LAKE KOSHKONONG WATER LEVELS AND GROWTH RATE OF TREES IN BORDERING FLOODPLAIN FORESTS

LAKE KOSHKONONG WETLAND ASSOCIATION
JEFFERSON COUNTY, WISCONSIN

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Jefferson County, Wisconsin

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PREFACE

On behalf of the Lake Koshkonong Wetland Association (LKWA), and in partial fulfillment of a Wisconsin Department of Natural Resources (WDNR) $10,000 River Protection Grant award, Natural Resources Consulting, Inc. (NRC) has completed an assessment of floodplain forest communities that border Lake Koshkonong.

The Lake Koshkonong Wetland Association (LKWA) was formed in 2003 in an effort to protect the existing wetlands on Lake Koshkonong and the Rock River and to promote the health of natural plants, fish, birds, and other forms of wildlife in the basin. Lake Koshkonong is a natural widening of the Rock River that was impounded in the early 1900’s. This is a very shallow lake with conditions marginally favorable for navigation by recreational boaters, especially as watercraft size increases. Because of these circumstances, the Rock-Koshkonong Lake District (RKLD), current owner of the dam, has proposed to modify the operating order, increasing the lake water levels by 6 to 8 inches throughout the growing season. The formation of the LKWA was prompted by this proposed increase in water levels due to local concern about adverse impacts to the more than 4000 acres of wetlands adjacent to the lake. The LKWA, although formed initially in response to this threat, has undertaken other projects within the basin such as: aquatic weed programs; wood duck nesting box construction; and osprey nesting platform construction. The LKWA has funded several preliminary studies on various wetland communities around the lake to assess the potential impacts of increased water levels.

More than 1000 acres of floodplain forests border Lake Koshkonong and are some of the highest quality of their type in southern Wisconsin. These communities are important migration corridors for wildlife habitat, neotropical interior bird species, fish spawning habitat during spring flooding, amphibian and reptile habitat, and have a substantial timber value. Floodplain forests have evolved to flourish under spring flooding conditions however, they are not well adapted to prolonged periods of inundation throughout the growing season. The primary objective of this study was to improve our understanding of the correlations between hydrology and the health of these floodplain forests in order to better understand the impacts of increased water levels on Lake Koshkonong. This study has valuable implications for protecting, enhancing, and promoting the health of these wetland communities by contributing to the overall management strategy for Lake Koshkonong and the Rock River.
ABSTRACT

This study illustrates the correlations between the growth rates of trees, the elevations at which they occur, and recent and historic water levels within floodplain forests adjacent to Lake Koshkonong in southern Wisconsin. Seven sample sites were selected, located near the outlet of Koshkonong Creek and just upstream from where the Rock River discharges into Lake Koshkonong. At each sample site, tree cores were collected and the elevation at the base of each tree cored was recorded. Approximately 4 to 6 trees of each representative species (Fraxinus pennsylvanica, Acer saccharinum, and Quercus bicolor) were selected for sampling at each site and a total of 74 trees were sampled. Relative water levels of the lake were obtained from the 73-year record from the gage on the Rock River at Fort Atkinson.

We found significant correlations in the growth rates of trees and the elevation at which they occur. Trees of all three species growing at higher elevations had higher average growth rates than trees growing at lower elevations. This correlation was strongest in swamp white oak for which 43% of the variation in growth rate was explained by variation in the tree’s elevation. We found only one tree in our seven sample sites that was growing at an elevation lower than the average late season water level in Lake Koshkonong. Of the trees we sampled 35% of the Green ash and 40% of the silver maple were growing at an elevation below the August to October mean water level that would result from setting the target elevation to 776.8 ft above mean sea level.

All three floodplain tree species had significantly higher average growth rates in response to fluctuating, high water levels over the short-term. Long-term water level increases were significantly correlated to the decreased growth rates of green ash. Swamp white oak had fairly significant correlations of decreased growth rates during rapidly raising water levels. There was essentially no long-term change in silver maple growth rate that could be explained by the increase in lake levels over the 73-year period of record.

Although, growth rates and water levels were not as highly correlated as anticipated or at least difficult to demonstrate (with the exception of green ash), the strong correlation between slow growth rates and low elevation alone is quite conclusive that adverse impacts will be associated with increasing water levels even slightly in Lake Koshkonong. At the particular elevation at which a tree grew it appeared to be able to compensate for water levels that rose slowly over time within the limits of the historical rise in water level. The fact that they seem to have compensated for an increase in the past, does not ensure that they will be able to tolerate another rise over a short period of time. There are certainly threshold water level elevations that these trees can tolerate before detrimental damage and mortality will result. Based on the elevation data, a large percent of the trees we surveyed are at that threshold condition.
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INTRODUCTION

The effects of prolonged flooding on individual tree species and woody vegetation have been studied extensively (Bell and Johnson 1974, Boules 1974, Broadfoot and Williston 1973, Coder 1994, Kozlowski 1984, Lieffers and Rothwell 1987, McKnight et al. 1980, Tattar 1972). Flooding stress has been identified as the primary limiting factor on above-ground tree productivity in forested wetlands, although adaptations of some species may result in stand productivity being optimized under certain flooding regimes (Burke et al. 1999). There have also been studies of the effects of flooding on below-ground productivity of wetland trees. Rodgers, et al. (2003) found no differences in rooting depth of Atlantic white cedar between two wetlands, one persistently flooded, the other only intermittently flooded, although root length density, root abundance, and root longevity were generally greater in the persistently flooded site. Most of the studies of the effects of flooding on forest tree growth have been on large rivers in the southern part of the United States, or on coastal plain wetlands (e.g. Cypress swamps) (Burke et al. 2003, Long and Nestler 1996). King (1995) found that differing flooding regimes affected regeneration, stress, and mortality of trees, and hence had an important affect on stand structure. He found that stress and mortality were substantially higher in larger diameter trees and that stress increased with flooding.

The effects of different flooding regimes on wetland and riparian plant communities have also been studied. Gradients in the composition of riparian and floodplain forest communities from the water to the higher elevation uplands are well known (Baker and Wiley 2004). These changes in forest community composition have been variously attributed to patterns of sediment erosion and deposition, fluvial landforms, and soil particle size and moisture status (Baker and Wiley 2004). Hydrology has repeatedly been found to be the most important single factor influencing forest community structure in wetlands and floodplains (Conner et al. 1981, Brinson et al. 1981, Brown 1981, Wharton et al. 1982, Brinson et al. 1984, Day et al. 1988). Correlations between levels of available moisture and growth rates of trees are well known. Although hydroperiod has been shown to have a major influence on growth rate of trees in southern and coastal floodplain forests, direct studies of growth rates in northern floodplain forests are few. A study by Baker and Wiley (2004) of the community structure of Michigan riparian forests is one of the few studies of northern riparian communities. Mitsch et al. (1991) found that the percent of growing season flooding and average water depth may be more accurate predictors of primary productivity than any other abiotic factors in forested wetland communities.

The Lake Koshkonong System

There is a 73-year record of water levels from a gage on the Rock River at Fort Atkinson, Wisconsin, approximately 5 miles above Lake Koshkonong. Water levels recorded for 73 years at Fort Atkinson can be used as a very accurate record of relative monthly mean water levels in Lake Koshkonong. There is a direct correlation among water levels at Fort Atkinson, water levels at the Indianford dam, and water levels in the entire lake system, including the extensive floodplain forests associated with the lake. The water table in the permeable soils of the Lake Koshkonong floodplain forests directly reflects the water level in the nearby lake.

The large open water area of the lake, originally an extensive deep and shallow marsh and shallow wild rice lake system, was formed by construction of the Indianford dam in 1851. Some of the best-developed floodplain forests bordering Lake Koshkonong are along Koshkonong Creek entering the northwestern shore of the lake, and along the Rock River inlet to the lake.
The forests currently found on the floodplains of Lake Koshkonong are dominated by silver maple (Acer saccharinum), green ash (Fraxinus pennsylvanica), and swamp white oak (Quercus bicolor). Some of these forests, including the ones sampled for this study, are typical well-developed floodplain forests of high quality. They have a closed canopy and contain very low light levels at the forest floor. The low light penetration to the ground level, and repeated natural disturbance associated with spring flooding of the soils, produces a very open understory having very little herbaceous vegetation in the forest groundlayer. Although these forests have been logged in the past, they are dominated by large trees at this time.

The purpose of this study was to discover correlations between growth rates of trees in the Lake Koshkonong floodplain forest with the elevations at which they occur and the variations in historic and recent water levels within the Lake Koshkonong.
STUDY SITES AND METHODS

For our sampling, we selected seven sites with mature floodplain forest occurring at various elevations, but primarily focused on those areas that are relatively low-lying and affected by flooding when Lake Koshkonong water levels are high (Figures 1 and 2). We obtained elevations of the ground level near the base of each tree we sampled; these averaged 777.6’ above MSL, and ranged from 776.3’ to 778.7’ (Table 1, Figure 3). Any lake stages above the recorded elevation for a tree would flood the ground surface near the base of that tree. The 10 swamp white oak trees that we sampled were found, on average, at elevations 0.6 ft higher than the ash and maple. Sample site D had the lowest average ground surface elevations (777.0’) and site C had the highest mean elevation (778.4’) (Figure 2a -- aerial). Five sample sites were located in the floodplain forest associated with the outlet of Koshkonong Creek (Figure 2a -- aerial), and two sample sites were just upstream from where the Rock River discharges into Lake Koshkonong (Figure 2b -- aerial).

We used the 73-year record of water levels from the gage on the Rock River at Fort Atkinson, approximately 5.5 miles above Lake Koshkonong, as our measure of relative water levels in the lake. A dam at Indianford, 5 river-miles below the lake, controls the water level in Lake Koshkonong. Water levels have been recorded at the dam at Indianford since 1984. Comparison of monthly mean water levels (Figure 4) shows that there is a very strong correlation between the water levels recorded at the Indianford Dam, which controls the level of the lake, and water levels of the Rock River at Fort Atkinson. Water levels recorded for 73 years at Fort Atkinson can be used as a very accurate record of relative monthly mean water levels in Lake Koshkonong.

We collected cores for measurement of ring widths from the three most dominant tree species, silver maple (*Acer saccharinum*), green ash (*Fraxinus pennsylvanica*), and swamp white oak (*Quercus bicolor*) on 16 and 17 August 2004. Approximately 4 to 6 cores were collected from each of the species that were present at each of the seven sample sites, for a total of 74 measurable cores (30 silver maple, 34 green ash, and 10 swamp white oak). Large trees at various topographic positions within each site were selected for coring in an attempt to obtain as many cores as possible that would provide a tree growth record extending at least 73 years before present (1932), the time when water levels began to be recorded at the Fort Atkinson gage.

We recorded the species and diameter at breast height (DBH) of each tree that we cored. The average DBH of all trees sampled was 53.2 cm, and ranged from 31.9 cm, a green ash, to 129.5 cm, a silver maple (Table 1). The green ash were on average the smallest trees we cored and silver maple the largest (Table 1). However, green ash and swamp white oak had average annual growth increments (ring widths) of only a little over half that of silver maple, so that the green ash cores had the longest average period of record (67 years) and silver maple the shortest (49 years) (Table 1). The longest cores obtained were approximately 27 cm long, the maximum length we could take with our coring tools.

All cores were mounted in wooden blocks and sanded smooth to prepare for measurement of ring widths. Annual growth increments were measured to the nearest 0.1 mm using an ocular micrometer mounted in a dissecting microscope at 10X magnification. All ring widths were measured starting with the 2004 increment and recorded as years before present (YBP). The annual rings of the ring-porous species, green ash and swamp white oak, were easier to discern than those of the diffuse-porous species, silver maple. However, with care the silver maple growth increments could be accurately measured because of a very
There are potentially some errors in the dataset that arose by not recognizing an annual ring, and consequently measuring two years of growth increment as a single ring. This kind of error will cause subsequent years before present to be shifted off by one year in the record. We will be able to correct these errors using a laborious process of matching growth increments between cores to recognize when the annual sequence has been shifted. However, to date we have not had sufficient time to complete this correction process, and the analysis presented here was done with the uncorrected ring width data. This correction is unlikely to qualitatively change any interpretations of the data, but is only likely to strengthen the growth relationships discovered in this study.

**Analysis**

The water level records we used in this analysis were recorded every five days, throughout the year, from 1932 through 2004 at the Fort Atkinson Gage, 5.5 miles upstream of Lake Koshkonong on the Rock River, Jefferson County, Wisconsin. During low to moderate flows, water levels at the Fort Atkinson Gage are highly representative of water levels in Lake Koshkonong. During higher flows there is about 0.2 ft to 0.4 ft difference in water levels between Fort Atkinson and Lake Koshkonong (pers. comm., Kenneth Johnson, WDNR Hydrologist). There is always a very strong correlation between monthly mean water levels at Fort Atkinson and Lake Koshkonong (Figure 4). Monthly means is the time scale useful for correlation of tree growth with lake water levels.

There are several ways that this water level data can be summarized to explore correlations between water level and tree growth, including different ways of expressing the average water level during different parts of one growing season, and a possible relationship between tree growth in one growing season and the previous season’s water levels. For the analysis presented here, we used the mean of all water levels recorded during two periods each year, 1 February to 31 July, and 1 August to 10 October, as the average early- and late-season water levels for that year. There is a positive, but weak, correlation between the average water levels during these two periods within a year (Figure 5). Only 16% of the variation among years in August to October water levels is explained by differences in February to July water levels of that year. 1986 was an extreme outlier year (over 5 standard deviations above the mean) for both water levels and tree growth increment and was eliminated from the dataset.

We used these two periods as our early and late-season water levels for two reasons: 1) The dam at Indianford controls mainly the late-season, base-flow water levels in Lake Koshkonong, and it is the effect of water levels influenced by the dam that is the main focus of this study (Montgomery Associates 2003); and 2) There is a large, but rather ephemeral, year-to-year variation in spring flood water levels; this spring variation is not much influenced by levels set at the dam. The interest of this study was focused on the effects of the water levels maintained through the later part of the growing season by the dam at Indianford, not on the effect of variable spring flooding. Average water levels, for each year’s early and late periods, were expressed as standard normal deviates from the overall mean water level for those months over the 73-year period of record. That is, water levels were standardized by subtracting the overall mean water level from the mean for each year, and dividing by the standard deviation of monthly mean water levels over the entire period of record.

The main purpose of this study was to search for correlations between the relative water levels experienced by a tree in any given year and the relative growth increment of that tree in that year. In
order to explore this relationship, the growth increment of the trees must be standardized so that trees with
different average growth rates can be compared. We standardized growth increments in two ways. Each
ring width was standardized by subtracting each annual growth increment from the overall mean for that
tree, and dividing this difference by the standard deviation of all ring widths measured for that tree. This
converted all ring width measurements into units of the number of standard deviations above or below the
mean for that tree. The mean of this standardized ring width variable is zero for each tree, and its
standard deviation is one, so all data is directly comparable.

A second method of standardization was required to explore the relationship between growth rate and
short-term fluctuations in water levels. We found some significant long-term negative relationships
between tree growth rates and water levels (see Results). Yet it appeared that over a shorter span of
years, growth of trees might have been greater during years with higher water levels. In order to examine
this relationship, it was necessary to express tree growth and water levels as deviations from shorter-term
running averages of ring width and water level.

Variation in water levels from year to year masks some of the apparent long-term increase in water levels
caused by changes in the dam at Indianford over the period of record (Figure 6). Ten-year average water
levels from the 1930’s through 2004 show that the ten-year, August to October, average water levels in
Lake Koshkonong have increased by approximately 1.0 ft over that period (Figure 7). At least for one of
the tree species we examined (green ash) there appears to have been a long-term slowing of growth rate
over this 73-year period of increasing average water levels (see Results). It appeared that within this
long-term trend there might be a short-term pattern of increased tree growth in years with higher water
levels.

To determine how the growth increment of any year deviated from the short-term average ring width, we
standardized the growth increment in each year to the 9-year running average centered on that year. We
calculated a 9-year average ring width, including the year to be standardized and the four preceding, and
four subsequent years. We subtracted this 9-year running mean from the ring width for that year, and
divided by the overall standard deviation of ring widths for that tree. This standardization transformed
the raw ring width score for a particular year into a measure of the deviation of that year from a 9-year
average. For this analysis we similarly transformed the water levels into standard normal deviations from
the 9-year running average water level.

Standardization of the data was calculated in Excel worksheets. Linear regressions and Analysis of
Variance (ANOVA) of tree ring width on water levels were performed with Excel and Systat 9.
RESULTS

Relative Elevation of Trees and Annual Growth Rates

We obtained the relative elevation of each tree that we sampled. These data allow us to examine whether the elevation of individual trees affects the relationship between relative water levels and tree growth. We examined whether the elevation of trees affected the relationship between their annual growth and water levels in three ways: 1) We performed a multiple linear regression of tree growth on mean August to October water level and relative tree elevation; 2) We divided the trees of each species into two groups, those above, and those below the mean of all elevations for that species, and determined whether the effect of August to October water level on annual growth rates was different for these two groups; and 3) We divided our seven sites into those that had an average tree elevation above the mean elevation of all sites, and those sites that had lower than average elevation, and determined whether the effect of August to October water level on annual growth rates was different for trees in these two groups of sites.

All three analyses provided the same results; within a species, tree elevation did not have a substantial effect on the relationship between annual tree growth rates and long-term variation in August to October mean water level. We hypothesized that trees at lower relative elevations might be affected more strongly by differences in water levels. If anything, there was a slight tendency for the long-term relationship between water level and annual tree growth rates to be stronger in those trees at higher elevations, but this difference was never significant. Variation in tree elevation did not add significantly to the relationship between water level and tree growth rate in the multiple linear regression.

In general, trees growing at lower than average elevations showed a stronger effect of short-term deviations in August to October water levels on deviations in annual tree growth relative to the 9-year mean (Compare Figures 14 and 15). Trees growing at low elevations (Figure 14) had greater increases in growth relative to the 9-year mean when water levels were high relative to the 9-year mean than did trees growing at higher elevations (Figure 15).

Relative Elevation of Trees and their Average Growth Rates

We also examined the relationship between the growth rate of individual trees averaged over the entire length of core that we collected, and the ground elevation at the base of that tree (Figure 16). The lifetime growth rate of each of the three tree species had a strong positive correlation with the elevation at which that tree was growing (P < 0.001). Trees of all three species growing at higher elevations had higher average growth rates than trees growing at lower elevations. This correlation was particularly strong in Swamp white oak for which 43% of the variation in growth rate was explained by variation in the tree’s elevation (Figure 16). For Green ash, 16% of variation in average growth rate was explained by variation in the tree’s elevation; even this level of correlation is very high for ecological data of this sort. A one-foot increase in the elevation of a tree was associated with an increase in predicted average annual growth increment of 0.55 mm (22% of the mean) for Green ash, 1.21 mm (27% of the mean) for Silver maple, and 1.35 mm (59% of the mean) for Swamp white oak.
Water Level Variation

Late growing season (August – October) average water levels in Lake Koshkonong have varied over a range of 6.4 ft, between a low of 774.8 ft in 1937, and a high of 781.2 ft in 1986, averaging 776.2 ft over the 73-year record. Without 1986, the next highest August to October water level was 778.3 ft in 1980. There are five years, 1938, 1972, 1980, 1986, and 1993, that are outliers in the water level records, all having exceptionally high water levels (Figure 6 – The extreme outlier, 1986, is removed in Figure 6). Each of these years has water levels that are more than two standard deviations above the mean water level; 1986 August to October water levels were 5.4 standard deviations above the mean.

In addition to large variations in water levels between years, the ten-year average August to October water levels have risen 1.0 ft from the 1930’s to the present day because of changes in the levels set at the Indianford dam (Figure 7). There were particularly large increases in water levels between the 1960’s and 1980’s, when mean water levels rose by 0.72 ft, and between the 1940’s and 1950’s when water levels rose 0.80 ft. Based on changes in mean water levels, the hydrologic record of Lake Koshkonong can be broken into three distinct periods (Table 2). Water levels were low from 1932 to 1949, intermediate, and changing rapidly (Figure 7) from 1950 to 1971, and relatively high from 1972 to 2004.

Long-term Trends in Tree Growth Rates

We found that annual growth increments of the three species of trees have varied differently over time and that they differ in their apparent response to changing water levels (Figure 8). Average growth rates of green ash appear to have declined over time, with increasing water levels; silver maple growth rates appear to have remained essentially unchanged throughout the period of record, and swamp white oak appears to have had relatively high growth rates in the 1930’s and 40’s, low rates of growth from 1950 to 1970, and somewhat higher growth rates since 1970 (Figure 8). Because each species may have a unique growth response to water level changes, there is no justification for pooling the data from the three species to examine growth rates of trees overall.

There are two different ways that we can analyze a relationship between water levels and tree growth rate over the entire period of record. We can regress the standardized annual growth increments measured for each tree on the water levels recorded in that year. Since there are three distinct hydrologic periods for Lake Koshkonong water levels (Table 2), we can also use Analysis of Variance (ANOVA) to determine if the tree had significantly different growth rates during those three periods.

The 73 year mean annual ring widths of green ash, averaged over all trees, have a highly significant (P<0.001) negative correlation with August to October water levels (Figure 9). Variation in August to October water levels explains 11% of the variation in green ash ring width among years. There is also a highly significant negative relationship between green ash ring widths and February to July water levels, but this relationship is not quite as strong, explaining 7% of the annual variation in ring width. The negative relationship between August to October water level and growth rate in green ash becomes much stronger if the four additional outlier water level years (1938, 72, 80, and 1993) are removed from the dataset (Figure 10). With these outliers removed, variation in August to October water level explains 26% of the variation in green ash ring width among years. According to the regression, predicted growth rate of green ash falls by approximately 0.6 standard deviations for every one-foot rise in water levels. A linear regression of ring width on water level does not provide a very good fit to the data (Figure 10). Expressing water level variation on a logarithmic scale makes the relationship between water levels and
growth rate of green ash even stronger, with log August to October water levels explaining almost one-third of the variation in green ash growth ($R^2 = 0.314$, $P < 0.001$).

The growth rates of neither silver maple nor swamp white oak show a strong correlation with either February to July or August to October Lake Koshkonong water levels (Figures 11 and 12). Average annual growth rate of silver maple does not change at all with August to October water level over the 73-year period (Figure 11). Swamp white oak also shows no significant correlation with long-term changes in either February to July or August to October water levels (Figure 12).

ANOVA may be a more powerful method for testing for significant differences in growth rates of the trees among different hydrologic periods during the history of records for Lake Koshkonong. By combining years within hydrologic periods, it removes the effect of inter-annual variation in water levels and examines growth rates averaged over the entire period. As in the regression analysis, ANOVA of green ash growth rate among water level periods shows a strong and steady decline in growth rate from the low water years before 1950 to the high water years after 1972 (Table 3). Water level periods explain 21% of the variation in green ash growth rates in this ANOVA.

ANOVA of the average annual growth increments of silver maple trees found that they grew significantly slower during the period between 1950 and 1971 when lake levels were rising rapidly, but that they had the same growth rate before or after that time (Table 3). However, this ANOVA comparing water level periods explained less than 3% of the total variation in silver maple growth, and is probably not very biologically meaningful. Swamp white oak had high average growth rates before 1950, when water levels were relatively low, very low average growth rates from 1950 to 1971, when water levels were rising rapidly, and seem to have recovered to moderate growth rates since 1972 (Table 3). This relationship of swamp white oak growth rate to water level period is intermediate in strength, explaining about 10% of the variation in growth rates.

**Short-term Correlations Between Tree Growth Rates and Lake Water Levels**

There were some long-term correlations between tree growth rates and annual water levels or hydrologic lake level periods that matched expected and explainable patterns (e.g. strongly decreasing growth rates of green ash with increasing water levels). However, close examination of Figure 8 suggested that within this long-term pattern of changing growth rates, some species might be responding positively to year-to-year variation in water levels. In other words, it appears in Figure 8 that, within a short time period, high water years tend to have greater tree growth rates. To examine this relationship we expressed the annual growth increment of each tree as a deviation from the 9-year running average growth rate of that tree (see above). This standardization transformed the raw ring width score for a particular year into a measure of the deviation of that year from a 9-year average. With this standardization we used linear regression to test whether growth rate responded to year-to-year variation in lake water levels.

All three tree species showed highly significant ($P < 0.001$) positive correlations between the departure of August to October water levels from the 9-year mean and the departure of annual growth increment from the running 9-year mean (Figure 13). Over the short term (9 years), when August to October water levels were above normal the average rate of tree growth was also above normal. This is the pattern that is apparent in Figure 8. Each species alone had a highly significant positive relationship with water levels, and some portion of the short-term variation in annual growth of each species could be explained by short-term variation in the August to October mean water level of the lake (Green ash, 7%; Silver maple, 6%; Swamp white oak, 15%). Because all three species responded similarly to short-term variation in
water levels, we combined the species by taking the overall average growth rate for each year (Figure 13). With the outlier high water years included, 10% of the variation in growth rate was explained by variation in short-term, August to October, water level variation (Figure 13). With the outlier high water years removed the relationship was stronger, with 17% of the variation in annual growth increment explained by fluctuations in water level.
DISCUSSION

Growth Rates and Elevation

The present target elevation of Lake Koshkonong (the level that the dam at Indianford attempts to maintain) is 776.2 ft. Average water levels between August and October are always somewhat higher than this target elevation (Figure 7) because the dam is maintaining a minimum lake level and does not control rises in lake levels that follow storm events. The average August to October water level in Lake Koshkonong since 1972 (without 1986) has been 776.55 ft. (0.35 ft above target) and there have only been 8 years in this 32-year period when the mean August to October water level was below the 776.2 ft target. The proposed target water level of Lake Koshkonong is 776.8 ft., a 0.6 ft. increase in the minimum lake levels maintained during base flows. The relationship between the target lake level in recent history and the actual August to October mean lake level suggests that average late season lake levels could be about 777.15 ft with a 776.8 ft target.

We sampled trees in each of our seven study sites to span the range of elevations at which that species grew in the site. We found no trees growing at a ground elevation at or below the current target lake elevation of 776.2 ft (Figure 3). Only one tree sampled was growing at an elevation lower than the average August to October lake level (776.55 ft) since 1972 (Figure 3). Individual trees of all three species that were growing at relatively high elevations had significantly higher growth rates than trees that were growing at low relative elevations. We found that the growth rate of Swamp white oak was particularly sensitive to the elevation at which the tree grew; the predicted growth rate of a Swamp white oak growing at the high end of the trees that we sampled was almost exactly double that of a tree growing at the lowest elevation on which we found oaks (Figure 3).

Increasing base flow (late season) water levels by 0.6 ft in Lake Koshkonong is likely to cause substantial mortality of trees over the long-term. We found only one tree in our seven sample sites that was growing at an elevation lower than the average late season water level produced by the current target water levels at the Indianford Dam (766.55 ft). Twelve (35%) of the Green ash, and 12 (40%) of the Silver maple we sampled were growing at an elevation below the likely August to October water level mean (777.15 ft) that would result from a target level at the Indianford Dam of 776.8 ft; eight trees were growing below the proposed target elevation. It is highly probable that these trees, and all trees growing at similar low elevations would be killed over time under the proposed water level regime. This tree mortality is likely to be most rapid and most dramatic in site D and E of the areas we sampled (Figure 2a), because the average ground surface elevation that we sampled in these two lowest sites was below 777.15 ft.

Virtually every study of plant communities in swamps and riparian areas has found that the community structure of forest trees is very strongly influenced by elevation, water level, or flood frequency and duration (Baker and Wiley 2004, Brinson et al. 1981, Brown 1981, Burke et al. 1999, Burke et al. 2003, Conner et al. 1981, Kearsley 1999, King 1995, Mitsch et al. 1991, Wharton et al. 1982). Small changes in elevation along the riparian gradient are associated with marked changes in the dominant trees species, because each species tends to be the competitive dominant over a much narrower range of elevations than those in which it could survive without competition. Although Swamp white oak grows at the highest average elevations of the floodplain forests we sampled, it also shows the greatest growth rate response to elevation of the three species we sampled (Figure 16), suggesting that it is the most sensitive of the three to higher water levels. Swamp white oak may be nearly, or completely, eliminated from the stands that
we studied over time if water levels are increased by 0.6 ft, since the elevation – growth rate relationship (Figure 16) predicts that the average growth rate of Swamp white oak would be decreased by almost 40%.

Growth Rates and Water Levels

All three floodplain tree species had significantly higher average growth rates in response to Lake Koshkonong water levels that were higher than the short-term (9-year) average. Over the short-term, when August to October water levels were high, trees had greater than average annual growth increments. There was essentially no long-term change in silver maple growth rate that could be explained by the increase in lake levels over the 73-year period of record. Swamp white oak had high growth rates before 1950, when water levels were lower than they are today, low growth rates between 1950 and 1971, when lake levels were steadily increasing, and intermediate growth rates since 1972, when the lake levels have been stabilized at a higher level. Green ash has shown steady reductions in average growth rates as August to October average water levels have risen by at least one foot over the 73-year period.

What can explain an apparent negative response of green ash growth rates to long-term increases in water levels, and a positive response to high water levels over the short-term? There are at least two possible explanations for this observed pattern. One possibility is that the apparent negative correlation of green ash growth rates with long-term increases in water levels is not related to the change in lake levels. In other words, that the observed correlation cannot be interpreted as cause and effect. The annual growth increment of green ash trees may inherently slow as the trees age. None of the ash trees sampled were much over 100 years old; many were 73 years old or younger; all of the trees were relatively young at the beginning of the available water level records. If these young trees were established in a recently cut or thinned forest, they may have had high available light levels and growth rates. As the forest canopy began to close and the trees began to compete more intensely for light, growth rate may have slowed independently of changes in the lake water levels.

A second possible explanation for a long-term decrease in green ash growth rate with rising water levels and a short-term positive response to high water tables is that fluctuating water levels are favorable for green ash growth, but that long-term flooding of the root system causes reduced growth. Most floodplain forest trees root to the depth of the water table to obtain moisture (Lieffers and Rothwell 1987, Rodgers, et al. 2003), however roots require oxygenated soil to grow (Kozlowski 1984). High water levels that last for a season or less may provide abundant moisture and excessive nutrient supplies beneficial for tree growth, but high water levels may not last long enough to cause the soil to become anoxic. Longer-term high water levels can cause deeper layers of soil to become anoxic, leading to death of tree roots that have penetrated to that depth (Lieffers and Rothwell 1987, Rodgers, et al. 2003). Long-term rising water levels may have decreased the depth of soil available for rooting of green ash. While deeper soil levels are no longer available for the growth of green ash roots, relatively high water levels that last for a season or less may still be favorable for green ash growth. It may not be possible with the present dataset to distinguish between these two possible explanations of the observed pattern.

Silver maple is probably the most flood-tolerant of the three floodplain trees studied. Baker and Wiley (2004) found that in Michigan riparian forests silver maple was most dominant in the lowest, most frequently flooded, forests, while green ash was most dominant in an intermediate position on the riparian elevation gradient. Kearsley (1999) found a similar pattern in the floodplain forest communities of Massachusetts. The silver maples in our sample grew at the same average elevation as the green ash, but
at substantially lower elevations than the swamp white oak (Table 1, Figure 3). However, our sampling was not designed to determine the elevations at which each species achieved its highest dominance in the forest communities. Silver maple typically grows in floodplain forests that are very frequently flooded, and grows in a zone of elevation just above cottonwood and willow species common in wet floodplain forests (Curtis 1959). Silver maple is likely to be very adept at producing new roots in the oxygenated zone of the soil as long-term increases in water levels make lower soil levels unavailable for root growth.

Swamp white oak grew at average elevations 0.7 ft higher than the other two species in our sample (Figure 3), and is probably the least flood tolerant of the three species. The relatively poor growth of swamp white oak during the period when lake levels were rising dramatically (1950 to 1971) may have been caused by rising water levels killing the lower roots of the trees, and relatively slow production of new feeder roots in the oxygenated zone of the soil. More recent partial recovery of swamp white oak growth rates may be the result of the production of new feeder roots in shallower parts of the soil profile under the recently more stabilized average lake levels.
SUMMARY

We predict the following changes in the floodplain forest communities of Lake Koshkonong if average late-season water levels are permanently increased by 0.6 ft:

1) Mortality of silver maple and green ash growing at lower elevations in the floodplains. Many trees at low elevations and at the lake edge can be expected to be uprooted as their root systems are flooded.

2) Low relative elevations in the forests may be colonized by other less valuable tree species (e.g. willow species and cottonwoods), or they may no longer be suitable for growth of trees and convert to wet meadow/shallow marsh communities.

3) A general reduction in the growth rate of all three of the dominant Lake Koshkonong floodplain forest trees. We expect this decline to be especially pronounced in green ash, given the evidence that its growth rate has already declined with higher late-season water levels in the lake.

4) A shift in community composition so that the relative dominance of silver maple increases in the floodplain forests at higher elevations, and swamp white oak is nearly, or completely, eliminated over time.
LITERATURE CITED


Coder, Kim D. 1994. Flood damage to trees. Warnell School of Forest Resources. The University of Georgia.


TABLES
Table 1. Summary characteristics of the 74 trees cored in the floodplain forests of Lake Koshkonong. “Core Years” are the length of record of the individual cores truncated at 73 YBP (years before present), which is the length of the water level records. “Number = 73 yrs” is the number of cores that contained this maximum length of record. Minimum and maximum “all species” ring widths are the smallest and largest of the average ring widths obtained for each of the 74 trees cored.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>DBH</th>
<th>Core Years</th>
<th>Number =73 yrs</th>
<th>Ring width (mm)</th>
<th>Elevation (ft) above MSL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Green ash</td>
<td>34</td>
<td>47.7</td>
<td>67</td>
<td>17</td>
<td>2.47</td>
<td>777.5</td>
</tr>
<tr>
<td>Silver maple</td>
<td>30</td>
<td>59.2</td>
<td>49</td>
<td>3</td>
<td>4.41</td>
<td>777.4</td>
</tr>
<tr>
<td>Swamp white oak</td>
<td>10</td>
<td>53.7</td>
<td>58</td>
<td>5</td>
<td>2.28</td>
<td>778.1</td>
</tr>
<tr>
<td>All species mean</td>
<td>53.2</td>
<td>58.7</td>
<td></td>
<td>3.23</td>
<td>777.6</td>
<td></td>
</tr>
<tr>
<td>All species min.</td>
<td>31.9</td>
<td>12</td>
<td></td>
<td>0.71</td>
<td>776.3</td>
<td></td>
</tr>
<tr>
<td>All species max.</td>
<td>129.5</td>
<td>73</td>
<td></td>
<td>7.33</td>
<td>778.7</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. August to October water level means and standard deviations for three distinct hydrologic periods in Lake Koshkonong.

<table>
<thead>
<tr>
<th>Years</th>
<th>Average Aug - Oct Water Level (feet)</th>
<th>Average Standard normal</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932 - 1949</td>
<td>775.49</td>
<td>-0.96</td>
<td>0.62</td>
</tr>
<tr>
<td>1950 - 1971</td>
<td>776.21</td>
<td>0.03</td>
<td>0.55</td>
</tr>
<tr>
<td>1972 - 2004</td>
<td>776.55</td>
<td>0.52</td>
<td>0.58</td>
</tr>
</tbody>
</table>
Table 3. Means and standard deviations of standardized annual growth increments for three
species of trees in three different periods of water level data for Lake Koshkonong. ANOVAs of
growth rate for each species are significant at $P < 0.001$. Means followed by the same lower case
letter do not differ significantly. $R^2 =$ the amount of total variation in growth rate explained by
water level period in the ANOVA.

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>Mean</th>
<th>Std. Dev.</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Green ash</td>
<td>1932 - 49</td>
<td>0.88 c</td>
<td>1.25</td>
<td>0.212</td>
</tr>
<tr>
<td></td>
<td>1950 - 71</td>
<td>0.02 b</td>
<td>0.88</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1972 - 04</td>
<td>-0.35 a</td>
<td>0.77</td>
<td></td>
</tr>
<tr>
<td>Silver maple</td>
<td>1932 - 49</td>
<td>0.07 b</td>
<td>0.82</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td>1950 - 71</td>
<td>-0.26 a</td>
<td>8.83</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1972 - 04</td>
<td>0.10 b</td>
<td>1.05</td>
<td></td>
</tr>
<tr>
<td>Swamp white oak</td>
<td>1932 - 49</td>
<td>0.51 c</td>
<td>1.13</td>
<td>0.095</td>
</tr>
<tr>
<td></td>
<td>1950 - 71</td>
<td>-0.40 a</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1972 - 04</td>
<td>0.09 b</td>
<td>0.99</td>
<td></td>
</tr>
</tbody>
</table>
FIGURES
FIGURE 2b. PROJECT LOCATION & ORTHOPHOTOGRAPHY
Lake Koshkonong Floodplain Forest Study

Location
Sections 13, 16, 17, 20, 21, T5N, R13E & Section 18, T5N, R14E, Jefferson County, Wisconsin

Project Information
NRC Project Number #: 04-104
Modified January 13, 2005

Legend
Sample Areas

0 300 600 Feet

Map Area Shown In Red

NRC Natural Resources Consulting, Inc.
119 South Main Street, Suite D
P.O. Box 128
Cottage Grove, WI 53527-0128
phone: 608-839-1998
fax: 608-839-1995

www.nrc-inc.net
Figure 3. Elevation of 74 Green ash, Silver maple, and Swamp white oak trees sampled in the floodplain forests of Lake Koshkonong. Trees of each species are arranged in order of increasing elevation on the x-axis. Elevation is in feet above mean sea level.
Figure 4. Comparison of monthly average Rock River water levels in feet above mean sea level recorded between 1984 and 2001 at the Indianford Dam, below Lake Koshkonong, and at Fort Atkinson, above the lake. A linear regression line and correlation coefficient are shown.

\[ y = 0.503x + 384.913 \]

\[ R^2 = 0.910 \]
Figure 5. Relationship between the average February to July water levels recorded during a year and the average water level recorded during August to October of that same year. Water levels are in feet above mean sea level (MSL).
Figure 6. Annual variation in average February to July (thin line) and August to October (thick line) water levels recorded between 1932 and 2004 on the Rock River at Fort Atkinson. Water levels are plotted in units of standard deviations above or below the overall mean. The extreme outlier year, 1986, is eliminated from the data.
Figure 7. Change in ten-year average water levels of Lake Koshkonong over a 73-year period of record (1932 to 2004). Water levels are expressed in feet above mean sea level (feet MSL).
Figure 8. Average annual growth increments for three tree species in floodplain forests, and mean annual August to October water levels for Lake Koshkonong. Tree growth and water level are expressed as standard normal deviations from the means from 1932 to 2004. Zero is the mean ring width for each tree species and for water levels over the entire period of record in this transformed dataset. The extreme outlier year, 1986, is not shown in this figure.
Figure 9. Linear regression of the average annual growth increment (ring width) of 34 green ash (Fraxinus pennsylvanica) trees on August to October water levels in Lake Koshkonong between 1932 and 2004. Both variables are expressed as standard normal deviations from the overall mean for the period of record.
Figure 10. Linear regression of the average annual growth increment (ring width) of 34 green ash (*Fraxinus pennsylvanica*) trees on August to October water levels in Lake Koshkonong between 1932 and 2004. Both variables are expressed as standard normal deviations from the overall mean for the period of record. This is the same dataset as used in Figure 9, but the outlier, high water years, 1938, 72, 80, 86, and 1993, have been removed from the dataset.
Figure 11. Scatter plot of the average annual growth increment (ring width) of 30 silver maple \((Acer saccharinum)\) trees on August to October water levels in Lake Koshkonong between 1932 and 2004. Both variables are expressed as standard normal deviations from the overall mean for the period of record. The linear regression is not significant.
Figure 12. Scatter plot of the average annual growth increment (ring width) of 10 swamp white oak (*Quercus bicolor*) trees on August to October water levels in Lake Koshkonong between 1932 and 2004. Both variables are expressed as standard normal deviations from the overall mean for the period of record. The linear regression is not significant.
Figure 13. Regression of the departure of annual growth increments from the 9-year running mean on the departure of water levels from their 9-year running mean for all three tree species combined. Both variables are expressed as standard normal deviations from the 9-year running means. The regression is highly significant (P < 0.001).
Figure 14. Regression of the departure of annual growth increments from the 9-year running mean on the departure of water levels from their 9-year running mean for trees of all three species that are growing at lower than average elevations. Both variables are expressed as standard normal deviations from the 9-year running means. The regression is highly significant ($P < 0.001$).
Figure 15. Regression of the departure of annual growth increments from the 9-year running mean on the departure of water levels from their 9-year running mean for trees of all three species that are growing at higher than average elevations. Both variables are expressed as standard normal deviations from the 9-year running means. The regression is significant (P < 0.01).

\[ y = 0.069x + 0.005 \]
\[ R^2 = 0.047 \]
Figure 16. Regressions of the average annual growth increments (in mm) of 74 Green ash (hollow diamonds), Silver maple (solid squares), and Swamp white oak (solid triangles) trees on the ground elevations at the base of each trees (in feet above means sea level). All three regressions are highly significant (P < 0.001).