our active floodplain and upland sites did differ in basal area, but this is likely due to differences in species composition and the characteristics of species abundant on each site. *B. nigra* individuals, which are abundant in the active floodplain, retain small diameters throughout their lifespan (Grelen, 1990); whereas as *Quercus* spp., can have very large diameters when mature (Sander, 1990). Therefore, the similarities in stand-level growth rates among forest stands we observed may be real, and not an artifact of differences in stand density or basal area.

Our results show that tree species respond differently to flooding. However, we found no differences in stand level tree growth between floodplains and uplands or between active and restricted floodplains. One explanation is that consistent stand-level tree growth occurs because community composition changes spatially as flood frequency declines. Our stands in the restricted floodplain are comprised of fewer flood-tolerant trees than stands in active floodplain, which could be a response to altered flood regime (Gergel *et al.*, 2002), and flood-intolerant species are even more abundant in upland stands. Thus, our results suggest that growth rates may be similar among sites because each forest community is comprised of species adapted to their current flood regime. The response in community composition may permit growth to be maintained as environmental conditions changed.

ACKNOWLEDGEMENTS

We are grateful to Tom Gower and Sean Burrows for use of the WinDENDRO Program as well as Crystal Van Cutsem and Tal Sutton for help with field sampling. Emily Stanley, Tom Gower, Steve Carpenter and two anonymous reviewers all provided insightful comments that improved this manuscript. Funding for this research was provided by National Science Foundation IGERT grant 9870703, Human and Dimensions of Social and Aquatic System Interactions; Environmental Protection Agency STAR grant R826600, Ecological Indicators; and the University of Wisconsin-Madison Zoology Department Davis Grant.

REFERENCES

- Anderson CJ, Mitsch WJ. 2006. The influence of hydrologic restoration on the productivity of a bottomland forest in Central Ohio. In *Olentangy River Wetland Research Park 2005 Annual Report*, Mitsch WJ, Zhang L, Tuttle C, Jones K (eds). The Ohio State University: Columbus, OH; 177–192.
- Baker TT, Lockaby BG, Conner WH, Meier CE, Stanturf JA, Burke MK. 2001. Leaf litter decomposition and nutrient dynamics in four southern forested floodplain communities. *Soil Science Society of America Journal* **65**: 1334–1347.
- Bakhiev AB, Treshkin SE. 1994. Dynamics of productivity of floodplain communities in the Amu-Darya delta in conditions of the territories varying hydrological regime. *Russian Journal of Ecology* **25**: 322–325.
- Balien EV, Naiman RJ. 2005. Abundance and production of riparian trees in the lowland floodplain of the Queets River Washington. *Ecosystems* **8**: 841–861.
- Brinson MM. 1990. Riverine forests. In *Forested Wetlands*, Lugo AE, Brinson MM, Brown S (eds). Elsevier Scientific Publishers: Amsterdam; 87–141.
- Brown S, Peterson DL. 1983. Structural characteristics and biomass production of 2 Illinois bottomland forests. *American Midland Naturalist* **110**: 107–117.
- Burke MK, Lockaby BG, Conner WH. 1999. Aboveground production and nutrient circulation along a flooding gradient in a South Carolina coastal plain forest. *Canadian Journal of Forest Research* **29**: 1402–1418.
- Conner WH, Day JW Jr. 1976. Productivity and composition of a bald cypress-water tupelo site and a bottomland hardwood site in a Louisiana swamp. *American Journal of Botany* **63**: 1354–1364.
- Curtis JT. 1959. *The Vegetation of Wisconsin: An Ordination of Plant Communities*. University of Wisconsin Press: Madison, WI.
- Disalvo AC, Hart SC. 2002. Climatic and stream-flow controls on tree growth in a western montane riparian forest. *Environmental Management* **30**: 678–691.
- Dixon MD, Turner MG. 2006. Simulated recruitment of riparian trees under natural and regulated flow regimes on the Wisconsin River, USA. *River Research and Applications* **22**: 1057–1083.
- Dudek DM, McClenahan JR, Mitsch WJ. 1998. Tree growth responses of *Populus deltoides* and *Juglans nigra* to streamflow and climate in a bottomland hardwood forest in central Ohio. *American Midland Naturalist* **140**: 233–244.

- Duschesne L, Ouimet R, Houle D. 2002. Basal area growth of Sugar Maple in relation to acid deposition, stand health and soil nutrients. *Journal of Environmental Quality* **31**: 1676–1683.
- Freeman RE, Stanley EH, Turner MG. 2003. Analysis and conservation implications of landscape change in the Wisconsin River floodplain, USA. *Ecological Applications* **13**: 416–431.
- Gergel SE, Dixon MD, Turner MG. 2002. Consequences of human-altered floods: levees, floods, and floodplain forests along the Wisconsin River. *Ecological Applications* **12**: 1755–1770.
- Gosselink JG, Lee LC. 1989. Cumulative impact assessment in bottomland hardwood forests. *Wetlands* **9**: 93–174.
- Grelen HE. 1990. River birch. In *Silvics of North America, Vol. 2, Hardwoods, Burns R, Honkala B (eds). United States Department of Agriculture, Forest Service: Washington DC*; 153–157.
- Heim RR Jr. 2002. A review of Twentieth Century drought indices used in the United States. *Bulletin of the American Meteorological Society* **83**: 1149–1165.
- Hosner JF. 1958. The effects of complete inundation upon seedlings of six bottomland tree species. *Ecology* **39**: 371–373.
- Johnson FL, Bell DT. 1976. Plant biomass and net primary production along a flood-frequency gradient in the streamside forest. *Castanea* **41**: 156–165.
- Johnson WC, Burgess RL, Keammerer WR. 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. *Ecological Monographs* **46**: 59–84.
- Kennedy HE. 1990. Green ash. In *Silvics of North America, Vol. 2, Hardwoods, Burns R, Honkala B (eds). United States Department of Agriculture, Forest Service: Washington DC*; 348–354.
- Kozlowski TT. 1984. Responses of woody plants to flooding. In *Flooding and Plant Growth, Kozlowski TT (ed). Academic Press: Orlando, FL*; 129–163.
- Kozlowski TT. 2002. Physiological-ecological impacts of flooding on riparian forest ecosystems. *Wetlands* **22**: 550–561.
- Kozlowski TT, Kramer PJ, Pallardy SG. 1991. *The Physiological Ecology of Woody Plants. Academic Press: San Diego, CA.*
- Kozlowski TT, Pallardy SG. 1996. *Physiology of Woody Plants (2nd edn). Academic Press: San Diego, CA.*
- Krauss KW, Doyle TW, Twilley RR, Rivera-Monroy VH, Sullivan JK. 2006. Evaluating the relative contributions of hydroperiod and soil fertility on growth of south Florida mangroves. *Hydrobiologia* **569**: 311–324.
- Liegel K. 1988. Land use and vegetational change on the Aldo Leopold Memorial Reserve. *Transactions of the Wisconsin Academy of Arts and Letters* **70**: 13–26.
- Martin L. 1965. *The Physical Geography of Wisconsin. The University of Wisconsin Press: Madison, WI.*
- McIninch S, Garbisch E, Biggs D. 1994. The benefits of wet-acclimating woody wetland plant species. *Wetland Journal* **6**: 19–23.
- Megonigal JP, Conner WH, Kroeger S, Sharitz RR. 1997. Aboveground production in Southeastern floodplain forests: a test of the subsidy-stress hypothesis. *Ecology* **78**: 370–384.
- Middleton BA, McKee KL. 2005. Primary production in an impounded baldcypress swamp (*Taxodium distichum*) at the northern limit of the range. *Wetlands Ecology and Management* **13**: 15–24.
- Mitsch WJ, Dorge CL, Wiemhoff JR. 1979. Ecosystem dynamics and a phosphorous budget of an alluvial cypress swamp in Southern Illinois. *Ecology* **60**: 1116–1124.
- Mitsch WJ, Gosselink JG. 2000. *Wetlands. John Wiley, NY: New York.*
- Mitsch WJ, Rust WG. 1984. Tree growth-responses to flooding in a bottomland forest in Northeastern Illinois. *Forest Science* **30**: 499–510.
- Mitsch WJ, Taylor JR, Benson KB. 1991. Estimating primary productivity of forested wetland communities in different hydrologic landscapes. *Landscape Ecology* **5**: 75–92.
- Mueller-Dombois D, Ellenberg H. 1974. *Aims and methods of vegetation science. Wiley, NY: New York.*
- Naiman RJ, Décamps H. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* **28**: 621–658.
- Nilsson C, Reidy CA, Dynesius M, Revenga C. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* **308**: 405–408.
- Odum EP, Finn JT, Franz EH. 1979. Perturbation theory and the subsidy-stress gradient. *Bioscience* **29**: 349–352.
- Pfeiffer SM. 2001. Groundwater/surface water interactions in a lowland savanna on the Lower Wisconsin River floodplain. *Masters Thesis, University of Wisconsin, Madison, WI.*
- Ponnamperuma FN. 1984. Effects of flooding on soils. In *Flooding and Plant Growth, Kozlowski TT (ed). Academic Press: Orlando, FL*; 9–45.
- Regent Instruments Inc. 1998. *WinDendro Reference Manual. Regent Instruments Inc.: Quebec, Canada.*
- Reily PW, Johnson WC. 1982. The effects of altered hydrologic regime on tree growth along the Missouri River in North Dakota. *Canadian Journal of Botany* **60**: 2410–2423.
- Robertson PA. 1992. Factors affecting tree growth on 3 lowland sites in Southern Illinois. *American Midland Naturalist* **128**: 218–236.
- Sala OE, Austin AT. 2000. Methods of estimating aboveground net primary productivity. In *Methods in Ecosystem Science, Sala OE, Jackson RB, Mooney HA, Howarth RW (eds). Springer: New York*; 31–43.
- Sander IL. 1990. Black oak. In *Silvics of North America, Volume 2, Hardwoods, Burns R, Honkala B (eds). United States Department of Agriculture, Forest Service: Washington DC*; 744–750.
- SAS Institute Inc. 1996. *SAS/STAT Software: Changes and Enhancements Through Release 9. SAS Institute Inc.: Cary, NC.*
- Tardif J, Bergeron Y. 1993. Radial growth of *Fraxinus nigra* in a Canadian boreal floodplain in response to climatic and hydrological fluctuations. *Journal of Vegetation Science* **4**: 751–758.
- Taylor JR, Cardamone MA, Mitsch WJ. 1990. Bottomland hardwood forests: their functions and values. In *Ecological Processes and Cumulative Impacts: Illustrated by Bottomland Hardwood Wetland Ecosystems, Gosselink JG, Lee LC, Muir TA (eds). Lewis: Chelsea, MI*; 13–86. 8.

- Turner MG, Gergel SE, Dixon MD, Miller JR. 2004. Distribution and abundance of trees in floodplain forests of the Wisconsin River: Environmental influences at different scales. *Journal of Vegetation Science* **15**: 729–738.
- Visser H. 1995. A note on the relation between ring widths and basal area increments. *Forest Science* **41**: 297–304.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth's ecosystems. *Science* **277**: 494–499.
- Wright RB, Lockaby BG, Walbridge MR. 2001. Phosphorus availability in an artificially flooded southeastern floodplain forest soil. *Soil Science Society of America Journal* **65**: 1293–1302.