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Estimating and modeling red oak acorn yield and abundance in the Mississippi Alluvial Valley

By

Jacob Nathaniel Straub

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Estimating and modeling red oak acorn yield and abundance in the Mississippi Alluvial Valley

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Red oaks (*Quercus* spp.; Section *Erythrobalanus*) produce acorns which are valuable forage for wildlife especially mallards (*Anas platyrhynchos*) and wood ducks (*Aix sponsa*). Scientists have limited information on amount, timing, and persistence of these acorns in the Mississippi Alluvial Valley (MAV). Conservation planners rely on precise estimates of acorns and other forage to estimate habitat needed by waterfowl in the MAV and other regions.

My study provided premiere landscape-scale, multi-year estimates of red oak acorn yield and on-ground abundance in the MAV. Mean yield of acorns was 534 kg(dry)/ha (42.3 acorns/ m^2) across all sites, years (falls-winters 2009-2012), and oak species. Yield varied more within years (CV = 11 - 29%) than when data were combined across years (CV = 11%). Yield was not synchronized in any year among MAV sites. However, yield usually was synchronized among species within sites suggesting local factors influenced acorn yield more than landscape-scale factors. Among sites and years, acorn abundance generally was greatest in January (sample mean = 371 kg/ha) and least in November (198 kg/ha). Acorns persisted to February only in years of above-average

yield. Except for Nuttall oak (*Quercus texana*), acorn persistence generally was stable regardless of yield from parent trees. Nuttall oak acorn persistence increased with yield perhaps revealing an evolutionary pressure that encourages masting. Red oak acorn abundance was linearly related to percentage of red oaks in the overstory, but this relationship differed in years of above- and below-average yield.

Currently, conservation planners use 166 kg/ha as a forage estimate of red oak acorns, moist-soil seeds, and aquatic macro-invertebrates in bottomland hardwood forests with 100% red oak canopy. I sampled at 5 sites throughout the MAV over 3 years; therefore, I recommend conservation planners consider adopting my predicted estimate of 247 kg of acorns/ha of forest land with 100% red oak canopy. Because acorns persist through most winters and generally reach peak abundance in January, often concomitant with peak abundance of mallards and other ducks in the MAV, biologists and conservation planners may have undervalued the potential of bottomland hardwood forests to support ducks in mid-late winter.

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CHAPTER I

RED OAK ACORN YIELD IN THE MISSISSIPPI ALLUVIAL VALLEY

Bottomland hardwood forests are diverse and productive ecosystems in the Mississippi Alluvial Valley (MAV) and southeastern United States. Historically, hardwood bottomlands were the dominant land-cover in the MAV and harbored as many as 70 endemic tree species (Fredrickson and Hansen 1983). Only about 20% of the historic area of hardwood bottomlands remain due to extirpation by agriculture and other human developments (Twedt and Loesch 1999). Landscape-level, human induced modifications, such as hydrologic engineering and extensive deforestation, have impacted important ecological functions of bottomland hardwood forests in the MAV (Denslow and Battaglia 2002, King et al. 2006). Also, commercial timber harvesting has influenced current forest composition, because highly selective cutting removed valuable red oaks disproportionately to other species. As a result, many remaining forest communities in the MAV are dominated by shade- and moisture-tolerant tree species with low commercial value (Conner and Sharitz 2005, Fredrickson 2005). Despite current and past impacts, extant and restored hardwood bottomlands provide timber and habitat for resident and migratory wildlife (Stanturf et al. 2000, Hamel 2003).

Among the diversity of overstory species found in bottomland hardwood forests, scientists and managers are especially interested in red oaks (*Quercus* spp; Section *Erythrobalanus*). Acorns from red oaks provide food for many wildlife, including waterfowl (Delnicki and Reinecke 1986, Kaminski et al. 2003). Many wildlife species rely on acorns during winter as a primary energy source; thus, abundance of acorns may be linked to wildlife population dynamics (Elkinton et al. 1996, Ostfeld et al. 1996, McShea 2000). In addition, intact acorns that survive winter may germinate and regenerate oak forests. Common red oak species in the MAV include cherrybark (*Q. pagoda*), Nuttall (*Q. texana*), pin (*Q. palustris*), water (*Q. nigra*), and willow oaks (*Q. phellos;* hereafter red oaks). Each species produces an acorn that varies in size (Bonner and Vozzo 1987, Aizen and Patterson 1990), and trees occupy a somewhat overlapping niche along hydrologic and soil gradients (Hodges 1997). Nuttall and pin oaks are considered most flood tolerant followed by willow, water, and cherrybark oaks (Hodges 1997).

A defining characteristic of oak acorn production is spatial-temporal variability in masting (Sork et al. 1993, Kelly 1994, Greenberg and Parresol 2002). Masting is defined as the synchronous intermittent yield of large seed crops in perennial plants (Kelly 1994). Components of masting include synchrony and temporal variability, which are unique terms. Synchrony is the extent that mast crops are correlated among years, sites, and species; temporal variability is among year variation in seed yield (Liebhold et al. 2004*b*). These components have not been examined regionally for red oaks in the MAV or other lowland forests in southeastern United States, although they have been investigated for other oaks in North America (Liebhold et al. 2004b, Pons and Pausas 2012).

Variability in acorn yield transcends spatio-temporo scales, species, individual trees, and years. Combinations of intrinsic and extrinsic factors influence acorn yield, which vary among and within species and years (Fearer et al. 2008, Miyazaki 2011). Therefore, precise estimation and prediction of acorn yields have been difficult. Further, different variables influence red oak acorn yield depending on spatial scale. For instance, local factors, such as tree size, condition, competition from con- and heterospecifics, canopy dominance, and hydrology may influence yield by individual trees (Healy et al. 1999, Lombardo and McCarthy 2008, Lashley et al. 2009); whereas, large scale weather events can influence yield at landscape scales (e.g., stand, regions; Sork et al. 1993). For example, Sork et al. (2003) found that spring temperatures and summer droughts were greatly correlated with acorn yield of 3 species of North American oaks.

Mangers and ecologists have limited information concerning spatial and temporal masting cycles in the MAV and elsewhere. Further, research that illustrates important factors influencing acorn crop size, regardless of scale, is scant, although this research has been conducted in the United States (Greenberg and Parresol 2002). Estimates of red oak acorn yield in southeastern United States are only from Mingo National Wildlife Refuge (NWR) in southeast Missouri, Sam D. Hamilton-Noxubee NWR in east-central Mississippi, and Monsanto Farm and Wildlife Management Area in east-central Arkansas (Minckler and McDermott 1960, McQuilkin and Musbach 1977, Young 1990, Guttery 2006). Although these studies have provided managers with useful information, they focused on one or few red oak species and have lacked large-scale spatial replication over a period of years.

My goals were to generate reliable, contemporary estimates of acorn yield and variability from red oak trees in the MAV and determine which variables best predicted acorn mast. Biologists and managers need reliable estimates of acorn yield in bottomland hardwood forests to assess potential foraging carrying capacity of these habitats for waterfowl and other wildlife and forest regeneration (Loesch et al. 1995, Kaminski et al. 2003). Therefore, my objectives were to 1) estimate precisely (i.e., CV ≤ 15%; Stafford et al. 2006, Kross et al. 2008) red oak acorn yield on public lands in the MAV, 2) examine variation in yield of acorns by individual red oak trees as functions of biologically relevant local scale factors, and 3) evaluate components of masting among species, sites, and years.

Study Areas

The MAV, a historic floodplain of the Mississippi River, extends from Cairo, Illinois to the mouth of the Mississippi River in Louisiana, a total length of about 800 km (Reinecke et al. 1989). It includes about 10 million hectares in 7 states of which nearly 2.6 million ha remain in hardwood bottomlands (Twedt and Loesch 1999). About 16% of the remaining hardwoods are on public lands (Twedt and Loesch 1999). The region extends between 29° and 37°N latitude and between 89° and 92°W longitude (Fig 1). The MAV is situated in a humid, subtropical region of the Northern Temperate Zone where annual precipitation ranges between 117 cm in the north and 165 cm in the south (National Climatic Data Center 2011). January temperatures range from 3ºC in the northern reach of the MAV, 7.5ºC in the central sub-region, and 11ºC in the southern reach, wheras temperatures in July average about 30ºC across the region.

Current land cover in the MAV is a mix of mostly agricultural land, bottomland hardwood and other forest communities, emergent and other wetlands, and urban areas (Twedt and Loesch 1999). The current distribution of hardwood bottomlands is skewed greatly toward the southern MAV, wherein the states of Arkansas, Louisiana, and

Mississippi have about 94% of the total hardwood bottomlands (Twedt and Loesch 1999).

I studied acorn yield by red oaks on one area in each of 5 states in the MAV, including 4 NWRs (Mingo [Missouri], Chickasaw [Tennessee], White River [Arkansas], and Tensas River [Louisiana]) and Delta National Forest [Delta NF; Mississippi]; Fig. 1). Thus, I established study plots in major hardwood bottomlands in 5 of the 7 states in the MAV. Although I did not select study areas randomly, I consulted with area managers to ensure there were adequate mature (i.e., >50 year old) bottomland hardwoods that generally flood annually.

Methods

Acorn Survey Design

I obtained a digital land cover map for the MAV from the Lower Mississippi Valley Joint Venture of the North American Waterfowl Management Plan (Twedt and Loesch 1999). I excluded all cover types except those labeled bottomland hardwood forest and wet bottomland hardwood forest. I then obtained a GIS boundary layer for each of my 5 study areas from Mississippi's Automated Resource Information System. I used Arc GIS 9.2 to restrict land cover files to these 5 areas. The result was digital coverage of bottomland hardwood forests within the boundaries of my 5 study areas. Finally, to facilitate walking accessibility to sample sites within areas, I used Arc GIS to identify all bottomland hardwood tracts within each study area that were 0.08-0.32 km from a road open to vehicular travel. I assumed these sample areas were representative of hardwood bottomlands in each area and not differently influenced hydrologically or otherwise by proximity of the road.

I used the GRTS package (Stevens Jr. and Olsen 2004) of Program R 2.8.1 (Stevens and Olsen 2004; R Development Core Team) to generate latitudinal and longitudinal coordinates for centers of 20 randomly placed, circular plots (0.2 ha) within the aforementioned forested areas of each site. I also selected 20 alternate plot centers if original plots were not suitable upon initial inspection (e.g., original data coverage misclassified the forest type). The GRTS package uses a spatial algorithm to select random points within a specified sampling universe at each site (Stevens and Olson 2004). This approach ensured plots were not clustered but randomly dispersed.

Within each plot, I inventoried all red oaks that were ≥25 cm diameter at breast height (DBH; 1.37 m above ground level), because these typically produce mast (Dey 1995). I then randomly selected 2 red oaks of the specified DBH class to sample regardless of species, because my goal was to estimate acorn yield by red oaks, as mast from these provides important food for wildlife (Reinecke et al. 1989, Kaminski et al. 2003, Heitmeyer et al. 2006). If a plot did not contain 2 red oaks ≥25 cm DBH, I chose the nearest alternate plot and randomly selected 2 trees of ≥25 cm DBH. Not all red oak species occurred at each study are; therefore, distribution of species varied within and among study areas.

To collect acorns from selected trees, I randomly chose a cardinal direction and then placed a 1-m^2 sampling trap halfway between the bole and the canopy drip line (Guttery 2006). I fabricated frames of traps from 2.5 x 10 cm treated lumber, joined at the ends, and mounted atop 4, 1.5 m lengths of electrical conduit, or I made traps of the same dimensions from PVC pipe. To the wooden or PVC frame, I attached a funnel-like piece of fiberglass window screening that extended downward from the frame approximately 45 cm vertically. At the distal end of the screening, I attached a wide mouthed plastic bottle to consolidate acorns that fell into the trap. I pushed legs of the trap 30-40 cm into the ground, giving the trap stability yet keeping it elevated to inhibit acorn depredation by ground-foraging grainivores.

I randomly selected and installed a trap under 200 red oaks across my 5 study areas. I visited all traps monthly from August 2009 – March 2012. Because of tree damage or mortality, flooding, excessive trap molestation from black bears (*Ursus americana*), I never retrieved samples from all trees in any year. As a result, number of sampled red oak trees and species varied by study area and year.

I recorded the following parameters for all sampled trees: species, DBH, crown area, and crown class. I recorded the following parameters for all plots: total red oaks by species and DBH of each red oak tree by species. I estimated crown area by calculating the mean of 4 radii (r), each measured in one of the cardinal directions, extending from outer edge of bole to canopy drip line, and using the following equation: crown area = πr^2. I designated crown class as dominant, co-dominant, intermediate, or suppressed following Smith (1962).

Laboratory Methods

I stored all acorn samples in a freezer at -10˚C at Mississippi State University. To process samples, I first thawed acorns, then separated them using a float test to identify sound acorns (i.e., those that sunk) from unsound (i.e., those that floated; Allen 1989, Barras et al. 1996). For each type of acorns, I halved them with shears and enumerated them as follows: 1) wholly intact, 2) either >50% or <50% seed damaged by insects (e.g., weevil [*Curculio* spp.] or gall wasp [Cynipidae]), 3) either >50% or < 50% of the seed apparently consumed by vertebrates (e.g., squirrels [*Sciurus* spp.]), 4) either >50% or < 50% of the seed covered by fungus, and 5) underdeveloped (i.e., aborted prematurely; Young 1990). Because I was interested in estimating total number of acorns produced by trees, my estimates and analyses included: 1) all sound whole acorns, 2) all sound partial acorns, and 3) all whole acorns that floated (i.e., not sound). I included the latter category because sometimes whole viable acorns floated because of low moisture content or air pockets under the pericarp of acorns (Allen 1989). Exclusion of buoyant, viable acorns would negatively bias estimates of yield and abundance of acorns potentially available to wildlife.

Statistical Analyses

Estimating Red Oak Acorn Yield in the MAV

I used a multi-stage sampling design to estimate red oak acorn yield within and among study sites in the MAV (Stafford et al. 2006, Kross et al. 2008, Leach 2011, Straub et al. 2012). I used the SURVEY package in R version 2.13.2 (R Development Core Team 2009) and incorporated appropriate sampling weights for 3 stages of sampling (i.e., plots, red oak trees within plots, and sampled crown area of each tree). I calculated probability of selecting a plot by dividing 1 by total area of hardwood bottomland available for sampling at each study area. Within each plot, I calculated probability of selecting a red oak tree by dividing 2 (*n* trees sampled per plot) by total number of red oaks of ≥25 cm DBH in the plot. Lastly, I calculated probability of placing a trap under the crown of selected red oak by dividing 1 by total estimated crown area of the sampled tree. I determined individual weights for each tree by calculating the inverse of the product of the 3 probabilities (Stafford et al. 2006, Kross et al. 2008, Straub et al. 2012).

I present results as the autumn-winter cumulative mean mass and mean number of acorns produced per m^2 red oak tree crown for each site and year. This approach enabled me to compare relative density (i.e., kg[dry]/ha or acorns/m^2) of acorn yield among individual trees (Canellas et al. 2007). I calculated coefficients of variation (CV) as the standard error (SE) of the mean mass or mean number of acorns divided by each respective mean (Stafford et al. 2006). Because my primary sampling unit was the seed trap, means and SEs were based on number of trees sampled per site and year. Within years, I produced a MAV-wide estimate of red oak acorn yield by using design based weights of individual trees. This approach skewed the MAV-wide estimate toward individuals from larger study areas, because these trees had disproportionate influence on the mean (Levy and Lemeshow 2011). I used design based weights from trees within years to estimate mean mass and mean number of acorns across all years and the MAV.

Covariates of Red Oak Acorn Yield

All Trees

I used a generalized liner model in R version 2.13.2 (R Development Core Team 2012) to model relationships between yield of sound acorns (i.e., acorns/m^2 red oak crown) and measured covariates. I used the autumn-winter cumulative number of acorns per trap as my response variable instead of mass, because 1) number and mass of acorns per tree were positively correlated ($r = 0.81$, $n = 493$, $P < 0.001$), 2) tested models fit variation in number of acorns better than mass, and 3) acorn numbers fit a negative binomial distribution ($\chi^2 = 283.6$, df = 423, $P = 0.99$) justifying use of a generalized linear models.

Covariates included fixed factors (i.e., study area [SITE], species [SPP], and crown class [CRWCL], plus continuous variables (i.e., DBH, basal area of conspecifics within plots [BA], number of heterospecifics [HETSPC] per plot, and 2 quadratic terms (e.g., DBH^2, BA^2). I included quadratic terms, because acorn yield is often non-linear relative to tree size (Greenberg and Parresol 2002, Leach 2011).

I used a generalized linear model and specified the negative binomial distribution and log link function to model cumulative number of sound red oak acorns captured per trap. I used a stepwise backwards selection procedure which included starting with the most complex model and removing the least significant term until model fit ceased improving (Juliano 2001). I based assessments of model fit on Akaike's Second Order Information Criteria (AIC*c*; Burnham and Anderson 2002). I removed an effect if a nested model had a lesser AIC*c* value than the higher order model (Zuur et al. 2009). I considered the highest-order interactions initially and then main effects, ensuring main effects were retained if interactions of these were supported.

I present untransformed parameter estimates (β) with 95% confidence intervals for best models. I exponetiated (e.g., antilog) parameter estimates to present them on their original scale (e.g., number of acorns/m^2; Guthery 2007, Kabacoff 2011). I grouped cherrybark and water oaks into one group as these species had the smallest sample sizes and to meet assumptions of homogeneity. As a result, my models created separate estimates for Nuttall, pin, and willow oaks and cherrybark and water oaks combined.

Mast Trees

Masting is defined as the synchronous intermittent production of large seed crops in perennial plants (Kelly 1994). My data were consistent with this trend as many trees produced few or no acorns among all years and sites. Therefore, I analyzed only trees that exhibited masting behavior (*n* = 78; hereafter mast trees). For each tree, I defined a masting year as one in which the annual standardized deviate of acorn yield was greater than the absolute magnitude of the variation below the mean (i.e.,[(mean number of acorns in year *t* – 3-year mean number of acorns) / SD among years];Lamontagne and Boutin 2007; 2009). I used similar modeling procedures as described above to model the effect of DBH, BA, SPP, HETSPC, and number of conspecifics (CONSPC) on mast trees. However, because sample size was substantially smaller, I reduced the complexity of the full model (Table 1.2).

Masting Characteristics

I assessed temporal variability in acorn yield for each red oak species within study areas and across species within areas using the following parameters (Herrera 1998, Koenig et al. 2003) 1) inter-specific synchrony (r_p), calculated as mean of all pair-wise Pearson product-moment correlations of annual means of acorn yield among species and years 2) mean individual synchrony (r_i), calculated as mean of all pair-wise Pearson correlations of annual yield for individual trees across years (Buonaccorsi et al. 2001), 3) community variability calculated as mean coefficient of variation (CV_c) of annual mean acorn yield among species across years and 4) individual variability (CV_i) calculated by averaging across individuals the coefficient of variation for acorn yield across years for each individual. I used acorn counts (acorns/m^2 of red oak canopy) in calculating all parameters. I calculated CV as SD/mean to be consistent with the literature (Koenig et al. 2003, Liebhold et al. 2004b), thus allowing comparisons with other masting studies. I calculated MAV-wide synchrony of acorn yield by taking the mean of all pair-wise Pearson correlations of annual mean across years (Table 1.4).

Results

Red Oak Acorn Yield

I estimated acorn yield from 161, 173, and 159 red oak trees during autumn-winters 2009-2010, 2010-2011, and 2011-2012, respectively. Distributions of acorn mass and number of seeds were heavily right skewed with few trees producing most acorns (Appendix A). For example, 9, 13, and 17 trees yielded ≥50% of all acorns produced during these 3 years. Accordingly, median mass and number of acorns for all sites and years were always less than yearly multi-stage means.

Across years, mass ($\bar{x}$ =1,790 kg/ha [SE = 318]; Fig. 1.2) and number of acorns ($\bar{x}$ = 120.9 acorns/m^2 [SE = 23.4]; Fig. 1.2) were greatest at Chickasaw NWR during 2010-2011. In contrast, acorn mass was least ($\bar{x}$ =100 kg/ha [SE = 59]; Fig. 1.2) at Mingo NWR during 2009-2010, and number of acorns fewest ($\bar{x}$ =9.0 acorns/m^2 [SE = 3.5]; Fig. 1.2) at Delta NF during 2011-2012. The MAV-wide estimates of acorn mass and numbers increased for each year, whereas variation decreased (Table 1.1). Across all years and study areas, red oak acorn mass was $\bar{x}$ =534 kg/ha (SE = 38) and $\bar{x}$ = 42.3 acorns/m^2 (SE = 5.5); coefficients of variation for each estimate was <15% (Table 1.1).

Mean mass of red oak acorns was most variable across years at Chickasaw NWR, where trees produced 13.8 times more acorns during 2010-2011 than the previous year

(Fig 1.2). By contrast, yield was most consistent across years at Tensas River NWR, where the disparity between most and least acorn mass was only two-fold (i.e., 190 and 452 kg/ha).

Variables Influencing Red Oak Acorn Yields

All Trees

I censored data from one tree at Mingo NWR from analysis of 2010-2011 and 2011-2012 data, because it was an outlier invoking disproportionate leverage on results. Models explaining variation in red oak acorn yield differed among years (Table 1.2) and were more complex (i.e., contained additional parameters) in 2010-2011 and 2011-2012 compared to 2009-2010. The variables SITE, DBH, and CRWCL were included in the reduced models for all years.

In 2009-2010, variation in acorn yield was best explained by a model with 9 parameters containing additive effects of SITE, DBH and CRWCL (Tables 1.2 Appendix B). Fixed effects from the best model indicated acorn yield was greatest at Delta NF ($\bar{x}$ = 33.8 acorns/m^2; 95% CI = 19.6 ─ 58.5) followed by White River NWR ($\bar{x}$ = 29.7; 95% CI = 14.0 ─ 63.2), Tensas River NWR ($\bar{x}$ = 15.3; 95% CI = 7.4 ─ 32.0), Mingo NWR ($\bar{x}$ = 6.6; 95% CI = 3.7 ─ 11.4), and Chickasaw NWR ($\bar{x}$ = 2.1; 95% CI = 1.1 ─ 3.9). Across study sites, acorn yield was related positively to DBH (β = 0.026, SE = 0.007, 95% CI = 0.011- 0.041). Acorn yield was greatest for trees with dominant crowns ($\bar{x}$ = 17.2; 95% CI = 9.5 ─ 31.1), followed by co-dominant ($\bar{x}$ = 9.2; 95% CI = 6.3 ─ 13.4), and suppressed crowns ($\bar{x}$ = 4.5; 95% CI = 2.0 ─ 10.2).

In 2010-2011, variation in acorn yield was best explained by a model with 17 parameters (Tables 1.2, Appendix B). Fixed effects indicated acorn yield was greatest for trees with dominant ($\bar{x}$ = 20.1; 95% CI = 12.2 — 33.2), followed by co-dominant ($\bar{x}$ = 12.3; 95% CI = 8.6 — 14.5), and suppressed crowns ($\bar{x}$ = 6.7; 95% CI = 3.1 — 14.5). Acorn yield was related to DBH, but this relationship varied by SITE. Acorn yield increased with DBH at Chickasaw NWR (β = 0.037, 95% CI: 0.016, 0.059) and Delta NF (β= 0.011, 95% CI: -0.020, 0.042) NWRs, but no effect of DBH on acorn yield was detected for trees at Tensas River NWR (β= 0.000, 95% CI: -0.034, 0.035) whereas yield decreased with DBH at White River NWR(β = 0.021, 95% CI: -0.054, 0.015) and Mingo NWR (β = -0.012, 95% CI: -0.042, 0.019). Acorn yield varied by species and was greatest for cherrybark and water oaks ($\bar{x}$ = 70.7; 95% CI = 36.3 — 137.9), followed by willow ($\bar{x}$ = 14.1; 95% CI = 8.0 — 25.1), Nuttall ($\bar{x}$ = 9.7; 95% CI = 6.2 — 15.0), and pin ($\bar{x}$ = 8.6; 95% CI = 4.6 — 15.9) oak acorns. Acorn yield increased with BA per plot (β = 0.329, 95% CI: 0.023, 0.645).

In 2011-2012, variation in acorn yield was best explained by a model with 16 parameters (Table 1.2, Appendix B). Acorn yield was related to DBH but the relationship varied by SITE. Acorn yield increased with DBH at Chickasaw (β= 0.029, 95% CI: 0.008, 0.051) and White River NWRs (β = 0.002, 95% CI: -0.035, 0.042), exhibited no detectable trend at Tensas River NWR (β= 0.000, 95% CI: -0.036, 0.037), and decreased at Delta NF (β= -0.015, 95% CI: -0.047, 0.018) and Mingo NWR (β = -0.005, 95% CI: -0.037, 0.026). Acorn yield was greatest for trees with dominant ($\bar{x}$ = 44.1; 95% CI = 26.5 — 73.6), followed by co-dominant ($\bar{x}$ = 22.9; 95% CI = 16.6 — 31.6) and suppressed crowns ($\bar{x}$ = 6.8; 95% CI = 3.3 — 14.2). Predicted number of acorns was greatest for willow ($\bar{x}$ = 59.2; 95% CI = 34.1 ─ 102.6), followed by cherrybark and water ($\bar{x}$ = 33.6; 95% CI = 16.8 ─ 66.8), pin ($\bar{x}$ = 17.8; 95% CI = 9.7 ─ 32.8), and Nuttall ($\bar{x}$ = 16.8; 95% CI = 11.2 ─ 25.2) oaks.

Mast Trees

Across years and sites, 78 trees (15.8%) masted (range = 46 – 425 acorns/m^2); these included 5 cherrybark, 23 Nuttall, 12 pin, 19 water, and 19 willow oaks. Variation in acorn yield was best explained by a model with 3 parameters (Table 1.2). The relationship between number of acorns produced was positively related to DBH (β = 0.008, 95% CI: 0.003, 0.013), although the effect was weak (i.e., 1 cm increase in DBH multiplied the expected number of acorns only by 1.008; 95% CI = 1.003 ─ 1.013).

Masting Characteristics

Inter-specific and individual synchrony and community and individual variability varied by red oak species within and among sites (Table 1.3; Fig 1.4). The community of red oak species sampled at Delta NF exhibited the greatest annual variability ($CV_{p\,=}$ 0.687), whereas those at Tensas River NWR exhibited the least (CV_p = 0.264). Cherrybark oaks at Mingo NWR had the greatest annual variability (CV_p = 1.274) among all red oak species-site combinations, although this estimate was based only on 3 trees (i.e., $\bar{x}$ = 2.7, 169.0 and 9.3 acorns/m^2 for years 1-3, respectively). By contrast, water oaks at Tensas River NWR (n = 9) showed the least annual variability (CV_p = 0.359) among all species-site combinations ($\bar{x}$ = 28.0, 48.9 and 71.4 acorns/m^2 for years 1-3, respectively).

Inter-specific acorn yield was synchronous at all study areas except White River NWR. Within sites, acorn yield was synchronous for all species except willow oaks at Tensas NWR. Across all sites, red oak acorn yield was not synchronized (mean pair-wise *r* = -0.212; Fig 1.3). However, acorn yield was synchronized between Chickasaw NWR and Mingo NWRs (*r* = 0.939) and between Delta NF and White River (*r* = 0.959; Table 1.4).

Discussion

Red Oak Acorn Yield

My study provided premiere landscape multi-year estimates of red oak acorn yield in the MAV. My sampling design did not discriminate among species of red oaks ≥25cm DBH or canopy dominance. Therefore, my estimates include variation from these sources. Although acorn yield varied among sites, years, species, and individual trees, the MAV-wide annual estimates of acorn yield were relatively consistent (range of annual CVs = 11 - 29%). Although some sites produced few acorns in some years, low mast production never occurred at all sites and in all years. Thus, annual mean yield of red oak acorns was always > 442 kg (dry) /ha across the MAV and ranged as high as 580 kg/ha. Individual variability also was great as some red oak trees produced >5,000 kg/ha of acorns in a year, but most trees (56%**,** *n* = 274) produced <150 kg/ha. Although I monitored trees for only 3 years, my data suggest red oak acorn yields are decoupled at the scale of the MAV, because I never observed a complete mast failure at any of my study areas.

Overall estimates of acorn mass were precise in each year except 2009-2010. However, across years, the CV was <11%. The CVs for estimates of acorn numbers were

>15% within each of the 3 years, but the across year CV was 13%. Thus, I met my a *priori* desired level of precision (i.e., CV ≤ 15% for estimates of acorn mass and numbers by combining data among years).

Sample size influences precision. Compared to other landscape-scale surveys of food resource abundance for wildlife, I achieved greater precision with fewer samples. For instance, Stafford et al (2006) sampled autumn waste-rice abundance in the MAV and collected 400, 690, and 500 samples in 3 years and achieved CVs of 24, 23 and 31%, respectively. In comparison, I collected 161, 153, and 169 samples during 3 years and achieved a CV < 15% in all but one year. Across years, I collected and processed 70% fewer samples (493 vs. 1,590) than Stafford et al. 2006 but achieved 30% more precision than these authors (i.e., CV = 10.9% vs. 15.4%). Similar patterns existed in surveys by Kross et al. (2008) and Straub et al (2012), who sampled wetland seed and tuber abundance in the MAV and Upper Mississippi River and Great Lakes Regions, respectively. Kross et al. (2008) collected >700 more samples than I did, yet their three-year CV was 12.5%. Additionally, Straub et al. (2012) collected >900 samples to achieve a CV of 11.4% across years.

Relationships between sample size and precision are important to consider when designing surveys to estimate resource abundance. I suggest the aforementioned differences may be due to sampling and collecting acorns from individual trees versus aggregates of a diversity of seeds from multiple parent plants (Stafford et al. 2006, Kross et al. 2008, Straub et al. 2012). Stafford et al. (2006) collected and estimated only rice abundance, but each core sample likely contained grains from multiple parent plants which could have introduced variation in mass of grains from different plants. Core samples collected by Kross et al. (2008) and Straub (2012) contained seeds and tubers from numerous individual moist-soil plants of different species. Because I sampled acorns from individual trees, my estimates were not confounded by variation from other individual trees or species, unless acorns from nearby trees were wind-blown or dropped by wildlife into my seed traps. I was not able to assess this possibility but believe it rarely or never occurred. Thus, I was able to achieve increased precision associated with my estimates of acorn mass with fewer samples. Although sampling from individual plants may be more time consuming, it is certainly practical with oak trees because researchers can easily return to each tree annually. As such, if researchers are interested in maximizing precision and minimizing samples needed, sampling individual trees is most efficient and effective.

To compare relative yields of acorns at sites across years, I will use criteria established by Greenberg and Parresol (2002): 1) poor (i.e., <60% of mean annual yield), 2) moderate (i.e., >60% and up to the mean), and 3) good acorn yield (i.e., > the mean). I used the MAV-estimate of 534 kg/ha as mean for comparisons. All sites had at least one year of good and poor yield except Tensas River NWR which had 2 poor years followed by a moderate year, which was the only site-year combination classified as moderate in my study. Among all 15 site-year combinations, there were 7 good and 7 poor combinations, plus the single moderate classification.

I cannot directly compare my results with those of other studies of acorn yield because of different methods used to measure (i.e., traps vs. visual counts) and express yield (numbers vs. mass of acorns) and because my study was first to estimate yield of acorns from a suite of bottomlan red oak species. I can however make valid comparisons to other studies in terms of patterns. For instance, the pattern in my study of few oak trees producing most acorns resulting in large individual variability was consistent with other acorn studies (Healy 1999, Greenburg 2000, Lashley et al. 2009). For example, I collected 571 acorns from one willow oak tree in 2010-2011 at Mingo NWR; while, in 2009-2010, I collected only 233 acorns from all 40 trees at that site. Heterogeneity in individual yield capability (Koenig et al., 1991; Sork et al.1993) and competition (Healy et al. 1999) may influence total yield. In my study, I selected red oak trees randomly and with minimal bias, thus my estimates did include the spectrum of acorn producers including those that produced no, few, or many acorns. Indeed, my results suggest that sampled red oak trees follow patterns of large individual variability similar with oaks elsewhere in North America (Sharp and Sprague 1967, Christisen and Kearby 1984, Koenig et al. 1991, Sork et al.1993, Liebhold et al. 2004*b*).

Although I did not measure effects of variation in acorn yield on wildlife populations, I suggest several predictions specific to wildlife using bottomland hardwood forests. Because acorn yield varied greatly among years at a site, non-migratory species that seasonally rely on acorns likely would be most affected by poor acorn crops (Christisen and. Korschgen 1955). In such instances, species such as mice (*Peromyscus* spp.), squirrels (*Sciurus* spp.), white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), and black bear (*Ursus americanus)* may switch winter diets from primarily red oak acorns to other foods (Korschgen 1981, Dickson 2001), which may result in increasing home range sizes with survival and other possible demographic consequences (Rogers 1987, Kelley et al. 1988, Costello 2010, Koike et al. 2012). Species that cannot find suitable alternative food items may experience population declines (Pelton 1989, McShea and Schwede 1993, Ostfeld et al. 1996, McShea 2000). Because of the current isolated nature of most bottomland hardwoods stands in the MAV (Twedt and Loesch 1999), the effect of mast crop failures may impact sedentary species (McShea et al. 2007). On the other hand, migratory species that annually forage in red oak dominated forests of the MAV (Dabbert and Martin 2000, Heitmeyer 2006), such as mallards and wood ducks, may be less adversely affected or not at all by poor acorn crops at the local scale. These species can potentially take advantage of the spatially asynchronous nature of red oak acorn yield in the MAV by dispersing to areas of increased acorn or other food abundance (Heitmeyer 2006). Unfortunately, studies that link population dynamics of migratory and non-migratory species to mast cycles in the MAV are non-existent, although they exist for other ecosystems inhabited by oaks (McShea 2000, Ostfeld and Keesing 2000, Clotfelter et al. 2007). I encourage researchers to extend my work by studying short and long-term implications of masting on wildlife populations to enhance understanding of wildlife foraging and population ecology in hardwood bottomlands in the MAV (Koenig and Knops 2000).

Variables influencing Red Oak Acorn Yield

Factors influencing yield of red oak acorns varied among years; however, several patterns emerged. Clearly, differences among sites, tree size, and crown classes explained variation in acorn annual yields. Large differences among sites were explained by asynchronous acorn yields within years. Acorn yield varied by ≤14 times between the most and least productive sites within years. Concomitantly, DBH varied substantially among sites.

Although DBH appeared in the most parsimonious models, it only occasionally had a positive linear effect on acorn yield and no effect in most site-year combinations. Therefore, acorn yield in the MAV seemed relatively invariant of DBH, which was consistent with other studies (Greenberg and Parresol 2002, Liebhold et al. 2004*b*, Lashley et al. 2009, Rose et al. 2012). For instance, across all sites in 2009-2010, a 1-cm increase in DBH only multiplied expected yield by 1.026 acorns/m^2. In 2010-2011 and 2011-2012, effect of DBH only explained variation in acorn yield at Chickasaw NWR, and there, a 1-cm increase in DBH only multiplied expected yield of acorns by 1.038 and 1.029 acorns/m^2 in these years, respectively. Finally, although DBH was the sole variable in the most robust model among trees that masted, it explained <10% of the variation in acorn yield. Clearly, tree size was not a consistent predictor of acorn yield among red oaks in the MAV. Nonetheless, a minimum 25 cm DBH and associated age generally are required for acorn production (Dey 1995).

Although I failed to find a strong relationship between acorn yield and DBH, red oaks with dominant crowns produced most acorns followed by those with co-dominant and suppressed crowns. I expected this result because dominant trees are known to flower and fruit abundantly (Goodrum et al. 1971, Healy 2002). Forest and wildlife managers can expect to attain maximal acorn yield from trees with dominant crowns. Indeed, releasing the crown of individual trees has shown to increase acorn yield (Healy 1997), but managers should be cautious not to thin oak stands excessively because thinning stands has resulted in decreased acorn yield at a large scale (Beck 1993, Healy 2002). I did not measure crown volume, but trees with developed crowns have the potential to yield more acorns because of increased branching and acorn production sites.

Although I was unable to find a linear relationship with tree size, my data indicate that dominant canopy red oaks consistently produced the greatest density of acorns.

I explored the possibility that numbers of conspecific red oaks per plot may influence acorn yield by sampled trees. I included this variable because, although oaks are monoecious, individual red oaks may benefit by increased density and flower pollination from neighboring conspecifics (Koenig and Ashley 2003, Sork et al, 2002). Alternatively, too many conspecifics might increase competition and reduce acorn yield (Healy 1997, Guariguata and Sáenz 2002). I failed to find any evidence that density of conspecifics affect acorn yield. However, a related variable, total basal area of conspecifics per plot did have an influence from the relationship of volume of red oaks present per plot. Leach (2011) found a non-linear relationship between basal area of conspecifics and acorn yield where number of acorns increased until a certain threshold and then decreased. Similar to Leach (2011), I found acorn yield increased, although linearly with basal area. I found that a 1-m^2 increase in basal area within plots multiplied expected yield by 1.39 acorns/m^2. I cannot explain why basal area of conspecifics influenced acorn yield only in one year during my study. Perhaps red oaks surrounded by increasingly larger conspecifics produced more acorns than conspecifics surrounded by smaller oaks. I suspect these larger red oaks had more developed crowns and thereby increased pollination efficiency of all neighboring conspecifics. My findings from 2010-2011 support the hypothesis that increased pollination efficiency increases acorn yield (Kelly and Sork 2002, Koenig and Ashley 2003).

Many interacting factors and events influence ontogeny of red oak acorns (Miyazaki 2011). Compounding these dynamic relationships is that red oak acorns require 2 growing seasons to mature (Johnson et al. 2009). Therefore, factors including weather conditions during female and male flowering episodes (Sork et al. 1993, Cecich 1997), arboreal removal of acorns (Koenig et al. 2001), and insect predation (Lombardo and McCarthy 2008) may influence numbers of sound acorns produced. However, my study was one of few to examine how local scale variables influence acorn crops from individual trees. Most studies have focused on large scale environmental change (Sork et al. 1993, Pons and Pausas 2012) and population level variability (Liebhold et al. 2004*a*). I developed models to predict red oak acorn yield by and among individual trees; the models explained 10-50% of overall variation. Apparently, variables such as DBH, density, and volume of conspecifics and heterospecifics do not have considerable influence on acorn yield within and among sites and years. Given the large variability among sites within years, I hypothesize that variation in red oak acorn yield in the MAV is driven largely by higher order influences (e.g., weather, hydrology, soil characteristics, etc.) and genetics more so than local scale influences. Indeed, there is a considerable knowledge gap regarding effects of site productivity, soil nutrients, and hydrology on yield of red oak acorns. These factors might be particularly pertinent for red oaks in hardwood bottomlands given the periodic and dynamic influx of allochtonous nutrients in alluvial floodplains compared to oaks that grow on more mesic and xeric sites (Hunter et al. 2008, McKee et al. 2012).

Masting Characteristics

According to Liebhold et al. (2004*b*), if yearly fluctuation in seed yield occurred randomly, then CV_p would approximate 1, whereas if "strict" masting occurred then CV_p of ~2 would be expected. Under strict masting, distribution of seed crops is predicted to be bimodal, wherein some years no seeds are produced, whereas other years many are produced (Kelly 1994). Polycarp species, such as *Quercus*, tend to exhibit "normal" masting, in which distribution of annual seed crops tend to be normally distributed among trees and trees produce at least some seeds every year but also have heavy production years (Kelly 1994). Similar to other studies on oak acorn yield in North America (Kelly 1994, Koenig et al. 2003, Liebhold et al. 2004*b*), the CV_p for most red oaks was ≤ 1. In one instance, CV_p was 1.2 for cherrybark oak at Mingo NWR, but this value was based on only 3 trees. Thus, most red oaks in my study exhibited "normal" masting. However, I monitored only for 3 successive years; therefore, I may not have encountered the full range of variation in acorn yield in the MAV. Consequently, I recommend further monitoring of the trees sampled in my study.

The annual variability recorded in acorn yield was within the range of other reported values for *Quercus* spp. in North America. Koenig et al. (2003) summarized annual variability in acorn yield and found that CV_p values ranged as great as 198 for California black oak (*Q.s kelloggii*) and as low 36 as for northern pin oak (*Q.s ellipsoidalis*). Although variability in acorn yield among the 5 species in my study (CV_p range = 36-127) was within the range reported for other masting studies, my values were toward the lower end of the range. Average CV_p for oaks reported by Koenig et al (2003) was 93, whereas the average among my 14 site-species values was 67. If values reported by Koenig et al. (2003) represent characteristics of *Quercus* spp. in general, red oaks in the MAV appear to exhibit less annual variability in acorn yield than oaks elsewhere. A possible reason for this difference may be nutrient availability. Red oaks in bottomland hardwood forests may receive a more consistent influx of nutrients compared to oaks in mesic and xeric environments (Hunter et al. 2008, McKee et al. 2012).

Clearly, red oak acorn yield is asynchronous spatially and temporally at the scale of the MAV (Fig 1.3). Nonetheless, acorn yield was highly synchronous between Mingo and Chickasaw NWRs and between Delta NF and White River NWR. Mingo and Chickasaw NWRs were the most northerly sites sampled in the MAV; the latter NWR is about 135 km southeast of Mingo NWR. Each site exhibited a near mast failure during 2009-2010, then had 2 good years of yield during 2010-2012. White River NWR, which is about 155 km northwest of Delta NF, had good acorn yield in 2009-2010, followed by a sharp decline in 2010-2011, and then a slight increase in 2011-2012. Because these sites were close geographically and showed synchrony in acorn yield, I suspect weather cues may have influenced acorn yield (Liebhold et al. 2004*b*, Peter and Harrington 2009). I agree and concur with Leach (2011) that poor acorn yield at Mingo and Chickasaw NWRs during 2009-2010 may have been caused by frost in late-spring 2008, which potentially killed red oak flowers that otherwise may have produced sound acorns in autumn 2009 (Goodrum et al. 1971, Sork et al. 1993, Kelly and Sork 2002, Koenig and Knops 2002). Weather events may be a primary proximate cue of synchrony in acorn yield. Although no frost events influenced acorn crops at White River NWR and Delta NF, I suspect other environmental cues were responsible for yield differences between these sites.

Environmental cues alone cannot completely explain synchrony between sites, because Tensas River NWR is only 60 km south and west of Delta NF and acorn yield at these sites was highly asynchronous. Although Tensas and White River NWRs and Delta

NF likely experienced similar weather conditions given their close proximity, there are stark differences in site, hydrologic, oak species, and soil conditions among these sites. Perhaps the most striking difference is forest species composition, which is indicative of relative differences among the sites. White River NWR and Delta NF are similar and characterized as a "low" bottomland hardwood forest, dominated by flood tolerant Nuttall and overcup oak (*Q. lyrata*) and bald cypress (*Taxodium distichum*) with a sparse or non-existent understory. Tensas River NWR is dominated by less flood tolerant species, such as water and willow oaks and sweet gum (*Liquidambar styraciflua*). Also, the mid- and understory is well developed and dense at Tensas River NWR, often comprised of vast amounts of saw palmetto (*Serenoa repens*). I suspect differences in species composition and local site conditions among these sites influenced asynchrony in acorn yield. Variation in red oak acorn yield in the MAV is apparently not simply a function of weather (Kelly and Sork 2002, Koenig and Knops 2005).

Although red oak acorn yield was asynchronous at the scale of the MAV, I found evidence of inter-specific synchrony within sites ($-0.25 \leq r \leq 0.99$; Table 1.3). In fact, inter-specific synchrony in acorn yield was evident at all sites, except White River NWR. At Delta NF, inter-specific synchrony was near perfect, because willow and Nuttall oaks had their greatest acorn crops in 2009-2010, followed by their least in 2010-2011 and a slight rebound in 2011-2012. Although the magnitude of acorn yield differed between the 2 species, their pattern across the 3 years was similar. By comparison, red oaks at White River NWR showed asynchrony, considering that Nuttall oak acorn yield showed large variation among years, whereas willow oak acorn yield increased annually. Inter-specific synchrony in mast yield has been reported for other oak and tree species

(Liebhold et al. 2004*a*, Liebhold et al. 2004*b*). Because inter-specific synchrony existed at 4 of 5 sites, I believe this phenomenon is further evidence that higher order influences, such as resource patterns (hydrology) or weather, influence annual yield of red oak acorns in the MAV. I suggest researchers evaluate effects of climatological, hydrological, soil, and other variables likely linked to acorn yield (Sork et al. 1993, Koenig et al. 1996, Pons and Pausas 2012).

Generally, inter-specific annual variability was less than intra-specific annual variability in yield at all 5 sites. This finding suggests that total acorn yield across species at a site was generally more uniform through time than was mast yield within species. This effect dampens the overall pulsed nature of masting at a site because, although some species might exhibit great annual variation, red oaks in general exhibited much less variability. This finding has implications for the grainivores of red oaks. Whereas some forests are dominated by one mast producing oak species, hardwood bottomlands in the MAV are known for their diversity of oaks and other mast producing hardwoods (e.g., *Carya spp.*; Johnson et al. 2009). Wildlife and other grainivores that depend on acorns during fall and winter in the MAV might have more stable food supplies compared to areas where oak and other mast producers are less diverse or abundant, because complete mast failures are less likely (McShea 2000, Greenberg and Parresol 2002).

Management and Research Implications

Acorn yield is temporally and spatially asynchronous in the MAV, and I never encountered a year when all 5 sites had a mast failure or a superabundant crop. At more local scales, forest managers can enhance acorn yield of individual trees by maintaining and managing for red oaks with dominant crowns. However, this approach must be balanced with the potential negative effects of removing some red oaks from the forest stand (Healy et al. 1999). Also, my results indicate that total red oak acorn yield at a site was generally more uniform through time than was mast production for individual species within a community. As such, managers have a greater probability of dampening the effect of mast failures if they manage for a diversity of red oaks as opposed to favoring just one species. Furthermore, managers do not need too great a density of oaks because I found that density and volume of neighboring oaks did not decrease individual tree yield.

My study was one of the few to examine local factors and their potential role in explaining acorn yield. Factors explaining variation in acorn yield are complex and for the most part unrelated to tree size or density and volume of conspecifics. I suggest researchers examine other factors that may influence red oak acorn yield in the MAV, such as age (Goodrum et al. 1971), weather (Koenig et al. 1996, Pons and Pausas 2012), hydrology, soil (Wolgast and Stout 1977), and other site-specific covariates. There is a considerable knowledge gap in site productivity, soil nutrients and hydrology for bottomland red oaks in particular. Given the annual fluctuations and importance of these variables in bottomland hardwoods, I suggest researchers design studies to explore relationships between acorn yield and soil and hydrology parameters.

Although my 3-year study is the longest tenured research on red oaks in the MAV, there were many important ecological questions I was unable to answer given this brief time period relative to other masting studies (Greenberg and Parresol 2002, Abrahamson and Layne 2003, Liebhold et al. 2004*a*). Answers to these questions could help inform conservation decisions. For instance, I was unable to determine inter-masting interval or time between large mast crops. Even if the inter-mast interval was as brief as 3 years, it would take at least 6 years of annual monitoring to detect this. If scientists had better understanding of the inter-mast interval they could better predict which years would have the greatest acorn yield. Also, masting in oaks has been at least partially explained by a resource depletion phenomenon (Sork et al. 1993, Koenig and Knops 2000). A common method to test this theory is to examine individual variation in endogenous cycles by calculating an autocorrelation function over many years (Koenig and Knops 2000, Liebhold et al. 2004*b*). Scientists calculate correlograms consisting of the ordered autocorrelation functions for time lags of 1-5 years. As such a minimum of 6 years of monitoring is required to adequately test this hypothesis. Because oaks are an integral forest component (McShea et al. 2007), I strongly suggest research continue for preferably >10 years with the goal of better understanding oak masting dynamics and bottomland hardwood ecology in general.

Table 1.1 Estimated multi-stage sampling means ($\bar{x}$), standard errors (SE), coefficients of variation (CV), and medians of acorn mass and numbers collected under crowns of red oaks in the Mississippi Alluvial Valley, autumns – winters 2009–2012.

		Mass (kg / ha)				Number (n acorns / m^2)			
Year	*n* trees	$\bar{x}$	SE	CV[a] (%)	median	$\bar{x}$	SE	CV[a] (%)	median
2009-2010	161	442	130	29.4	42	23.7	4.7	19.8	2
2010-2011	173	574	82	14.3	188	49.2	8.9	18.2	11
2011-2012	159	580	66	11.4	179	53.1	8.6	16.2	14
All years	493	534	58	10.9	113	42.3	5.5	13.1	7

[a] CV=[SE/mean] x 100

Table 1.2 Models used to explain variation in yield of sound red oak acorns in bottomland hardwood forests in National Wildlife Refuges (NWR) and a National Forest in the Mississippi Alluvial Valley, autumns-winters 2009-2012.

Autumn-winter/mast trees	Model[a]	K	AIC_C	ΔAIC	deviance explained
2009-2010	Reduced model = SITE +DBH + CROWN CLASS	9	1054.0	0.0	34.2
	Saturated model[b]	24	1062.8	8.8	43.2
2010-2011	Reduced model = SITE x DBH +BA + CROWN CLASS + SPECIES	17	1318.9	0.0	49.0
	Saturated model[b]	24	1324.0	5.0	52.8
2011-2012	Reduced model = SITE x DBH + CROWN CLASS + SPECIES	16	1385.3	0.0	34.8
	Saturated model[b]	24	1397.8	12.6	37.0
Mast trees	Reduced model = DBH + BA	4	888.6	0.0	9.5
	Saturated model[c]	9	895.8	7.2	17.4

[a] Explanatory variables include study site (SITE), tree diameter at breast height (DBH), tree canopy crown class (CRWCL), species (SPP), basal area of red oaks (*Quercus* spp; Section *Erythrobalanus*) ≥25 cm DBH per sample plot (BA), number of heterospecifics per sample plot (HETSPC) and number of conspecifics per sample plot (CONSPC).

[b] Saturated model = (DBH x SITE) + (BA x SITE) + SPP + CRWCL + HETSPC + DBH^2 + TREE $DENSITY^2$

[c] Saturated model = DBH + BA + SPP + CONSPC + HETSPC

Table 1.3 Coefficients of variation (CV_p,CV_i) and degree of synchrony (r_p, r_i), for 5 species of red oak species at 5 study areas in bottomland hardwood forests in the Mississippi Alluvial Valley, autumns-winter 2009-2012.

Study area	Species	n^a	CV_p^b	CV_i^c	r_p	r_i^d
Chickasaw	Cherrybark	3	0.755	1.183		0.126
	Nuttall	17	0.598	1.099		0.521
	Pin	14	0.684	1.078		0.838
	Water	6	0.883	1.196		0.427
	all red oaks	40	0.638	1.115	0.750	0.563
Delta	Nuttall	31	0.559	1.242		0.141
	Willow	8	0.757	1.113		0.179
	all red oaks	40	0.687	1.201	0.999	0.186
Mingo	cherrybark	3	1.274	1.537		0.997
	Pin	25	0.514	0.961		0.520
	Willow	12	0.708	1.083		0.641
	all red oaks	40	0.605	1.040	0.549	0.530
Tensas River	Nuttall	12	0.491	0.852		0.607
	Water	9	0.359	0.754		0.129
	Willow	11	0.525	1.164		-0.056
	all red oaks	32	0.264	0.934	0.415	0.244
White River	Nuttall	18	0.530	1.159		
	Willow	3	0.599			
	all red oaks	22	0.467	1.137	-0.250	
MAV	all red oaks		0.304	[e]	-0.212	

[a] Sample sizes refers to number of trees sampled.

[b] Calculated as coefficient of variation (CV=[SD/mean]x100) of the annual means across years.

[c] Calculated by averaging coefficient of variations for acorn yield across years within individual red oak trees.

[d] Calculated as mean of all pair-wise Pearson correlations between individual trees across years.

[e] Blanks denote small sample size and no calculation of parameter.

Table 1.4 Correlation coefficients of annual mean red oak acorn yield among 5 study sites in the Mississippi Alluvial Valley 2009-2012.

	Delta	Mingo	Tensas River	White River
Chickasaw	-0.925	0.939	0.252	-0.995
Delta	[a]	-0.999	-0.602	0.959
Mingo			0.570	-0.969
Tensas River				-0.349

[a] Blanks denote meaningless autocorrelation.

Figure 1.1 Locations of study areas within the Mississippi Alluvial Valley (red outline) where red oak acorn production was estimated during falls and winters, 2009-2012.

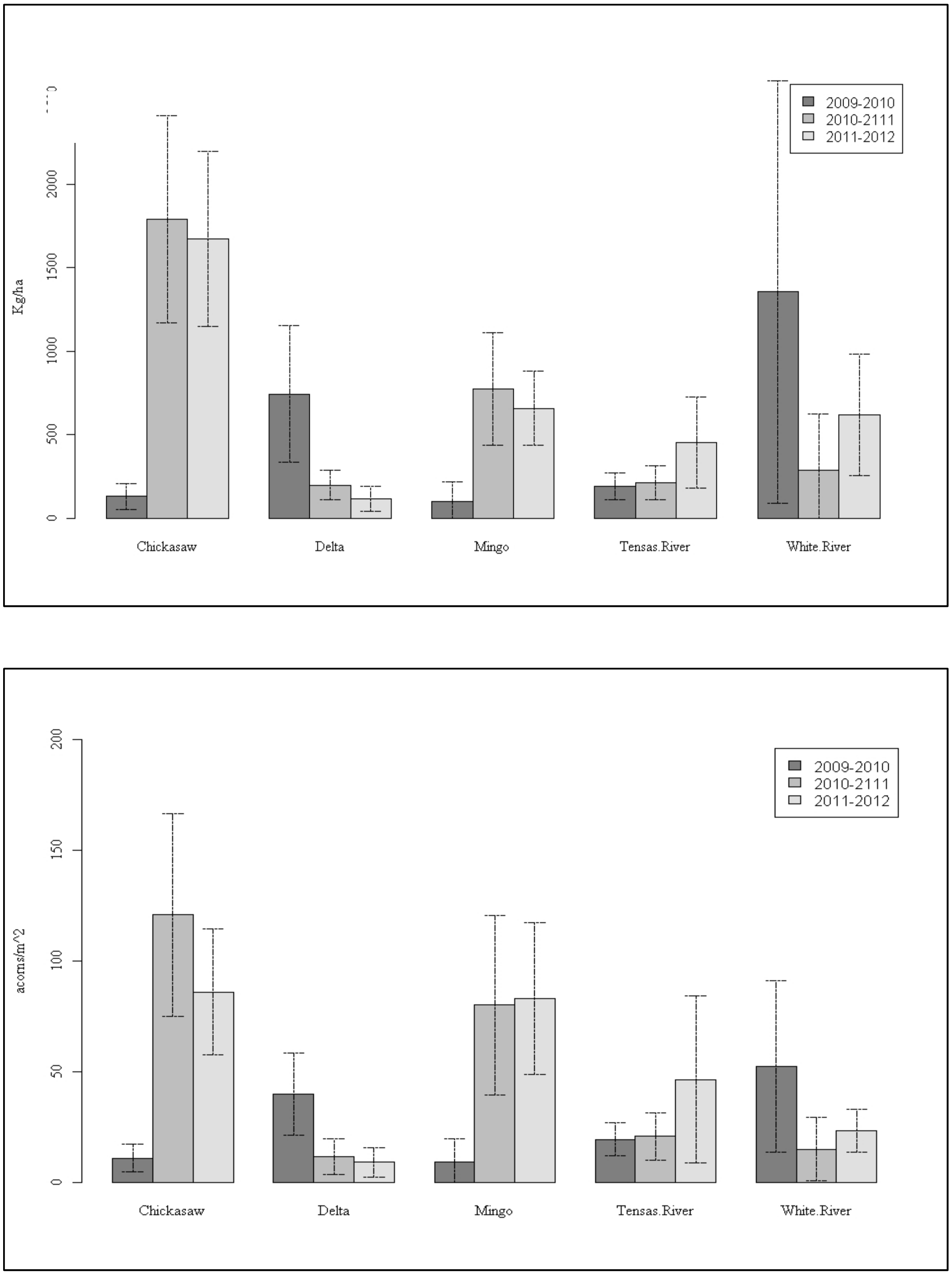

Figure 1.2 Annual acorn yield by mass (above) and number (below) from red oak trees at Chickasaw, Mingo, Tensas River and White River National Wildlife Refuges and Delta National Forest during falls and winters 2009-2012.

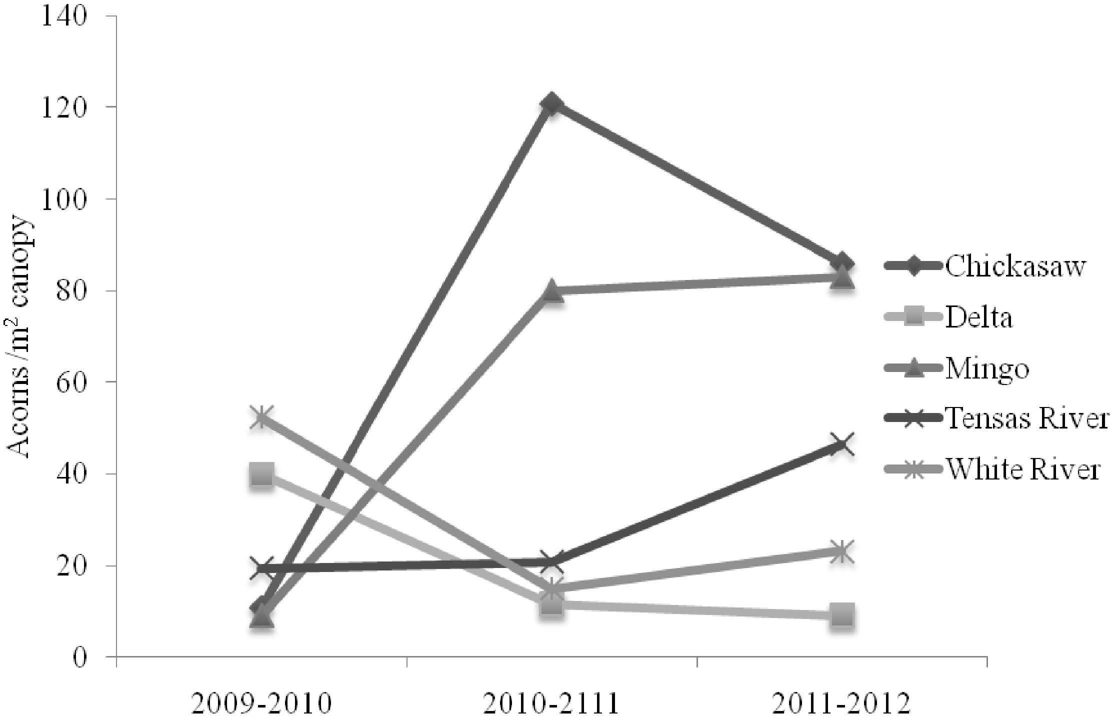

Figure 1.3 Time series of mean annual yield of red oak acorns at Chickasaw National Wildlife Refuge (NWR), Delta National Forest, Mingo NWR, Tensas River NWR, and White River NWR during falls and winters, 2009-2012.

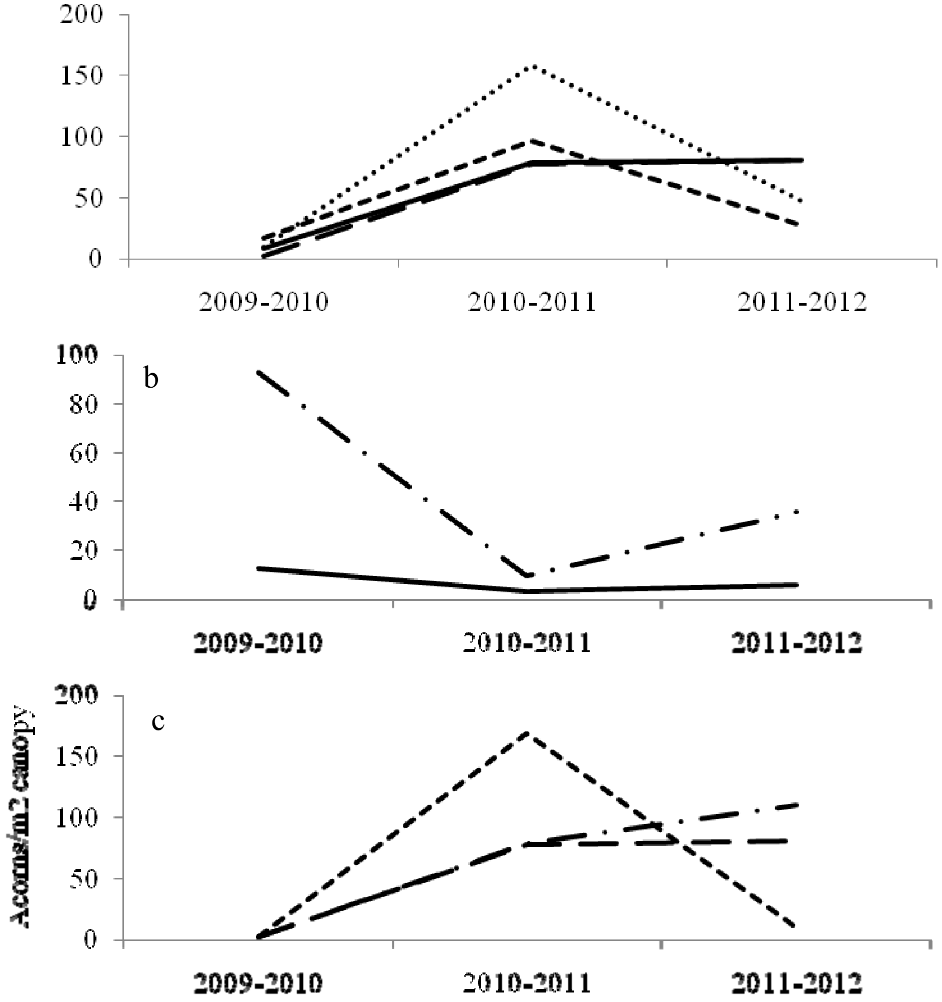

Figure 1.4 Time series of mean annual acorn production at Chickasaw National Wildlife Refuge (a), Delta National Forest (b), Mingo National Wildlife Refuge (c), Tensas River National Wildlife Refuge (d) and White River NWR (e) during falls and winters, 2009-2012.

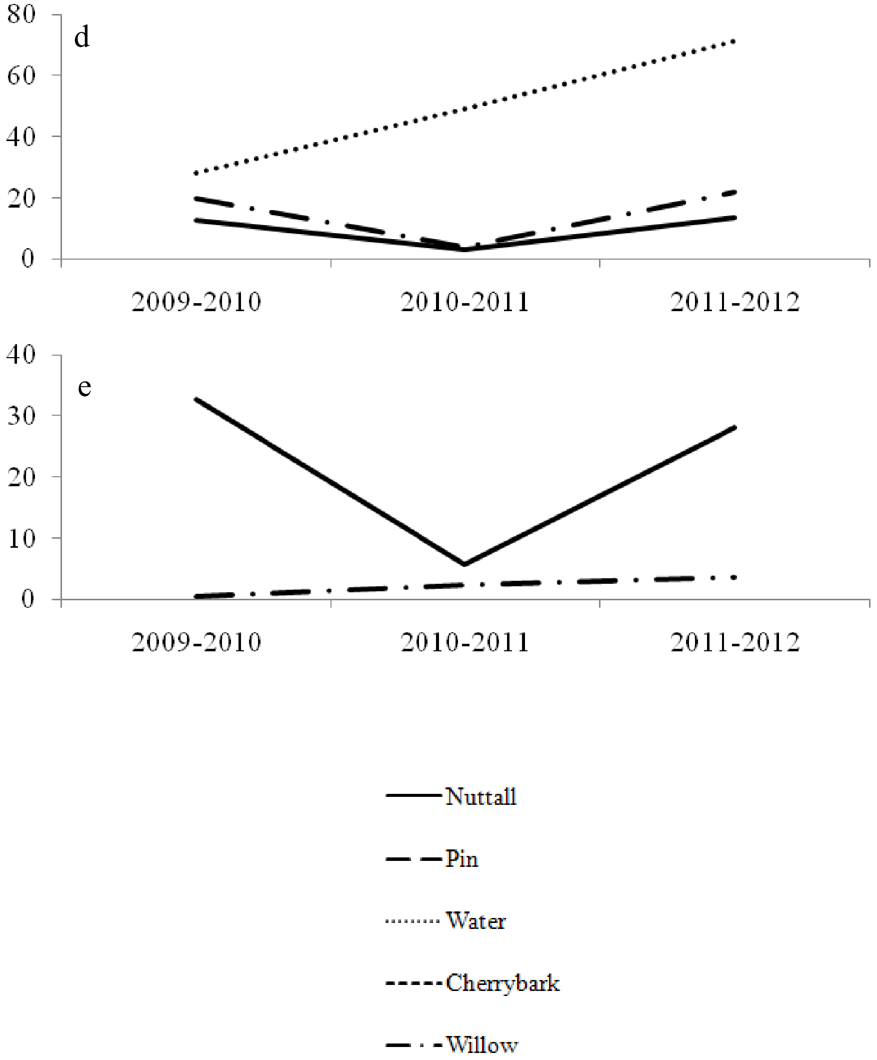

Figure 1.4 (continued)

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CHAPTER II

RED OAK ACORN ABUNDANCE AND PERSISTANCE IN THE MISSISSIPPI ALLUVIAL VALLEY

Bottomland species of red oak (*Quercus* spp.; Section *Erythrobalanus*) trees are ecologically and economically important in the Mississippi Alluvial Valley (MAV) and southeastern United States, and their value transcends these regions nationally and internationally. Common species in the MAV include cherrybark (*Q. pagoda*), Nuttall (*Q. texana*), pin (*Q. palustris*), water (*Q. nigra*), and willow oaks (*Q. phellos*; hereafter "red oaks"). All provide quality timber, and their acorns are valuable forage for wildlife especially ducks (Delnicki and Reinecke 1986, Kaminski et al. 2003). Some waterfowl and other wildlife rely on acorns during winter as a primary energy source; thus, abundance of acorns may be linked to wildlife population dynamics (Elkinton et al. 1996, Ostfeld et al. 1996, McShea 2000). Herein, I define abundance of acorns as number or mass of seeds per unit area on the ground or under water (≤45 cm) and potentially available as waterfowl and other wildlife forage

Acorns of red oaks vary in size (Bonner and Vozzo 1987, Aizen and Patterson 1990), and species occupy overlapping niches within hardwood bottomlands related to hydrology and hydroperiods (Hodges 1997). Nuttall and pin oaks produce the largest acorns and are considered the most flood tolerant red oaks, followed by willow, water, and cherrybark oaks (Hodges 1997). Currently, bottomland hardwoods in the MAV cover only about 20% of their historic range due to agriculture and other human encroachments (Twedt and Loesch 1999). Further, hydrology and hyrdroperiods still vary within and among years but have been dramatically altered due to an extensive levee and drainage systems along the Mississippi River and some of its tributaries (Klimas et al. 2009).

Despite tree species compositional and structural changes in the MAV, it remains one of North America's most important regions for waterfowl, especially wintering mallards (*Anas platyrhynchos*) and breeding and wintering wood ducks (*Aix sponsa*; (Fredrickson and Heitmeyer 1988). Ducks consume acorns of bottomland red oaks for energy, protein, and other nutrients for life-cycle processes (Reinecke et al. 1989, Kaminski et al. 2003, Heitmeyer et al. 2005). Acorns provide high levels of metabolizable energy and important fatty acids (Heitmeyer and Fredrickson 1990, Barras et al. 1996). Fatty acids from acorns are essential for wintering mallards and wood ducks building lipid reserves for spring migration and subsequent reproduction (Heitmeyer 2006). Conservation planners of the Lower Mississippi Alluvial Valley rely on precise and accurate assessments of forage potential from different major habitats used by waterfowl in this region (Loesch et al. 1995, Stafford et al. 2006, Kross et al. 2008). However, no landscape scale estimates of red oak acorn abundance exist for the MAV. Also, the relative amount, patterns, and timing of peak acorn abundance in bottomland hardwoods in the MAV are unknown.

Compared to other waterfowl foods, temporal availability of acorn abundance is important to consider when predicting estimates of acorn forage during winter. For example, parent plants of agricultural and moist-soil plants mature and drop their seeds during summer-fall (Foster et al. 2010, Hagy and Kaminski 2012). After these seeds dehisce, they gradually decline in abundance due to granivory (Stafford et al. 2006, Hagy and Kaminski 2012) and decomposition (Nelms and Twedt 1996, Greer et al. 2009). In comparison, oaks drop their seeds from fall-early spring (Chapter 1). Further, red oak acorns retain their energy over winter, in flooded and unflooded states, and energy content of acorns is consistent among years (Leach et al. 2012). Instead of abundance peaking at some point during fall and then gradually declining, the nature of oak seed maturation and phenology dictates that acorn abundance follows a much different seasonal pattern. However, the pattern of this relationship among oak species and in relation to size of the acorn crop are unknown. Cleary, having better understanding of when acorn abundance is greatest, its relationship with acorn yield, and how many acorns survive winter will further our understanding of bottomland hardwood ecology as it relates to waterfowl and other wildlife forage.

Availability of acorns as forage for wildlife is a function of many factors including species-specific differences, when and where they fall, yield, acorn predation and dispersal rates, and duration acorns are exposed. Clearly, when acorn yield is slight, so is abundance; however, large acorn crops can yield little abundance if acorns dehisce before maturity (Goodrum et al. 1971, Sork 1984). Because acorns can be depredated in tree crowns before they fall (Koenig et al. 2001), species that ground forage for acorns may encounter reduced abundances. Furthermore, bottomlands can flood deeply, preserving sound acorns that sink from foraging waterfowl and mammals but which are not available to wildlife (Allen 1989). Although peaks in acorn yield are known to occur at irregular intervals within and among years (Koenig et al. 1996), persistence of acorns on the ground has received little attention (McShea and Schwede 1993, Verdú et al. 2011). Herein, I define persistence of acorns as the ratio of presumably sound acorns on the ground to amount of sound acorns collected from seed traps and standardized for the area sampled.

My goals were to generate reliable estimates of monthly abundance of red oak acorns in the MAV at 2 spatial scales defined subsequently. Biologists and managers will use estimates of acorn abundance to assess potential foraging carrying capacity of these habitats for waterfowl and other wildlife and forest regeneration (Loesch et al. 1995, Kaminski et al. 2003). Therefore, my objectives were to 1) estimate monthly red oak acorn abundance during fall-winter beneath the crown of parent trees (hereafter crown-scale abundance), 2) estimate seasonal persistence rate of acorns and determine if it varies among red oak species, and 3) determine the relationship between forest-scale red oak acorn abundance and percentage of canopy trees comprised of red oaks. I define forest-scale abundance as mass or number of acorns collected from plots at various and random levels of red oak canopy dominance.

Study Area

The MAV, a historic floodplain of the Mississippi River, extends from Cairo, Illinois to the mouth of the Mississippi River in Louisiana, a total length of about 800 km (Reinecke et al. 1989). It includes portions of 7 states and about 10 million hectares of which nearly 2.6 million ha remain in hardwood bottomlands (Twedt and Loesch 1999). About 16% of the remaining hardwoods are on public lands (Twedt and Loesch 1999). The region extends between 29° and 37°N latitude and between 89° and 92°W longitude (Fig 1). The MAV is situated in a humid, subtropical region of the Northern Temperate

Zone where annual precipitation ranges between 117 cm in the north and 165 cm in the south (National Climatic Data Center 2011). January temperatures range from 3ºC in the northern reach of the MAV, 7.5ºC in the central sub-region, to 11ºC in the southern reach, whereas temperatures in July average about 30ºC across the region.

Current land cover in the MAV is a mix of mostly agricultural land, bottomland hardwood and other forest communities, emergent and other wetlands, and urban areas (Twedt and Loesch 1999). Current distribution of hardwood bottomlands is skewed greatly toward the southern MAV, wherein Arkansas, Louisiana, and Mississippi have about 94% of the total hardwood bottomlands (Twedt and Loesch 1999).

I studied on 5 areas in 5 states in the MAV, including 4 NWRs (Mingo [Missouri], Chickasaw [Tennessee], White River [Arkansas], and Tensas River [Louisiana]) and Delta National Forest [Mississippi]; Fig 1). Thus, I established study plots in major hardwood bottomlands in 5 of the 7 states in the MAV. Although I did not select study areas randomly, I consulted with area managers to ensure there was adequate mature (i.e., >50 year old) bottomland hardwoods that generally flood annually.

Methods

Study Design

I randomly selected 20 0.2-ha circular plots within mature hardwood bottomland forests at each study area (Chapter 1). At each plot, I randomly selected and sampled acorn yield from 2 oak trees. Because I was interested in estimating red oak acorn production in total, I did not discriminate selection of sample trees among species. Selected red oaks included cherrybark, Nuttall, pin, water, and willow oaks. Not all species occurred at each study area, so species composition and sample sizes varied by site. I sampled abundance of acorns found on the ground or underwater at 2 distinct spatial scales within each 0.2 ha circular plot: 1) at systematic locations within each plot (hereafter forest-scale), and 2) under the canopy of randomly selected red oak trees within plots (hereafter crown-scale). I sampled crown-scale abundance monthly from November 2009-2011 – February 2010-2012. I sampled forest-scale abundance monthly November 2009 – February 2011. Therefore, I collected crown-scale data over 3 years and forest-scale data for 2 years.

Acorn Collection

To collect acorns from sample trees, I randomly chose a cardinal direction and then placed a 1-m^2 square sampling frame (hereafter trap) halfway between the bole and the canopy drip line (Guttery 2006, Chapter 1). I fabricated frames of traps from 2.5 cm x 10 cm treated wooden boards, joined at the ends, and mounted atop 4, 1.5-m lengths of electrical conduit. To the wooden frame, I attached a funnel-like piece of fiberglass window screening that extended downward from the frame approximately 45 cm vertically. At the distal end of the screening, I attached a wide mouthed plastic bottle to consolidate acorns that fell into the trap. I pushed conduit legs of the trap 30-40 cm into the ground, giving the trap stability yet keeping them elevated to deter acorn depredation by ground-foraging grainivores. For comparison with tree-level abundance, I summed totals of all sound and unsound whole acorns collected to date after each visit to traps.

Abundance Sampling

Crown-scale

I established a permanent 0.5-m^2 circular ground plot at each randomly selected red oak tree with an acorn trap. To establish the circular plot, I first assessed the location of the trap. Because I was interested in relating abundance of acorns from the plot to those collected in the trap, I placed the circular plot near the trap and completely under the canopy of the sampled tree. Potential locations of the plot include between the trap and bole of tree, either side of the trap under the tree canopy, or between the trap and edge of the canopy. I chose a second random direction if the initial direction was under the canopy of another red oak tree. After selecting a direction under sample trees, I placed 2 fluorescent orange 25-cm pin flags 0.5 - 2.0 m from the trap. I used pin flags to mark the perimeter of 0.5-m^2 circular ground plots. I removed the fluorescent flagging from the pins to reduce conspicuousness of sample areas to grainivores and humans. I placed a 0.5-m^2 circular hoop on the ground that touched the pin flags, so I sampled the same exact area through time.

To collect acorns from the ground within the hoop, I first removed all leaf and other litter to reveal apparent sound acorns (Allen 1989). Acorns with dead embryos rattle when shook and pericarps are soft. Therefore, I shook and squeezed all acorns to determine their relative soundness in the field. I enumerated and recorded all apparently sound acorns and then replaced only sound acorns in the plot. I also replaced leaf and other litter in the plot, so it would appear undisturbed. I did not sample plots if they were inundated >45 cm or ice-covered, which could negatively bias my acorn detection. I recorded crown area (m^2) and red oak species from all sampled trees.

Forest-scale

I sampled forest-level acorn abundance by collecting all visible red oak acorns in 12 0.5-m^2 circular subplots systematically placed within the aforementioned 0.2-ha plots. I sampled from each study area monthly from November 2009-2011 - February 2010-2012. I oriented subplots along 2 perpendicular transects that bisected the plot center. I spaced subplots evenly apart and systematically to represent most variation within the plot. I changed orientation of transects monthly to avoid sampling same locations on the ground among months. I looked for acorns at all 12 subplot locations regardless if the location was under the canopy of a red oak tree, because acorns fall beyond the canopy of parent trees due to wind or dispersal mechanisms (Janzen 1971). This approach allowed me to relate abundance of acorns at the forest-scale to percentage of red oak canopy trees in the plot's overstory. Because I was not interested in within plot variation, I combined all sound red oak acorns collected within subplots. I determined acorn soundness as described previously. My sampling unit is aggregate sound acorns in 6.0 m^2 (e.g., 0.5 m^2 x 12). When subplots were inundated (16%; $n = 550$ subplots), I sampled the same locations using a sweep net and a correction factor based on this procedure (Weegman et al. 2010). I placed all collected acorns from subplots in a single labeled plastic bag for each plot ($n = 20$ per site/month) and transported samples to Mississippi State University, where I counted, dried, and weighed each sound acorn. I extrapolated dried masses to kg/ha and report a separate independent estimate for each sampling period each year. At each plot I measured percentage canopy comprised of red oak trees.

Statistical Analyses

Crown-scale abundance

I computed separate arithmetic means and 95% confidence intervals of crown-scale acorn abundance for each month (November - February), study site, and year. Because subplots were 0.5 m^2, I multiplied number of acorns by 2 to express results as acorns/m^2. I made inferences about differences in monthly means based on effect sizes and overlap of confidence intervals (Johnson 1999, Nakagawa and Cuthill 2007).

Forest-scale abundance

Because variation in acorn yield was great within years and among study sites, I categorized site-year combinations into good or poor acorn yields following Greenberg and Parresol (2002). I deemed acorn yield as poor at Chickasaw, Mingo, and Tensas River NWRs in 2009-2010 and Delta NF in 2010-2011. I considered acorn yield good at Delta NF in 2009-2010 and Chickasaw and Mingo NWRs in 2010-2011. I was unable to obtain accurate red oak canopy data at White River NWR, so I excluded this site in analyses. Thus, I considered 4 site-year combinations as poor and 3 as good acorn yield. I considered one site-year combination to have moderate acorn yield (Chapter 1).

Exploratory analyses indicated model residuals had large degrees of heterogeneity among study areas, showed non-linear patterns when plotted against proportion of tree canopy comprised of red oak species and contained autocorrelation among plots sampled repeatedly within winters. To stabilize residual variance, I examined 8 error covariance structures (Appendix C) using the WEIGHTS statement in the *nlme* package of R 2.13.1 and assessed them for increased variance stability using Akaikes information criteria corrected for small sample sizes (Burnham and Anderson 2002, Zuur et al. 2009). I accounted for autocorrelation among plots using the CORRELATION statement in the *nlme* package. I developed models using compound symmetry and autoregressive order one correlation structures and then compared these 2 temporal models with a model with no temporal correlation. Of the 3 models, I chose the model with the least AIC_c (Burnham and Anderson 2002) score as most explanatory of variance.

I used weighted regression and the *nlme* package of R. 2.13.1 to model the relationship of acorn abundance at forest-scale. I analyzed separately good and poor acorn yield years. I designated the dependant variable as abundance of acorns (kg[dry]/ha) per plot. I specified proportion of tree canopy comprised of red oak (%RO) species and sampling month as independent variables. I built 5 competing models to explain acorn abundance including the singular and additive effects of independent variables, an interaction term (i.e., %RO x month), and a null model. I compared models using a model selection approach, and considered the model with least AIC_c score as most explanatory of variation in acorn abundance (Zuur et al. 2009). I did not include sites and years as categorical effects in my analyses, because doing so would have temporally and geographically restricted my inferences and generalizations of acorn abundance among sites and years.

Persistence rates

To reiterate, I defined acorn persistence as the ratio of apparently sound acorns on the ground to total number of sound acorns collected in the trap to date for each tree per year. I calculated persistence rates for each species and month, as number of acorns found on the ground per m^2 divided by total number of acorns recovered to date in the 1-m^2 trap. Calculation of persistence required that number of acorns on the ground never exceeded those recovered in the trap (i.e., persistence > 1.0). When persistence >1 (16%; n = 843), I adjusted all proportions to 1.0. Despite large annual differences in acorn yield among sites and years (Chapter 1), I did not include sites and years as categorical effects in my analyses, as explained above. Because acorn persistence rates often are related to yield of acorns (i.e., density dependence; (Fletcher et al. 2010), I included the variable yield in my analysis (Chapter 1). Thus, I used logistic regression and analysis of covariance and designated species as a fixed factor and yield of acorns as a continuous covariate.

I started with a model which included the interaction of species and yield of acorns and each independently, because red oak acorn persistence interacted ($P < 0.05$) by oak species and acorn yield. If no interaction was detected, I used step-wise backwards selection and removed the least significant variables sequentially until all remaining variables were significant ($P < 0.05$). I sampled plots repeatedly over time (repeated measures); therefore, sampling units were not independent. Also plots were nested within sites. To avoid violation of independence, I conducted separate analyses for each month (November-February). To account for correlation of plots within study area, I used a mixed model and specified study area as a random grouping factor. Because of small sample sizes for cherrybark (n = 99) and water oak (n = 33), I combined data for these 2 species. I performed all analyses using the *glmmPQL* package in Program R 2.13.1., which revealed extensive overdispersion; therefore, P-values were adjusted using a quasi-binomial distribution (Crawley 2005).

Results

Crown-Scale Abundance

Abundance of acorns on the ground beneath the canopy of sampled red oak trees differed across months, sites, and years (Table. 2.1). The most acorns found in any subplot were 304 seeds (608/m^2) from a Nuttall oak at Chickasaw NWR in February 2011. Distribution of acorn abundance was right-skewed, primarily because I did not recover any acorns at plots 57% of the time across all sites, years, and months. With 2 exceptions, greatest acorn abundance among sites and years occurred in either December or January. One exception occurred at Mingo NWR in 2009-2010, where abundance was greatest in November followed by 3 months of decline. The other exception was at Chickasaw NWR in 2010-2011; there, acorn abundance increased each month from November through February. Chickasaw NWR was the only site where acorn abundance (Nuttall oak 73%, water oak 19%) increased from January to February in winters 2010-2012. All other site-year combinations showed decreased acorn abundance from January to February. In 4 of 11 site-year combinations, acorn abundance was zero during February.

Species-specific Acorn Persistence

I obtained seed-trap and ground-plot data for acorn abundance from 223, 230, 240, and 148 red oak trees in November, December, January, and February 2009-2012, respectively (Table 2.1). In November-January, acorn persistence rates varied by the interaction of oak species and yield of acorns per tree (November, $\chi^2_{3,223} = 12.745$, $P = 0.005$; December, $\chi^2_{3,230} = 8.729$, $P = 0.033$, January, $\chi^2_{3,240} = 12.058$, $P = 0.007$). In

November, Nuttall oak acorn persistence rates increased with yield, whereas persistence did not very among other oak species (Fig 2.1). For each additional Nuttall oak acorn produced, expected persistence rate multiplied by 1.028%. For mean yield of acorn across years, sites, and trees within sites, persistence was greatest for pin oak (55.1%), followed by cherrybark and water oaks (each 51.5%), willow oak (43.2%), and Nuttall oak (35.5%; Fig. 2.2). In December, persistence rates of Nuttall and pin oak acorns increased with yield, whereas persistence of willow, cherrybark, and water oak acorns was constant (Fig 2.1). For each additional acorn, expected persistence rate was multiplied by 1.009 and 1.006%, for Nuttall and pin oaks, respectively. At the mean level of acorn yield, persistence rates were greatest for cherrybark and water oak acorns (81.7%), followed by pin (81.1%), willow (74.2%), and Nuttall oak acorns (72.6%; Fig. 2.2). In January, Nuttall oak acorn persistence rates increased rapidly relative to acorn yield, whereas pin, cherrybark, and water oak acorns increased at a lesser rate (Fig 2.1). Acorn persistence rates slightly decreased with yield of willow oak acorns (Fig 2.1). For each additional acorn, the expected persistence rate multiplied by 1.011% for Nuttall oak and 1.004% and 1.001% for cherrybark and water oaks combined and pin oaks, respectively. With each additional willow oak acorn, the expected persistence rate declined by 0.998% At the mean level of acorn production, persistence rates were greatest for willow oak acorns (46.3%), followed by pin (45.5%), cherrybark and water (42.0%), and Nuttall oak acorns (32.0%; Fig. 2.2). In February acorn persistence rates varied by the additive effect of species ($\chi^2_{3,148} = 11.496$, $P = 0.009$) and acorn yield per tree ($\chi^2_{1,148} = 12.395$, $P < 0.001$). Persistence rates for all red oak species increased slightly with yield (Fig 2.1). For each additional acorn produced, the expected persistence rate increased by 1.005%. At the mean level of acorn production, persistence rates were greatest for Nuttall oak (44.1%), followed by cherrybark and water (29.2%), pin (27.1%), and willow oaks (12.9%; Fig. 2.2).

Forest-scale Abundance

I obtained 239 and 229 forest-scale samples of red oak acorn abundance during poor and good masting years, respectively. Percentage of canopy comprised of red oak trees across the MAV averaged 45.0% (SE = 5.6%, range = 8.3-89.6%), but varied by study area (Table 2.2).

In good and poor masting years, I used the same error variance structure, because model selection procedures indicated this was best (Appendices C and D). For good and poor masting years, autocorrelation was best modeled (i.e., least AIC_c) as a first order autoregressive function (ρ), indicating residuals from samples taken in months nearest each other (e.g., November – December) were more correlated than months farther apart (e.g., November – February). During poor masting years, residuals from Tensas River NWR had the greatest variation ($\sigma = 5.41$), followed by Chickasaw ($\sigma = 4.67$), Delta NF ($\sigma = 2.27$), and Mingo NWRs ($\sigma = 1.65$). The exponential function parameter (δ) was 2.96, whereas the first order autoregressive function (ρ) was 0.49.

In good masting years, residuals from Chickasaw NWR had the greatest variation ($\sigma = 157.42$), followed by Delta NF ($\sigma = 27.88$) and Mingo NWR ($\sigma = 18.36$). The exponential function parameter (δ) was 2.72, whereas the first order autoregressive function (ρ) was 0.62.

In poor masting years, red oak acorn abundance was best modeled by percentage of canopy comprised of red oaks (Table 2.3). Acorn abundance increased linearly with percentage of red-oak canopy (*β* = 10.12, 95% CI: 2.23 - 18.01, *P* = 0.013). At 45% (i.e., the MAV-scale mean value) and 100% red oak canopy, model parameters predicted 4.4 and 9.9 kg[dry]/ha of acorns (Figure 2.3), respectively. In good masting years, red oak acorn abundance was best modeled by monthly percentage of canopy comprised of red oaks (Table 2.3). Acorn abundance increased most rapidly relative to percentage of canopy comprised of red oaks in December (*β* = 308.36, 95% CI: 198.06, 418.65), followed by January (*β* = 271.42, 95% CI: 174.01, 368.85), November (*β* = 233.55, 95% CI: 136.13, 330.96), and February (*β* = 141.82, 95% CI: 14.19, 269.46). A 1% increase in red oak canopy increased acorn abundance by 3.08 kg/ha (95% CI: 1.98, 4.19) in December, 3.18 kg/ha in January (95% CI: 1.74, 3.69), and 1.42 kg/ha (95% CI: 0.14, 2.69) in February (Fig, 2.4). During November-January, at 45% and 100% red oak canopy, model parameters predicted 103.7 and 247.8 kg[dry]/ha of acorns (Fig. 2.4), respectively.

Discussion

Yield of acorns varied greatly among sites and years (Chapter 1), thus; crown-scale acorn abundance paralleled this variability. Among all sites and years, crown-scale abundance was greatest in January ($\bar{x}$ = 371 kg/ha, SE = 123) and least in November (198 kg/ha, SE = 64.4); however, site-specific variation was great. Three consistent temporal patterns emerged concerning maximal crown-scale acorn abundance, and these patterns generally were site-specific. One pattern showed least acorn abundance in November, followed by maximal abundance in December or January with a slight decline in February. This pattern primarily occurred at Delta NF and Tensas River NWR. A second pattern showed an increase in acorn abundance from November-February. This pattern primarily occurred at Chickasaw NWR. A final pattern showed a continual decrease in acorn abundance monthly. This phenomenon primarily occurred at Mingo NWR. These patterns may be driven by a combination of species-specific phenology in seed maturation (Fujii 1993, Espelta et al. 2009) and concomitant influences of grainivores and dispersal mechanisms (Janzen 1971). Phenology of oak seed maturation is a function of annual temperature and precipitation events which differ along a north-south gradient in the MAV. Red oak trees in the southern portion of the MAV resist dormancy longer than conspecifics in the north. This phenomenon may partially explain why acorn abundance was least from sites in the southern MAV during November, because acorns hadn't matured and dehisced from parent trees. In contrast, red oaks in the northern MAV enter dormancy sooner, and seeds begin dropping in October with greatest abundance often in November.

Confounded with spatial and temporal variation in seed-maturation phenology is the dynamic influence of seed predators (Sork 1984). Although I did not collect information on occurrence and relative abundance of seed predators, I noticed variation across sites in sightings and other evidence of whitetail deer (*Odocoileus virginianus*), eastern gray squirrel (*Sciurus carolinensis)*, and black bear (*Ursus americana*), all of which use acorns greatly in autumn and winter (Smith and Follmer 1972, McShea and Schwede 1993, Feldhamer et al. 2002). Also, large flocks of common grackles (*Quiscalus quiscula)* and blue jays (*Cyanocitta cristata)* consume large quantities of acorns (Johnson and Webb III 1989, Steele et al. 1993). These and other species that consume acorns from MAV hardwood forests (Heitmeyer et al. 2005) may have influenced monthly variation in acorn abundance. Humans also collect acorns for afforestation, but acorn collection was not allowed on any of my sites and I never observed any people engaged in this activity. Thus, acorn predation and dispersal likely were related only to wild animals. In addition to seed maturation phenology and grainivores, oak acorn abundance in bottomland hardwoods may be influenced by the impact that hunting may have on abundance and distribution of acorn predators. Finally, effects of hydrology and soil moisture apparently interact and affect acorn yield and subsequent abundance. Indeed, all aforementioned factors likely interacted and contributed to amount and timing of acorn abundance (Table 2.3). My monthly estimates of acorn abundance include variation from these factors, but I was unable to partition and estimate their individual or interacting effects. Quantitative assessments on impacts of these variables on acorn abundance will be valuable for forest ecologists and managers, especially given the wide diversity and range of intrinsic and exogenous factors across the MAV. Although my research provides initial estimates of abundance of red oak acorns in the MAV during fall-winter, there remains a need to link abundances with potential for forest regeneration in light of the decline in oak species across North America (McShea et al. 2007).

Although Chickasaw and Mingo NWRs are geographically close in the northern MAV, their site-specific timing of maximal acorn abundance was distinctly opposite. This phenomenon contradicts my assumption that seed-maturation phenology should drive acorn abundance. As expected, Mingo NWR, which was farthest north, had peak abundance in November. However, at Chickasaw NWR, which is about 135 km southeast of Mingo NWR, acorns fell November through February. I believe this pattern was largely driven by differences between pin and Nuttall oaks, the dominant species at

Mingo and Chickasaw NWRs, respectively (Chapter 1). Although these species occupy a similar niche in hardwood bottomlands (Fredrickson and Heitmeyer 1988), they apparently have markedly different seed-maturation adaptations (Bonner and Vozzo 1987). Little is known about seed maturation of Nuttall oak or evolutionary pressures that have influenced this adaptation, although other oak species have been studied (Bonner 1974, Bonner and Vozzo 1987). Because Nuttall oak is an abundant species in the MAV (Table 2.4), it has large and nutritious acorns (Kaminski et al. 2003), and it continually drops seed during winter, I hypothesize that it is an especially important species among red oaks in the MAV regarding winter forage for waterfowl and other wildlife and recruiting seedlings into forest communities.

In the 4 site-year combinations where I did not find any acorns in crown-scale plots in February, all coincided with poor masting years. Therefore, there is a reduced chance of seedling establishment in such years, at least under parent trees experiencing poor mast yield. This finding is similar to Haas and Heske (2005) who failed to find any northern red oak acorns (*Quercus rubra*) on ground plots at 4 upland locations in central Illinois during a poor mast year. Although I failed to find acorns in February in some years and sites, this result does not necessarily mean that seed germination did not occur. Grainivores can cache acorns collected from ground or tree crowns and place them in favorable locations for germination (Vander Wall et al. 2005). However, given the minimal amounts of acorns found in February in poor mast years, I suspect secondary dispersal contributes negligibly to acorn germination in the MAV.

During good masting years, I found at least some acorns ($8/m^2$) and sometimes many acorns ($>50 /m^2$) on the forest floor in February. Furthermore, I found evidence that acorn persistence into February was positively related to annual yield by parent trees for all species, especially Nuttall oak. I found no evidence that large yields of acorns were related to decreased ground persistence during winter. In fact, in February, I only found 4 ground plots (6% of all February samples) without acorns when ≥10 acorns were recovered from the parent tree. Therefore, successful recruitment of oaks into seedling cohorts in the MAV does not seem a problem of a seed source, at least during mast years. Consistent with Puerta-Piñero et al. (2010), my results suggest the greatest likelihood of successful seedling establishment occurs in the next year after greatest acorn yield. Although I did not monitor acorn persistence through germination, which typically occurs in late winter-spring in the MAV (Bonner and Vozzo 1987), I hypothesize that negligible seed predation would occur between the time I stopped monitoring acorns and seed germination.

Red oaks in the MAV exhibit mast seeding (Chapter 1), whereby individuals produce episodic, large seed crops that are synchronous with those of the other individuals in the population (Kelly 1994). A common explanation for this pattern is the predator-satiation hypothesis (PSH; Kelly and Sork 2002). The PSH predicts that seeds will escape predation differentially based on number of seeds produced. In masting years, escape is greatest because more seeds are produced than can be consumed by predators. One approach to testing the PSH is to examine the form of functional response grainivores have on seeds (Holling 1959a, Holling 1959b). Fletcher et al. (2010) reviewed the form of the relationship regarding proportion of available seeds consumed and amount of seeds available; however, I modified this relationship to compare persistence with acorn yield (Fig. 2.5). Type I functional responses do not support the predator satiation hypothesis, because seed persistence remains constant across all levels of seed yield. Types II and III responses are satiating functions, because proportion of available seed consumed decreases at high levels of seed availability. Type III responses differ from Type II responses in that proportion of available seed harvested increases at low levels of seed availability, because predators switch their food of interest when it becomes more available in the environment (Jeschke et al. 2002).

Across months and oak species, except for Nuttall oak, my results suggest predation of acorns in the MAV followed a Type I functional response, because persistence of acorns on the ground remained relatively constant across all levels of yield by parent trees (Fig 2.3). Nuttall oak persistence rates tended to increase with yield, suggesting a Type II response by this species. Regarding species other than Nuttall oak, there are a few reasons why these patterns may have emerged. First, unlike some ecosystems like shrubby oak-lands in western United States where there is a specialist grainivore like the acorn woodpecker (*Melanerpes formicivorus*), MAV grainivores are considered generalists in their diet (Heitmeyer et al. 2005). As a result, there is no single species that targets areas with great abundances of acorns, at least not to the degree that I could detect differential persistence through winter. Historically, this outcome may not have been the case, because millions of now extinct passenger pigeons (*Ectopistes migratorius*) congregated in southern hardwood forests to consume acorns, especially in mast years (McKinley 1960). This type of predation by passenger pigeons would be considered Type II or III response and may have influenced structure and composition of pre-settlement forests in North America (Ellsworth and McComb 2003). Nowadays, thousands or millions of grackles exploit acorns in MAV hardwood bottomlands, but their impact may not be invoking Type II or III responses. Furthermore, the abundance and distribution of mallard and wood duck populations and extent and duration of flooded hardwood bottomlands providing access to this habitat by waterfowl are less than in pre-settlement times (Reinecke et al. 1988). In winters when MAV hardwoods were inundated, these ducks may have invoked Type II or III responses and impacted subsequent forest regeneration. Without these major granivores, compounded by vast losses and fragmentation of hardwood forests in the MAV, dynamics of acorn persistence, oak regenerational capacity, and forest stand composition may be vastly different than during pre- settlement era. Therefore, understanding form and function of acorn persistence through winter in the MAV today will help ecologists understand the best approaches to meet reforest- and afforestation goals.

Another reason acorn persistence rates remained relatively constant across all levels of yield by parent trees relates to characteristics of winters in the MAV and its effects on foraging wildlife. Prolonged ice cover and deep snow are rare in the MAV; hence, accessibility of food resources generally is not constrained in winter. This pattern contrasts sharply with northern latitude forests where acorns are an important food in winter but may be covered by snow or ice (Sork 1984). Wildlife that utilize acorns from MAV hardwoods also use soft mast (e.g., sugar berry [*Celtis laevigata*], persimmon [*Diospyros virginiana*]) and other hard mast species (Hickories and Pecans [Carya spp.]) and aquatic and terrestrial insects (Batema et al. 2005, Foth 2011). Because of this diversity and abundance of other food resources, acorns in the MAV likely receive less foraging pressure. This possibility emphasizes need to recognize the importance and implications of forage diversity in hardwood bottomlands (Stanturf et al. 2000).

Although oaks are economically and ecologically valuable, afforestation that encourages monocultures of oaks or all hard mast producing trees may promote cascading effects through the food chain (Elton 1966, Fretwell 1977).

Nuttall oak was the only species that exhibited some evidence of predator satiation (i.e., Type II response). One explanation for this finding may be a function of seed size. Nuttall oak acorns are the largest and heaviest of the red oak species in the MAV. These large acorns may be used or selected less by wood ducks (*Aix sponsa*) and other ducks compared to smaller acorns (Barras et al. 1996). As a result, the suite of potential grainivores for Nuttall may be less. Because there is potentially less use of and competition for Nuttall oak acorns by grainivores, they may have reached satiation sooner than grainivores foraging on smaller red oak acorns. For smaller size acorns, the suite of grainivores consuming them may be greater at sites where a gradient in acorn size exists. Therefore, satiation may rarely occur and persistence remains constant across the range of yield. A competing explanation for finding evidence of satiation in Nuttall oak acorns and not in other species also pertains to size of the acorn. Grainivores may not eat as many Nuttall oak acorns as they do willow, water, or cherrybark until they will cease foraging because of physical constraints of ingesting and digesting large acorns and amount of metabolizable energy derived from relatively few large Nuttall oak acorns compared to the mass of many smaller acorns (Kaminski et al. 2003). Therefore, the evolutionary strategy to produce less but larger seeds may benefit Nuttall oak in bottomlands of the MAV, at least when it pertains to seed persistence through winter (Leishman et al. 2000, Gómez 2004).

I collected acorns from directly under the crown of parent trees (e.g., crown-scale abundance). I also estimated acorn abundance from random transects in heterogeneous hardwood forested plots to make comparisons with increased utility for foresters and wildlife managers who have knowledge of the relative species compositions of their stands. Red oak overstory composition averaged 45% and ranged from 8-90% across sites in the MAV. In masting and non-masting years, I discovered a linear relationship between forest-scale acorn abundance and percentage of red oak in the overstory. However, in non-masting years, acorn abundance at 100% red oak canopy was less than 10 kg/ha and did not vary monthly. During a masting year, acorn abundance exceeded 245 kg/ha at 100% red oak canopy for all months except February.

The linear relationship between abundance of all red oak acorns and proportion of red oaks in the canopy suggests no evidence for differential acorn predation at varying compositions of overstory red oaks. If grainivores were actively seeking dense patches of acorns, one might expect more seed predation and subsequently less abundance in stands with increased composition of masting red oaks (Fletcher et al. 2010). Conversely, predation may be less in forests with relatively low amounts of red oaks leading to increased abundance in these areas. Either scenario would result in a non-linear pattern. This finding is useful for conservation planners who are accustomed to relating amount of red oak acorn forage available relative to the composition of red oaks in the overstory (Table 2.5; Reinecke and Kaminski 2007).

Management Implications

I assessed crown- and forest-scale red oak acorn abundance from 5 study areas in the MAV over 3 consecutive years. I encountered great amounts of spatial and temporal variation; however, some important findings have emerged. Across all sites, in masting years, peak on the ground acorn abundance occurred in January. From a waterfowl foraging perspective, this pattern contrasts with agricultural and moist-soil seeds which are most abundant in early fall in the MAV and across Tennessee (Stafford et al. 2006, Hagy and Kaminski 2012). Further, red oak acorns retain their energy during winter, regardless of flooding, and energy content of acorns is consistent among years (Leach et al. 2012). Instead of abundance peaking at some point during fall and then declining, my data indicate that acorns persist as potential food through winter. However, in poor masting years, I found very few (< 3 sound acorns/m^2) acorns by January. Thus, the "boom and bust" nature of acorns as a food source for waterfowl has challenging implications for foraging habitat conservation planning purposes, the goal which is to predict how much foraging habitat is potentially available and required to support target populations of wintering waterfowl. Because waterfowl are mobile and I never encountered a year when all sites had poor yield, I suggest conservation planners adopt my values that are represented by mast years and summarized in Table 2.5. This recommendation assumes that every year ducks will encounter this much forage from acorns somewhere in the MAV. However, conservation planners should be mindful that annual abundance may be depauperate locally. Given the large variability in acorn abundance recorded over sites and year, an improvement to predicting capacity of hardwood forests to support populations of wintering waterfowl might best be achieved by using a spatially explicit model which incorporates the various sources of variability (Conroy et al. 1995, Carter and Finn 1999).

In evolutionary terms, inter- and intra-annual consistency (or inconsistency) of acorns as a food resource for waterfowl remains largely unstudied (Stephens and Krebs 1986, Stephens et al. 2007). I encourage researchers to address the micro- and macro-scale movements, abundance, and distribution of wintering wood ducks and mallards in relation to acorn and aquatic invertebrate abundances, 2 species that rely greatly on these resources in the MAV in winter (Wehrle et al. 1995, Kaminski et al. 2003, Heitmeyer 2006). In the MAV, there has been research documenting use of rice fields and moist-soil wetlands by mallards as a substitute for bottomland hardwood wetlands (Manley et al. 2004, Pearse et al. 2008, Havens et al. 2009, Hagy and Kaminski 2012). However, there is very little known about use and distribution of mallards regarding use of hardwood forests (Kaminski et al. 1993, Davis et al. 2009, Davis and Afton 2010). Research that links annual fluctuations in food resource abundance, waterfowl movements and survival, and other biological outcomes possibly linked to fitness are valuable and desperately need for waterfowl conservation.

To date, conservation planners of the Lower Mississippi Alluvial Valley Joint Venture (LMVJV) have used 166 kg/ha as the composite waterfowl forage estimate of red oak acorns, moist-soil seeds, and aquatic macro-invertebrates in bottomland hardwood forests at 100% red oak canopy (Reinecke and Kaminski 2007). This estimate was based primarily on a long term study of pin oaks at Mingo NWR (McQuilkin and Musbach 1977). Estimates of acorn abundance currently used by the LMVJV were within my 95% confidence limits during a mast year but about 60% less. My study indicates peak acorn abundance is linearly related to percentage of red oak trees in the overstory and varies up to 2 orders of magnitude during a masting and non-masting year

(Table 2.5). I recommend conservation planners adopt my landscape-scale contemporary estimate of red oak acorn abundance of 247 kg/ha with 100% red oak canopy (Table 2.5). Because acorns are a food resource that persists through winter and reaches peak abundance during January, I contend conservation planners have undervalued the potential of bottomland hardwoods to provide energy for wintering ducks. As such, conservation programs that secure, enhance, or protect remaining tracts of mature hardwoods are vital for foraging waterfowl and other wildlife, especially in the face of potentially emerging ecosystems services market (Jenkins et al. 2010) and an apparent late-winter decline in food abundance in other wintering habitats in the MAV and geographically close regions (Greer et al. 2009, Stafford et al. 2010).

Table 2.1 Red oak acorn abundance in bottomland hardwood forests in the Mississippi Alluvial Valley within Chickasaw (CNWR), Mingo (MNWR), Tensas River (TRNWR), and White River (WRNWR) National Wildlife Refuges and Delta National Forest (DNF) from November through February 2009-2012.

		November			December			January			February		
Year	Site	*n*[a]	acorns/m^2[b]	95% CIs	*n*	acorns/m^2[b]	95% CIs	*n*	acorns/m^2[b]	95% CIs	*n*	acorns/m^2[b]	95% CIs
09-10'	CNWR	39	2.4	-1.2 - 6.0	32	3.1	0.0 - 6.3	29	0.6	-0.1 - 1.3	34	0.0	0.0 - 0.0
	DNF	32	16.8	4.4 - 29.1	22	43.5	-7.3 - 94.2	21	39.6	-6.3 - 85.5	15	7.9	-4.4 - 20.1
	MNWR	32	1.9	0.8 - 3.1	35	0.5	0.1 - 0.9	34	0.1	-0.1 - 0.2	35	0.0	0.0 - 0.0
	TRNWR	35	5.4	2.4 - 8.3	26	6.5	2.9 - 10.2	31	2.1	0.9 - 3.3	35	0.7	0.3 - 1.2
	WRNWR		[c]		27	8.8	2.9 - 14.8						
10-11'	CNWR	36	20.6	10.6 - 30.7	30	57.0	26.2 - 87.8	37	62.8	27.4 - 98.1	38	68.3	29.2 - 107.3
	DNF	38	0.5	0.2 - 0.9	37	0.6	0.2 - 1.0	36	0.3	0.0 - 0.6	38	0.0	0.0 - 0.0
	MNWR	39	25.2	12.9 - 37.6	37	25.4	14.8 - 35.9	39	18.5	9.8 - 27.2	27	9.7	3.1 - 16.3
	TRNWR	38	3.0	1.1 - 4.9	38	6.6	2.2 - 11.0	37	2.9	0.5 - 5.2	37	0.0	0.0 - 0.0
	WRNWR	38	1.9	0.9 - 3.0	37	4.7	2.2 - 7.2	36	4.2	1.3 - 7.0			
11-12'	CNWR							23	34.0	16.3 - 51.7	36	53.6	29.4 - 77.7
	DNF	40	0.5	0.1 - 0.8	36	4.6	0.6 - 8.5				33	2.4	-0.6 - 5.5
	MNWR	16	23.0	10.3 - 35.7				22	18.9	5.7 - 32.1			
	TRNWR	38	2.2	0.4 - 4.0	32	17.4	6.9 - 28.0	24	20.3	1.3 - 39.4	21	16.4	-3.1 - 35.9
	WRNWR							15	5.7	1.0 - 10.5			

[a] *N* red oak trees sampled.

[a] Mean number of whole and partially sound acorns (i.e., those that sink in water) collected from 0.5-m^2 plots beneath the canopy of trees where acorn yield was estimated (Chapter 1).

[c] Blanks denote sites were not sampled.

Table 2.2 Mean composition (%) of red oaks in the overstory at 4 sites in the Mississippi Alluvial Valley where red oak acorn abundance was sampled during autumn-winters, 2009-2011.

	%		
Site	Mean	Maximum	Minimum
Delta National Forest	41.7	83.3	8.3
Mingo National Wildlife Refuge	60.0	85.4	25.0
Chickasaw National Wildlife Refuge	26.3	52.1	8.3
Tensas River National Wildlife Refuge	51.8	89.6	16.7
All Sites	45.0	89.6	8.3

Table 2.3 Candidate models explaining variation in red oak acorn abundance from 4 study areas in bottomland hardwood forests, autumn-winters 2009-2011 in good and poor masting years.

Masting year[a]	Model	K[c]	AIC_c	ΔAIC_c	ω_i
Good	Month * % RO[b]	13	2845.5	0.0	0.704
	Month + % RO	10	2847.6	2.1	0.241
	% RO	7	2850.6	5.1	0.055
	Month	9	2867.4	21.9	0.000
	null	6	2870.0	24.5	0.000
Poor	% RO	8	1834.6	0.0	0.783
	null	7	1838.5	3.9	0.114
	Month + % RO	11	1839.2	4.5	0.081
	Month	10	1842.9	8.3	0.013
	Month * %RO	14	1843.3	8.7	0.010

[a] from Greenberg and Parresol 2002

[b] Percentage of overstory canopy trees composed of red oak (RO).

[c] number of estimable parameters

Table 2.4 Factors hypothesized to influences red oak acorn abundance at 5 study areas in the Mississippi Alluvial Valley including the most abundant species found at each site (second most abundant in parentheses), mammal abundance, hunting pressure, and hydrological variables.

		Mammal Abundance				Hydrology		
Study Site	Abundant red oak	Deer	Black bear	Gray Squirrel	Hunting pressure	Depth	Duration	Peak abundance
Mingo NWR	pin (willow)	++[a]	--	++	-	+	+	November
Chickasaw NWR	Nuttall (water)	--	--	-	-	++	-	February
White River NWR	Nuttall (willow)	+	++	+	+	++	++	[b]
Delta National Forest	Nuttall (willow)	-	+	++	++	+	+	Dec-Jan
Tensas River NWR	water (willow)	+	++	+	+	-	-	Dec-Jan

[a] Plus and minus symbols indicate the hypothesized degree of influence of the selected factor.

[b] Peak abundance was unknown at White River National Wildlife Refuge because excessive flooding precluded consistent sampling.

Table 2.5 Abundance of sound red oak acorns in masting and non-masting years in the Mississippi Alluvial Valley in relation to percentage composition of red oak within the forest canopy, compared to values currently used by the Lower Mississippi Valley Joint Venture (LMVJV).

	kg/ha		
%	Masting year	Non-masting year	LMV JV
30	65	3	37
40	91	4	50
50	117	5	62
60	143	6	75
70	169	7	87
80	196	8	99
90	222	9	112
100	248	10	124

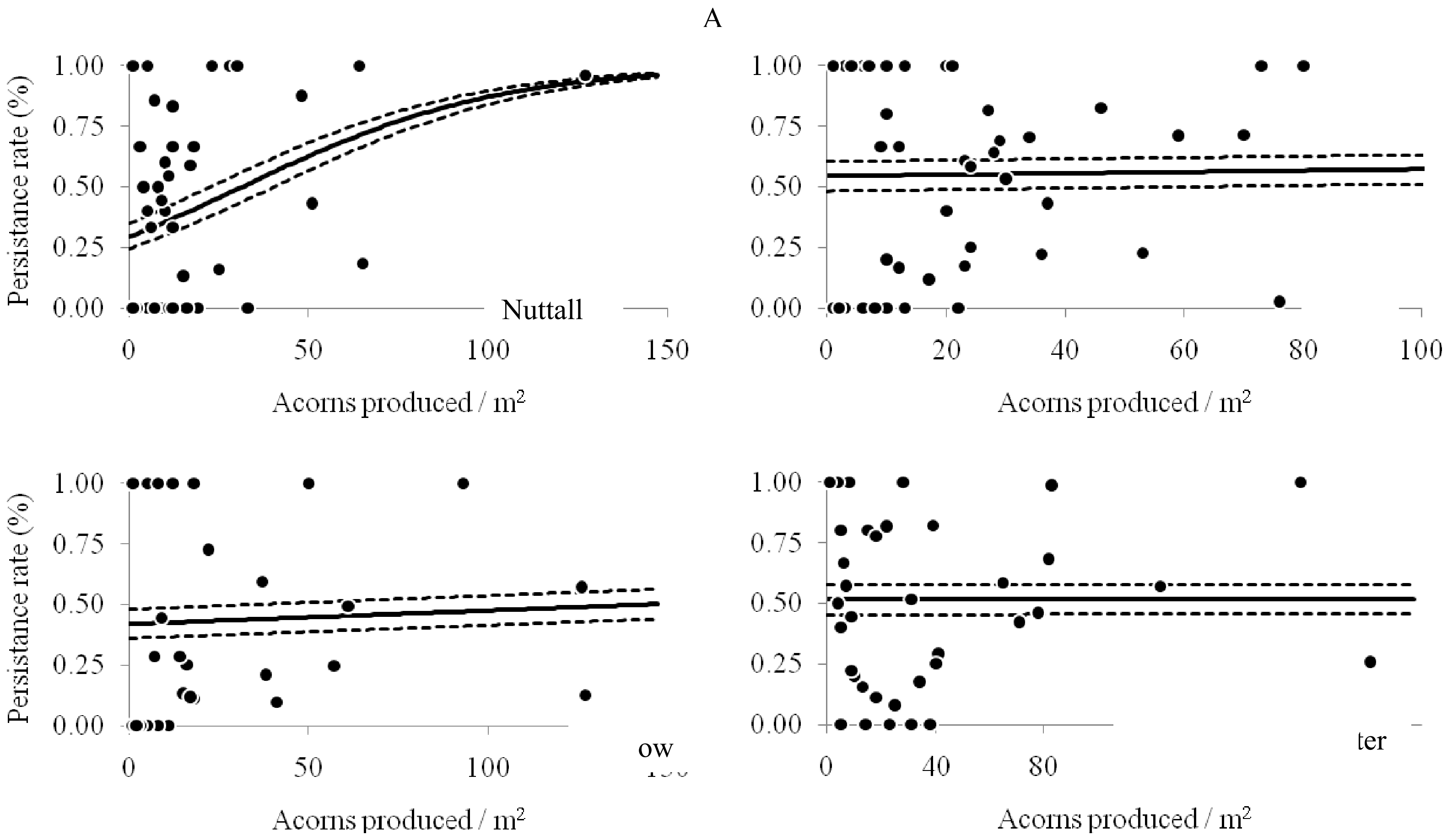


Figure 2.1 Persistence rates* with 95% confidence intervals of Nuttall, pin, willow and cherrybark and water oak acorns during November (A), December (B), January (C) and February (D) from bottomland hardwood forests in the Mississippi Alluvial Valley, 2009-2012.

*Persistence rate represents ratio of number of acorns found on the ground beneath parent trees divided by number of acorns estimated produced by parent trees. Sample units are individual trees and are represented by dots (•)

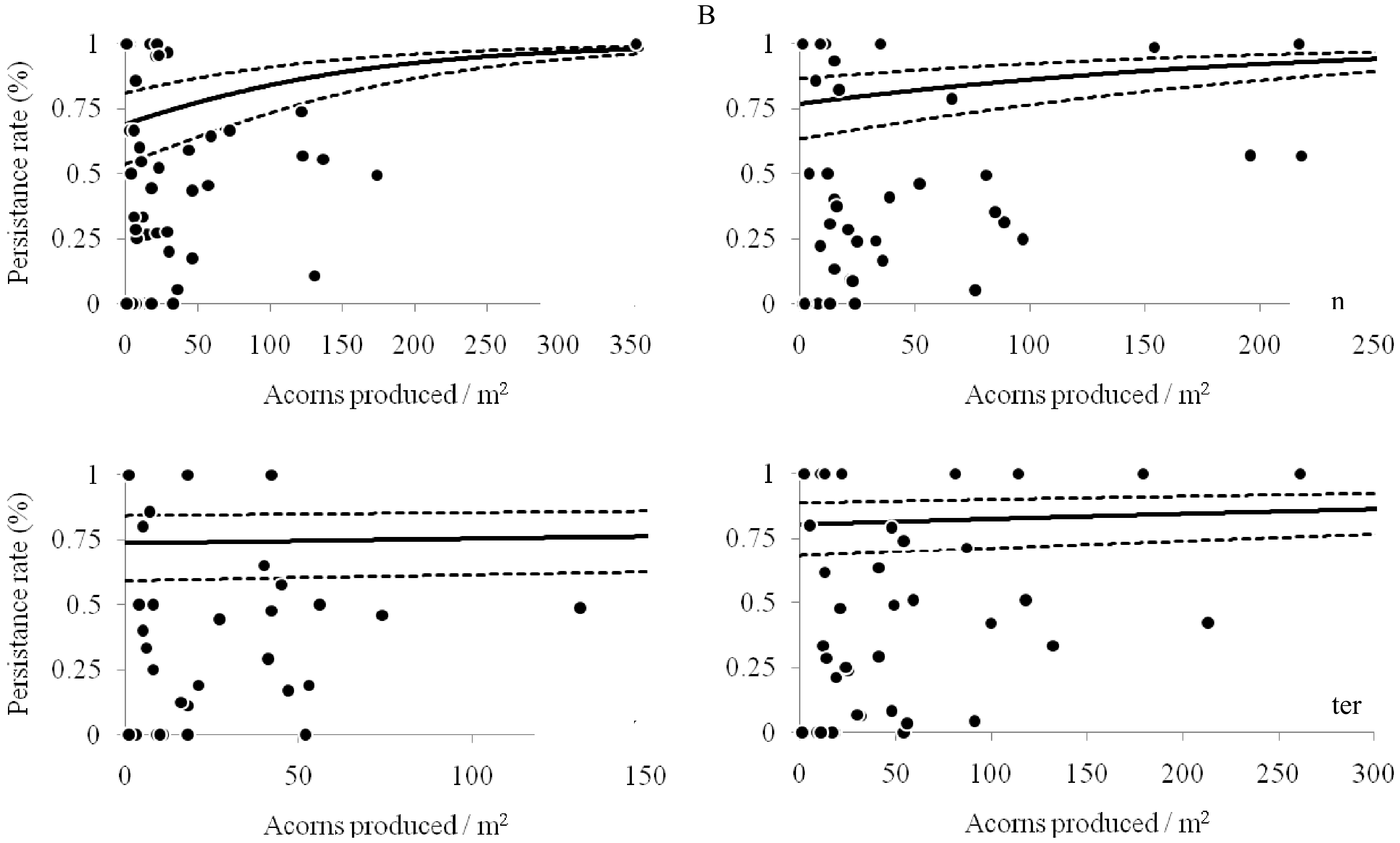
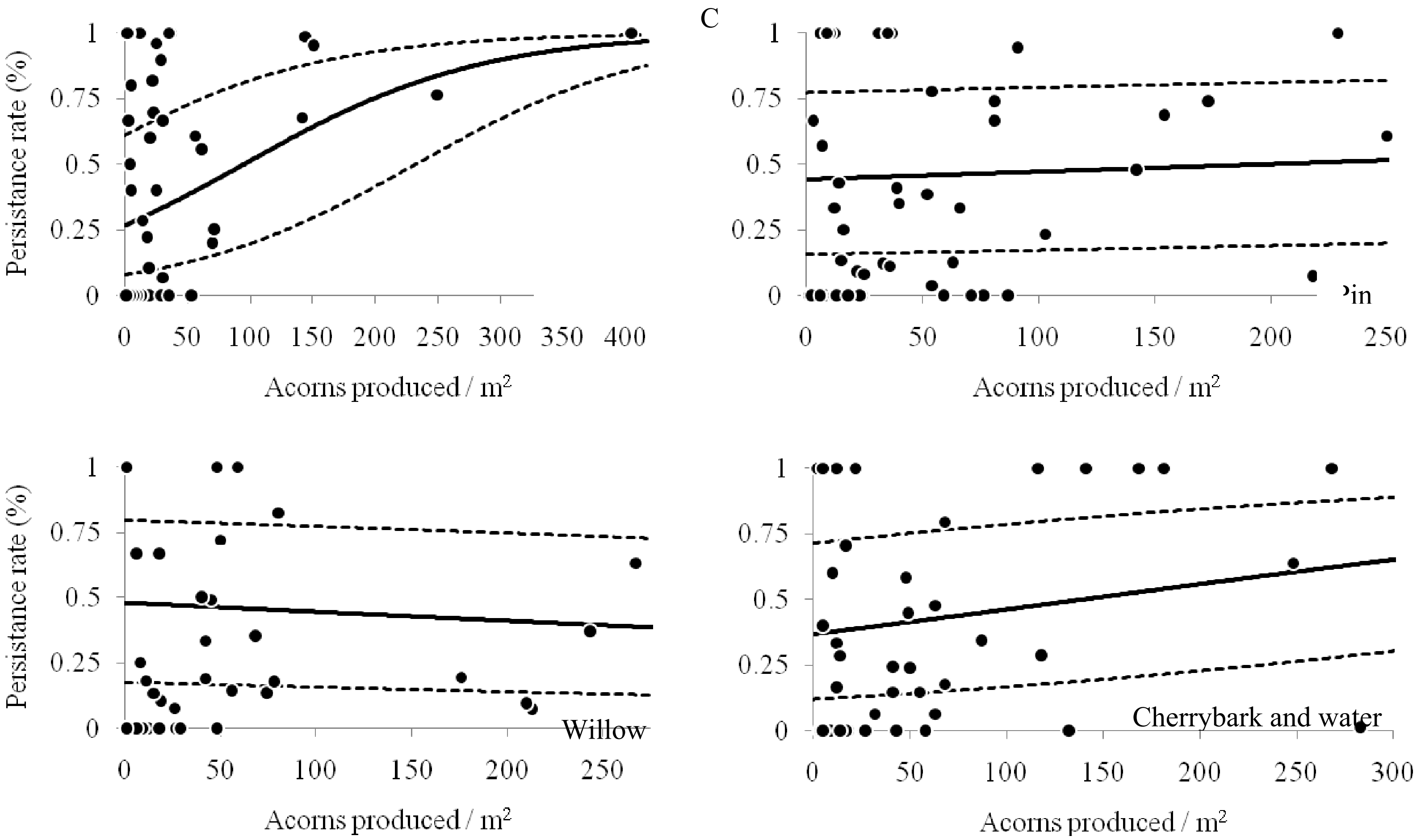


Figure 2.1 (continued)



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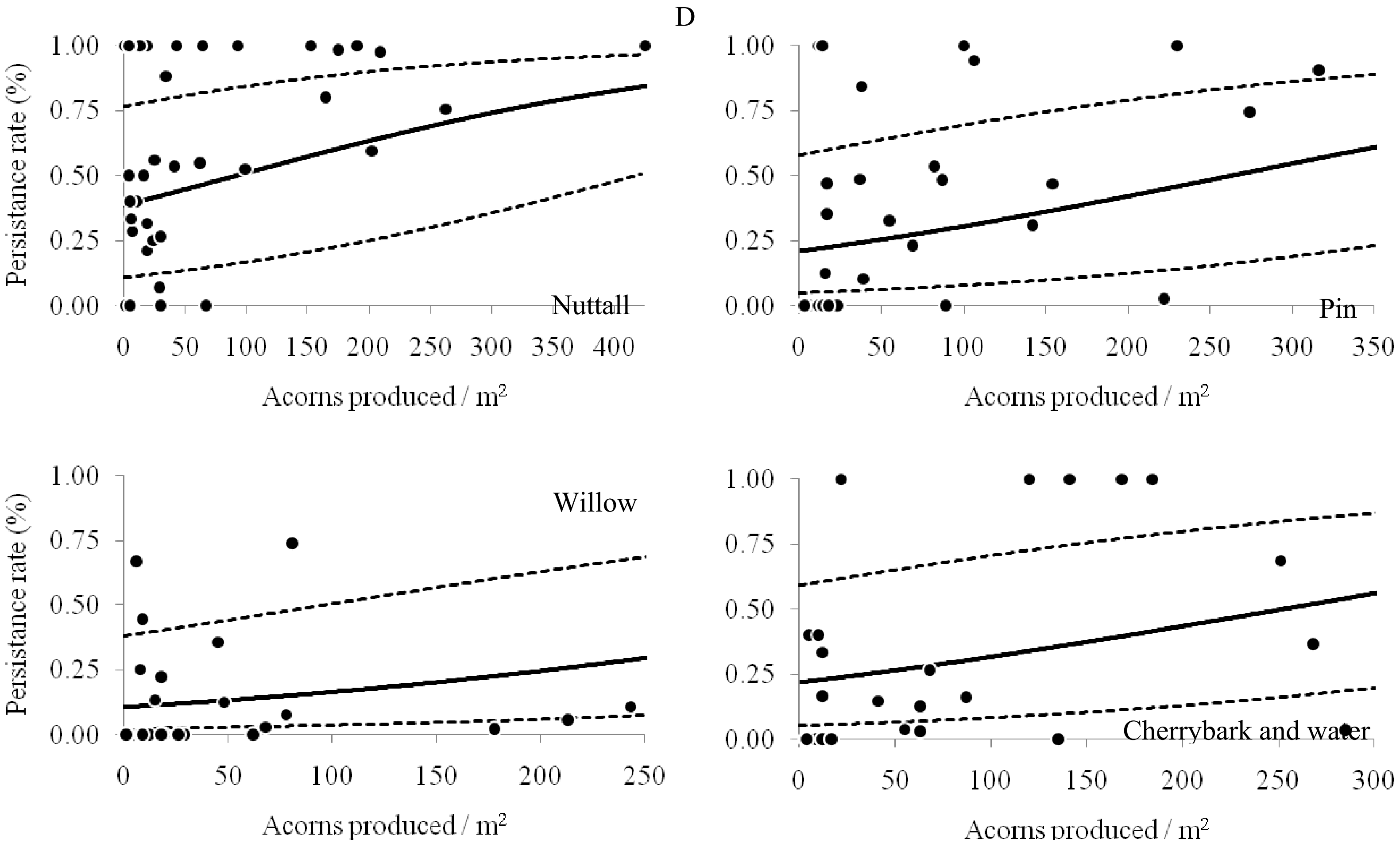

Figure 2.1 (continued)

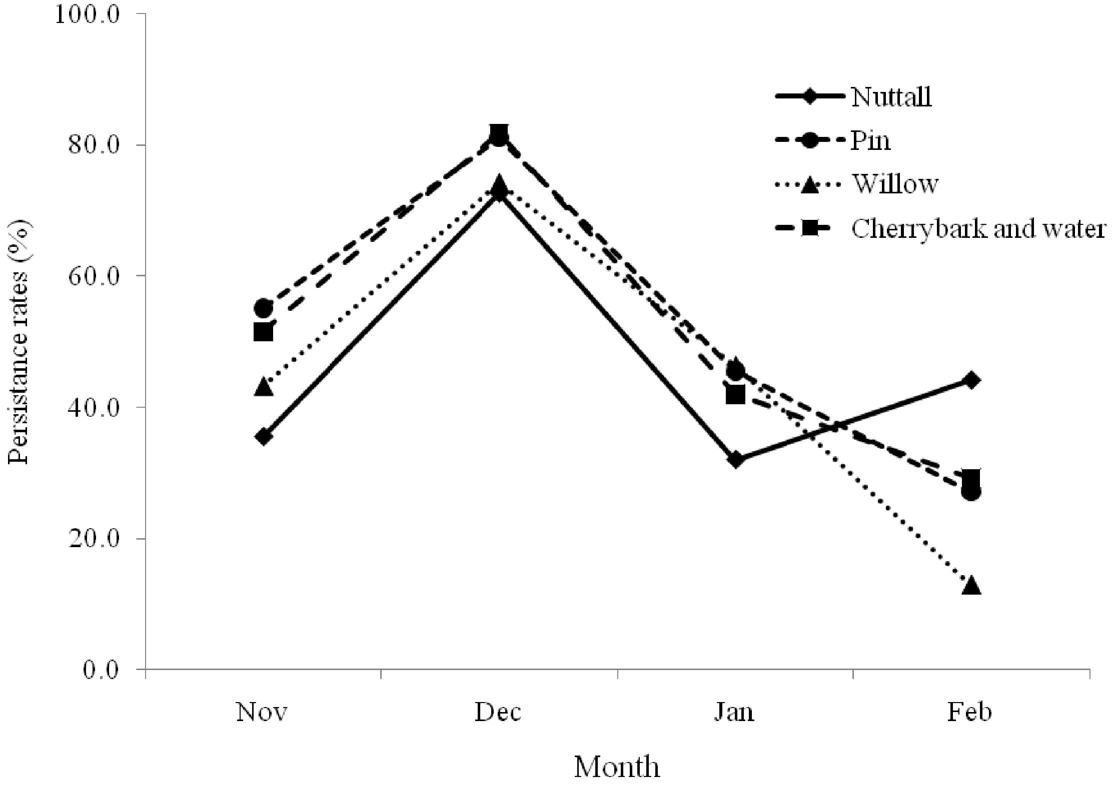

Figure 2.2 Monthly acorn persistence rates relative to species-specific mean yield for Nuttall, pin, willow and cherrybark and water oaks from bottomland hardwood forests in the Mississippi Alluvial Valley, autumn-winters 2009-2012.

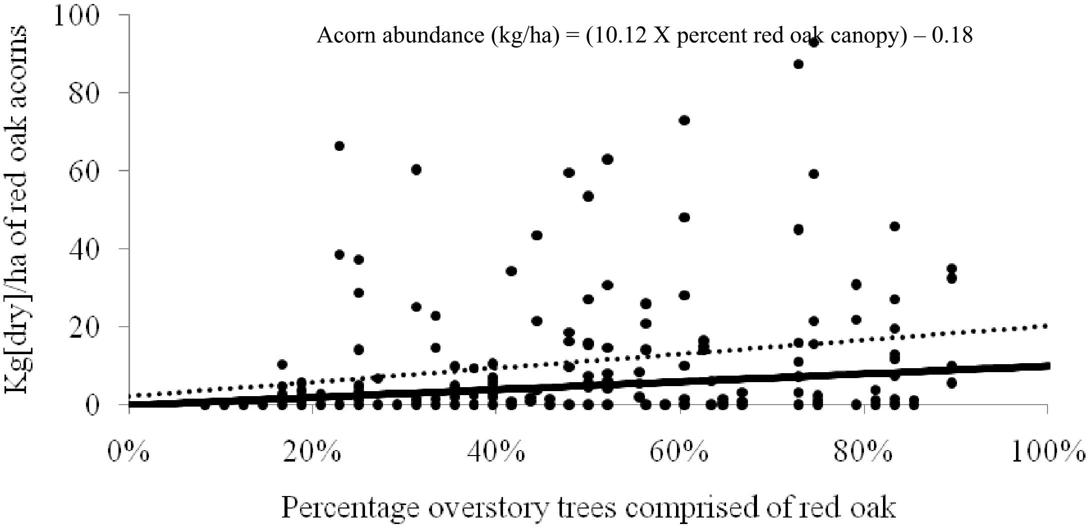

Figure 2.3 Relationship between red oak acorn abundance* and percentage of overstory trees comprised of red oaks in hardwood bottomlands in the Mississippi Alluvial Valley during non-mast years 2009-2011.

* Dotted line represents upper 95% confidence interval and dots represent sample values.

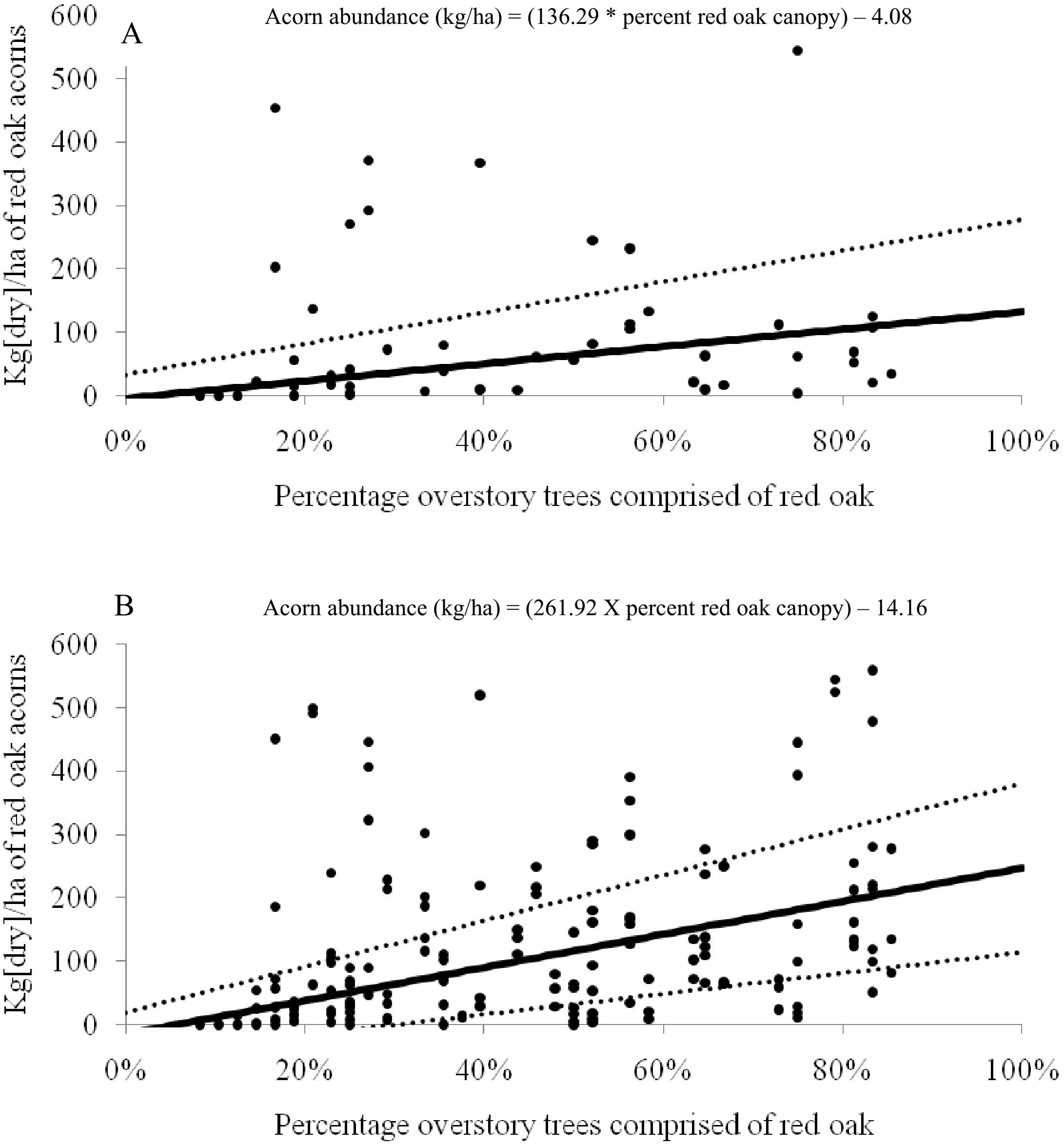

Figure 2.4 Relationship between red oak acorn abundance* and percentage of overstory trees comprised of red oaks in hardwood bottomlands in the Mississippi Alluvial Valley during February (A) and November, December and January (B) in mast years 2009-2011.

*Dotted line represents upper 95% confidence interval and dots represent sample values.

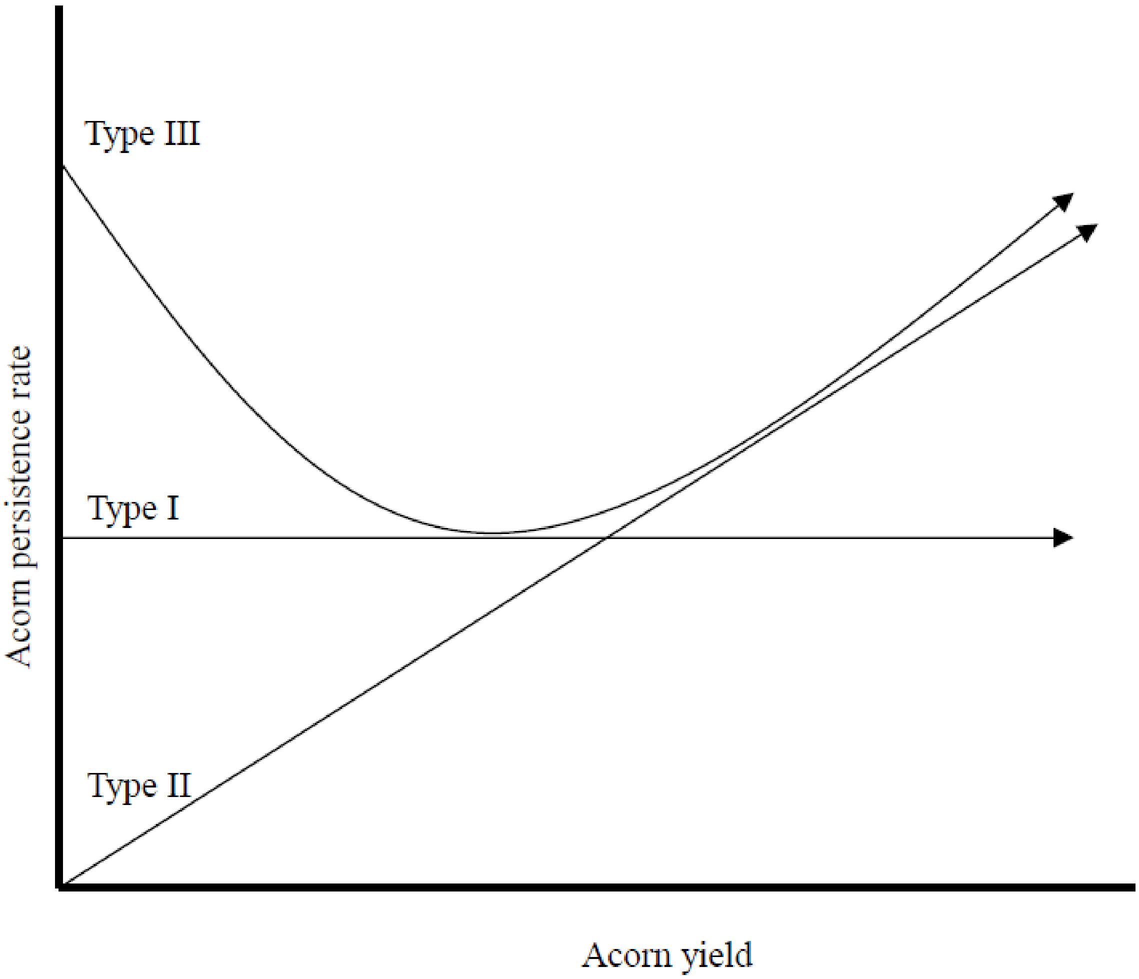

Figure 2.5 Theoretical relationship between red oak acorn yield* and acorn persistence# rates for Type I, II, and III functional responses.

*Acorn yield refers to the number of acorns produced by parent trees and collected in seed traps.

#Persistence is the ratio of presumably sound acorns on the ground to the yield from seed traps and standardized for the area sampled.

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CHAPTER III

EVALUATION OF VISUAL SURVEYS TO PREDICT RED ACORN YIELD IN THE MISSISSIPPI ALLUVIAL VALLEY

Red oak (*Quercus* spp.; Section *Erythrobalanus*) acorns are a valuable and extensively used food resource for wildlife and are fundamental for oak regeneration. A natural history review of the silvicolous species inhabiting hardwood bottomlands in Mississippi Alluvial Valley (MAV) reveals that most species utilize acorns to some extent during winter (Christisen and Korschgen 1955, Korschgen 1981). The common red oak species in the MAV include cherrybark (*Q. pagoda*), Nuttall (*Q. texana*), pin (*Q. palustris*), water (*Q. nigra*), and willow oaks (*Q. phellos*; hereafter "red oaks"). Notwithstanding the importance of red oak acorns as wildlife forage, their abundance often is correlated with reproductive output, survival, movements and body condition of many species (Rogers 1987, Pelton 1989, McShea and Schwede 1993, Feldhamer et al. 2002). Therefore, many ecologists consider acorns a keystone food resource (Rice et al. 1993, Wolff 1996). Undoubtedly, reduction in range or extirpation of oaks and their acorns from eastern forests would have devastating effects on native wildlife and humans (Ostfeld et al. 1996, Healy and McShea 2002, McShea et al. 2007).

Because of the far reaching impacts of acorns on wildlife populations and forest ecology, estimating annual yields of acorns has been paramount for researchers. Methods to assess yields include numerous quantitative and qualitative approaches. Quantitative approaches include seed traps, which catch acorns as they fall from the parent tree (Guttery 2006, Thornton 2009, Leach 2011), visual surveys such as time-constrained acorn counts (Koenig et al. 1994), and score counts of twigs and acorns on a subsample of oak limbs (Whitehead et al. 1969). Qualitative visual surveys rely on an observer's subjective assessment and use of categorical ranks such as "good" or "poor" yields (Christisen and Kearby 1984). Except for seed traps, these other approaches often are termed hard mast indices (HMIs).

Although seed traps provide quantitative assessments of acorn yields that can be standardized to unit area of tree crowns, traps require assembly, transportation, maintenance, and periodic monitoring. Furthermore, seed traps only collect acorns not harvested by arboreal predators of acorns (e.g., birds, squirrels), thus estimates of total yield are always biased low. Seed traps can yield quantitative estimates of mast reaching the ground; however, depending on arboreal removal, they may not accurately predict overall seed productivity. Indeed, HMIs are much less time consuming and labor intensive and require far less equipment than use of seed traps. The HMIs are typically conducted once each fall before most seeds fall (Koenig et al. 1994). Although HMIs do not provide an estimate of acorn abundance, they provide data to compare relative yield among trees, sites, and years, assuming HMIs are correlated positively with estimates of acorn abundance.

Although others have evaluated visual surveys with seed trap data for some oak species in upland forests (Perry and Thill 1999), no study has evaluated HMIs for the suite of red oaks inhabiting bottomland in the MAV. Conducting HMIs in bottomland hardwood forests presents challenges that may inhibit effectiveness of HMIs compared to upland forest. For example, bottomland hardwoods in the MAV contain diverse communities of native vines (e.g., poison ivy [*Toxicodendron radicans*], Virginia creeper [*Parthenocissus quinquefolia*]) that occupy mid- and upper crowns of these forests. Vines deter investigators' view of the canopy making HMIs difficult to conduct. Nonetheless, I designed a study to evaluate 4 separate HMIs to predict annual red oak acorn abundance in the MAV.

I used data from 3 years and 577 trees at 7 sites in the MAV and compared estimated acorn yield derived from seed traps with the aforementioned HMIs. Specifically, my objectives were to 1) determine which HMI best predicted actual number of acorns collected from seed traps, 2) compare results from my study with similar studies on other oak species in North America, and 3) make a recommendation as to which method is most effective to monitor mast production from MAV red oaks.

Study Area

The MAV, a historic floodplain of the Mississippi River, extends from Cairo, Illinois to the mouth of the Mississippi River in Louisiana, a total length of about 800 km (Reinecke et al. 1989). It includes 7 states and about 10 million hectares of which nearly 2.6 million ha remain in hardwood bottomlands (Twedt and Loesch 1999). About 16% of the remaining hardwoods are on public lands (Twedt and Loesch 1999). The region extends between 29° and 37°N latitude and between 89° and 92°W longitude (Fig 1). The MAV is situated in a humid, subtropical region of the Northern Temperate Zone where annual precipitation ranges between 117 cm in the north and 165 cm in the south (National Climatic Data Center 2011). January temperatures range from 3ºC in the northern reach of the MAV, 7.5ºC in the central sub-region, and 11ºC in the southern reach, whereas temperatures in July average about 30ºC across the region.

Current land cover in the MAV is a mix of mostly agricultural land, bottomland hardwood and other forest communities, emergent and other wetlands, and urban areas (Twedt and Loesch 1999, Pearse et al. 2012). The current distribution of hardwood bottomlands is skewed greatly toward the southern MAV, wherein Arkansas, Louisiana, and Mississippi have about 94% of the total hardwood bottomlands (Twedt and Loesch 1999).

I studied on 7 areas in 5 states in the MAV, including 5 National Wildlife Refuges (Mingo [Missouri], Chickasaw [Tennessee], White River [Arkansas], Tensas River [Louisiana] and Noxubee [Mississippi]), a National Forest (Delta [Mississippi]), and a private research forest (Monsanto Farm and Wildlife Management Center research Farm [Arkansas]).

Methods

Study Design

I randomly selected 20, 0.2-ha circular plots within mature hardwood bottomland forests at each of the aforementioned study areas (Chapter 1), except Monsanto Farm and Wildlife Management Center. There, I adopted a study design, previously used by Guttery (2006) to estimate willow oak acorn yield. At each plot, I randomly selected and sampled acorn yield from 2 oak trees, using an acorn trap (hereafter, trap; Chapter 1). However, I sampled one oak per plot at Monsanto Farm and Wildlife Management Center, consistent with Guttery's (2006) procedure. Because I was interested in estimating total production of red oak acorns across species at each site, I did not discriminate selection of sample trees among species. My selected tree species included cherrybark, Nuttall, pin, water, and willow oaks. Not all species occurred at each study area, so species composition and sample sizes varied. I sampled trees ranging in size from 25-141 cm DBH ($\bar{x}$ = 59.0 cm, SE = 1.9, n = 312).

Acorn Collection

To collect acorns from sample trees, I randomly chose a cardinal direction and then placed a 1-m^2 square trap halfway between the bole and the canopy drip line (Guttery 2006, Chapter 1). I fabricated frames of traps from 2.5 cm x 10 cm treated wooden boards, joined at the ends and mounted atop 4, 1.5-m lengths of electrical conduit. To the wooden frame, I attached a funnel-like piece of fiberglass window screening that extended downward from the frame approximately 45 cm vertically (Guttery 2006). At the distal end of the screening, I attached a wide mouthed plastic bottle to consolidate acorns that fell into the trap. I pushed conduit legs 30-40 cm into the ground, affording stability to the trap yet keeping them elevated above ground or water and to deter acorn depredation by animals. For comparisons with HMIs, I summed totals of all sound and unsound acorns (i.e., acorns that sink or float in water, respectively; Allen and Kennedy 1989), including partially consumed and/or fragmented acorns, collected over the entire collection period of November 2009-2011-February 2010-2012. I included totals of all of previously mentioned acorns and parts to compare these data with HMIs described in the following section.

Hard Mast Indices

I surveyed each tree once during autumns 2009-2011. I conducted surveys before seed drop from mid-August to mid-September each year. In all surveys, I used Eagle Optics *Denali* 8 power by 42 mm lens diameter binoculars. I conducted all surveys to eliminate inter-observer bias. At each sample tree, I randomized the order of types of surveys used to quantify HMIs to reduce bias associated with non-independence of methods. I used the following methods to assess visual acorn counts: 1) Koenig (Koenig et al. 1994), 2) Whitehead (Whitehead et al. 1969), 3) Graves (Graves 1980), 4) recorded percentage of crown containing acorns (Whitehead et al. 1969; hereafter CROWN%), and 5) after all surveys were completed I calculated percentage of trees with acorns (%TWA).

For the Koenig method, I randomly selected a portion of the crown and counted all mature acorns seen through binoculars during a 15 second sample period. I then moved to another random portion of the canopy and repeated this procedure. I used the combined counts as HMI for the tree in analysis.

I followed procedures from Whitehead (1969) and scanned the upper canopy with binoculars and assigned a score based on percentage of the crown containing acorns. I assigned numerical scores of 0, 1, 2, or 3 to the respective crown coverage with acorns of 0-5%, 6-33%, 34-66%, and 67-100%. Next, I examined the terminal approximate 1 m of an upper canopy tree limb and counted total number of twigs and associated mature acorns. I did this 5 times for each tree and determined percentage of twigs that harbored acorns on all 5 tree limbs. To assign a numerical score to percentage of twigs with acorns, I used the same percentage categories and scores (i.e., 0-3) as described previously. Lastly, for twigs containing acorns, I counted acorns to derive an average number of seeds per twig. I assigned scores of 0 - 4, when average number of acorns were <1, 1-2, 3-4, 5-6, and >6 per twig, respectively. Each tree received a cumulative index score which was the sum of scores assigned for the percentage of crown bearing acorns, percentage of twigs with acorns, and average number of acorns per twig. For example, if I classified a tree as having 100% of its crown containing acorns, 100% of its twigs harboring acorns and average number of acorns per twig equal to 7, the cumulative index would be 10 (i.e., 3 + 3 + 4).

I modified classes from Graves (1980) to assess subjective ranks for each tree. I scanned the crown of each tree and assigned a single index score for each tree based on observed acorns. I used the following scores: 0 = few or no acorns, 1 = scattering of single seeds over entire crown or a few clusters of acorns over one-fourth of the crown, 2 = some clusters with a scattering of single seeds evenly distributed over the entire crown or clusters of seeds only on half the crown, and 3 = seeds in clusters evenly distributed over entire crown.

I modified procedures from Whitehead (1969) to calculate CROWN%. First I visually divided the canopy into 10 equal-distant sections. I then scanned each section independently for exactly 5 seconds with binoculars and recorded if acorns were present in that section. I summed the total sections containing acorns for each tree crown and divided by total amount of sections to arrive at CROWN%. I recorded percentage increments of 10%. I used percentage increments as the index in analysis.

Lastly, I used results from the CROWN% to calculate the %TWA at the population level. For each site-year combination of red oaks, I classified all trees into 2 groups; those bearing acorns and those not bearing acorns. I classified trees with a CROWN% score of 10% or below as not producing acorns. From this I calculated the %TWA for each site-year combination.

Statistical Analyses

I compared HMI scores from individual trees for the Koenig, Whitehead, Graves and CROWN% HMIs with total annual yield of acorns collected in traps using Pearson product-moment correlation analysis (R Development Core Team 2006). I also compared mean population level acorn yield with for all the aforementioned HMIs and the %TWA HMI. I transformed acorn yield raw data using a natural log to linearize relationships. Because the Koenig HMI produced continuous data, I used simple linear regression to regress log transformed data on HMI values (R Development Core Team 2006). For the Whitehead and Graves HMIs (qualitative measures), I used mean acorn density across sample trees for each corresponding value class. Potential differences in acorn densities among classes were inferred using 95% confidence intervals (CI) if CIs did not overlap. I also summarized site-year means of all acorns collected in traps (acorn/m^2), sound acorns (kg[dry]/ha), and each corresponding HMI to make relative comparisons over sites and years. I computed correlation coefficients for each site-year mean acorn yield (acorns/m^2 and kg/ha) with each HMI.

Results

For individual trees, all HMIs were positively correlated with acorn yield from seed traps (Table 3.1; Figure 3.1). The CROWN% produced the greatest correlation (r = 0.730), whereas the Koenig method generated the least (r = 0.688). Nonetheless, there was a linear relationship between the Koenig ($R^2 = 0.47$, $F_{1,\,546} = 489.4$, $P < 0.001$) HMI and corresponding acorn yield data (Fig 3.2).

All increases in Graves HMI classes corresponded directly with mean number of acorns from traps and there was no overlap in ranges among any Graves HMI classes (Table 3.2). Similarly, mean number of acorns from traps increased with each Whitehead HMI class, except class 9 (Table 3.2). Ranges in acorn yield always overlapped among adjacent Whitehead HMI classes (Table 3.2). The most commonly assigned acorn classes were 0 (20% of all trees; $n = 473$) and 1 (40% of all trees ,$n = 481$;) for Whitehead and Graves methods, respectively.

Population estimates of mean number and biomass of acorns separately were positively related to mean HMIs (Tables 3.3 and 3.4). The CROWN% performed best (i.e., $r = 0.932$) in predicting acorn counts and biomass (i.e., $r = 0.679$). All HMIs were better at predicting acorn number than biomass.

Discussion

All HMIs were positively related ($0.642 \leq r \leq 0.932$) to acorn yield estimated from trap samples. The difference between all methods in predicting numbers of acorns only was $r = 0.042$ at the tree level and 0.071 at the population level, and was 0.085 in predicting biomass (kg [dry]/ha) at the population level. Because of this similarity in predicting acorn yield, I discuss the advantages and disadvantages of each HMI.

The Whitehead HMI was most time consuming and technical to complete. This method involves recording 3 separate parameters for each tree including counting numbers of twigs on the terminal 1 meter of a randomly selected branch. I was challenged judging length of a tree branch in the canopy, especially when canopy heights of oaks exceeded 25 m. I surveyed 3 different sections of the upper canopy; therefore, each survey took around 4 minutes. An advantage of the Whitehead HMI is that it inherently accounts for number of seeds produced per twig, although counting twigs and associated acorns is difficult, especially for willow, cherrybark, and water oaks which have relatively small acorns. Although index scores can range from 0 to 10, I never scored any trees a value of 10 and only 7 trees (1.6%) a value of 9. The species that received scores of 9 were 2 each of willow, cherrybark, and water oak and one pin oak. I never scored a Nuttall oak a value of 9, although I encountered this species most commonly. Because the Whitehead method is partially based on number of acorns per twig, it may discriminate against scores ≥8 for Nuttall Oak, given the large acorn size of this species. Number of acorns per twig were greatest for cherrybark ($\bar{x} = 2.44$, SE = 0.72, $n = 30$), followed by willow ($\bar{x} = 2.34$, SE = 0.29, $n = 125$), water ($\bar{x} = 2.22$, SE = 0.45, $n = 33$), pin ($\bar{x} = 1.82$, SE = 0.43, $n = 92$) and Nuttall oak ($\bar{x} = 1.71$, SE = 0.33, $n = 162$). As such, the Whitehead HMI should be used with caution when comparing different species, because the maximum obtainable index varies by species. Furthermore, I found large overlaps in the mean acorn yield for adjacent Whitehead index classes suggesting a lack of the precision in each index class. Despite these drawbacks, my results indicate the Whitehead HMI performed consistently second best regarding predicting acorn yield.

The Koenig method has been used successfully by researchers (Koenig et al. 1994, Garrison et al. 1998). The Koenig method requires two 15 second counts of acorns seen through binoculars; thus, this method was quickest. An advantage of this index is that it generates a continuous variable that can be analyzed with standard statistics. All other HMIs generate categorical ranks. Additionally, an observer needs no knowledge of relative acorn production (e.g., poor, average, or good); therefore, the Koenig method is less subjective than other HMIs. Furthermore, unlike the Whitehead HMI, the Koenig method does not require ambiguous decisions regarding estimating the terminal meter of a branch. The Koenig method was developed for use with oaks in coastal western U.S. coast including coast live (*Q. agrifolia)* and California black oak (*Q. kelloggii)*, which are species with crowns near the ground. Thus, acorns can be counted at ground level without binoculars (Koenig et al. 1994). As such, applicability of this method to tall bottomland oaks and other hardwoods in the MAV may be limited. However, Koenig HMI is an index; thus, relative values may render comparisons among sites and years useful. This method is limited regarding how fast an observer can count seeds. This limitation is pronounced on trees with abundant acorn crops. My data suggest that after 50-60 acorns are detected the linear relationship begins to flatten (Fig 3.1A). A Koenig score of 60 equates to counting 2 acorns per second, which limited my ability to count acorns this rapidly. Other investigators may have similar challenges. Therefore, the Koenig method may become increasingly unreliable when acorn yield is superabundant. In relation to the other methods evaluated, my results indicate the Koenig HMI was least effective at predicting yield of individual trees. When I re-analyzed Koenig HMI data using only values of ≤60 (i.e., 2 acorns/sec), I found the correlation coefficient increased to 0.740 ($R^2 = 0.47$, $F_{1, 428} = 181.8$, $P < 0.001$), which would have made it the most effective method in predicting individual tree acorn yield. This confirms the limitation of the Koenig index across the range of acorn yields.

The Graves method required a thorough scan of the upper tree canopy and generally took less than 3 minutes to complete. However, this method requires an observer to estimate subjectively one of 4 yield classes (e.g., list all 4 classes). A drawback of the Graves method is that it can be observer-biased. One observer's assessment of "light" may be another observer's assessment of "medium" or another yield class. In my study, I eliminated multiple observers confounding effects, because I was the only observer. It is unlikely that one observer would be involved in future large-scale acorn surveys. Researchers interested in subjective surveys should be mindful of the potential differences among observers and limit number of observers. Because the Graves HMI has only 4 classes, I found different acorn yields for each class. If researchers are interested in ranking their mast producing trees with a 4 scale system, then this method can be used recognizing that each rank will produce different yields. Reagrding predicting acorn yield at either the individual tree or population level, the Graves class consistently ranked third or fourth best.

The CROWN% HMI also required scanning the upper tree canopy, which generally took less than 2 minutes to complete. This method is based on the Whitehead HMI; therefore, correlation coefficients between each differed only by 0.004. Whitehead (1969) suggested that an observer scan the canopy of the tree for about 2 minutes then "estimate" the CROWN%, making this a subjective estimate. However, I attempted to reduce the subjectivity by visually dividing the upper canopy into 10 sections and then recording number of sections containing acorns. If all 10 sections contained acorns, then I scored that tree 100% CROWN%. A drawback of this method is remembering, during counting, where one divides the 10 sections of the canopy. To my knowledge, I was the first investigator to relate the CROWN% HMI to yield of acorns from seed traps. Greenberg and Warburton (2007) found that CROWN% was correlated ($r > 0.95$) with %TWA at the population level, although their study lacked acorn yield data. In my study, the CROWN% HMI also was correlated ($r = 0.94$) with %TWA HMI. Greenberg and Warburton (2007) showed strong relationships between the %TWA HMI and the Whitehead HMI for red and white oaks. Because of the strong correlation, they recommend forest mangers use %TWA to index and monitor trends in acorn yield. However, based on among years and sites variation in acorns yields in my study, I suggest CROWN% was a better predictor than %TWA and consistently was the best predictor of red oak acorn yield in the MAV, at the individual tree and population levels.

The %TWA HMI is an estimate that can be derived after completing other HMIs in the field. To calculate this index, one must classify each tree based on presence or absence of acorns in the canopy then calculate the ratio of producing versus non-producing trees. For example, if I classified 75 of 100 oak trees as producing acorns, then the %TWA index = 0.75. Greenberg and Warburton (2007) derived %TWA HMI by assigning presence or absence of acorns on individual trees using 3 separate approaches, when: 1) CROWN% was < 5.5%, 2) CROWN% was < 33.5%, and 3) Whitehead HMI = 0. They found all 3 methods were correlated with the Whitehead index of acorn yield. Because the %TWA HMI is calculated from a population of individuals, it cannot be correlated with individual tree yield. Of the HMIs assessed in this study, %TWA was least effective in predicting yield of acorns by count, and only the Koenig method performed worse regarding predicting acorn biomass. These results may be related to sample sizes being too small. Greenberg and Warburton (2007) analyzed data from >10 independent survey routes conducted over 21 years; thus, their sample size exceeded 200. On the other hand, I analyzed 3 years of data from 7 sites but I didn't survey each site all years. Therefore, in comparison, my sample size was 12. With additional years of surveys, the %TWA may become increasingly robust in estimating yield of red oak acorns in the MAV.

Hard mast indices pertaining to the individual trees were below values reported by Perry and Thill (1999), who conducted 5 separate HMIs on white oak (*Q. alba*) in the Ouachita Mountains in Arkansas. They reported regression coefficients for the Koenig, Graves, and Whitehead methods of 0.870, 0.850 and 0.850, respectively; whereas, I recorded 0.688, 0.703 and 0.728 for these same HMIs. At the population level, my correlation coefficients in predicting acorn yield ranged from 0.866 to 0.937, which were slightly less than values reported by Greenberg and Warburton (2007; $0.972 \leq r \leq 0.997$), although they did not relate their HMIs to actual yields of acorns. My coefficients may have been less than others, because I did not partition and analyze data by species.

There are various other factors that may influence efficiency and efficacy of HMIs. Factors such as time of day, sun angle, percentage cloud cover, precipitation, canopy closure, and wind speed can influence an observer's view of the canopy. Some factors are not systematic in how they would affect the reliability of the HMIs. For example, I found on windy days that all HMIs were challenging to conduct because of constant motion of the canopy and leaves, which made detecting acorns with binoculars difficult. Anecdotally, I found conducting HMI surveys were most difficult when there was no cloud cover, the sun was at its highest peak, and wind was strong. I found that species with small acorns such as willow, water, and cherrybark oaks were more difficult to count compared to Nuttall and pin oaks with larger acorns. Also, temporal and species-specific variation in acorn color may have influenced my results. I conducted surveys from mid-August through mid-September. Acorns at Mingo NWR in northern MAV were darker than elsewhere because of their advanced maturity, and these were easiest to see. By contrast, acorns from my southern sites were mostly green during this period and blended with the surrounding leaf foliage. To the best of my ability, I controlled for many of the factors by conducting surveys consistently in the morning, when wind was light and there was some cloud cover. However, I cannot assess the extent of interaction that may have occurred among these factors. Nonetheless, because correlation coefficients in my and other studies were similar, I'm confident these factors did not inhibit my results more so than other studies.

Management Implications

My data indicate that HMIs are effective in determining relative red oak acorn yield from individual trees and population means of trees in the MAV. However, although HMIs are economical and less time consuming to conduct, they do not produce estimates of yield. Scientists and managers needing estimates of acorn yield should consider using seed traps (Chapters 1 and 2). If relative comparisons in acorn abundance are desired among regions or years, HMIs will suffice in place of quantitative yield data from seed traps. I found the CROWN% HMI was consistently the most accurate predictor of acorn yield from seed traps, although all HMIs produced similar results. Given the similarities among HMIs, I recommend an approach that is simple to conduct and requires minimal time in the field. Greenberg and Warburton (2007) recommended standardizing mast surveys across states and regions and suggest %TWA as an applicable index for large-scale monitoring. Although I recognize the need and importance of standardizing protocols across regions, I recommend forest managers in the MAV use the CROWN% HMI because it was: 1) most efficient, 2) the best predictor of acorn yield in traps at the individual tree and at the population levels, 3) correlated ($r = 0.94$, this study; $r > 0.95$; Greenberg and Warburton 2007) with the population level %TWA, thus enabling easy comparison with CROWN% and other HMIs.

Although I surveyed many red oak trees (>400 trees) over 3 years in the MAV, I can only make limited inferences regarding population-level efficiency of the HMIs because at this level my sample sized is limited (i.e., $n < 15$). I suggest the continuation of research at my study areas using the %CROWN HMI for at least 5 additional years to make a more robust and accurate assessments of this approach.

Table 3.1 Pearson product moment correlation coefficients between hard mast indices and number of acorns collected from seed traps under red oak trees in the Mississippi Alluvial Valley, 2009-2011.

HMI[a]	df	*F*-statistic	*r*	*P*
CROWN%	464	528.4	0.730	< 0.001
Whitehead	440	496.9	0.728	< 0.001
Graves	472	496.9	0.703	< 0.001
Koenig	546	489.4	0.688	< 0.001

[a] Hard Mast Indices represent percentage of crown containing acorns (CROWN%) and others described in the methods (Greenberg and Warburton 1997, Whitehead 1969, Graves 1980, and Koenig et al. 1994).

Table 3.2 Mean red oak acorn yield collected in traps in the Mississippi Alluvial Valley 2009-2011for each index class of the Whitehead and Graves hard mast indices.

	Whitehead[a]		Graves[b]	
Index class	*n*	$\bar{x}$	*n*	$\bar{x}$
0	95	3.5 ± 2.2[c]	119	3.6 ± 1.8
1	12	6.3 ± 7.3	178	21.7 ± 5.7
2	16	6.4 ± 3.4	118	71.9 ± 15.9
3	52	8.3 ± 3.5	59	136.5 ± 25.5
4	68	18.6 ± 6.0		
5	41	45.9 ± 22.2		
6	63	69.3 ± 21.0		
7	44	99.2 ± 29.1		
8	43	134.2 ± 33.3		
9	7	125.6 ± 44.0		

[a] from Whitehead (1969)

[b] from Graves (1980)

[c] ± 95% confidence interval

Table 3.3 Mean annual red oak acorn yield in relation to mean hard mast indices at 7 study sites in the Mississippi Alluvial Valley and Interior Flatwoods from 2009-2011.

		Yield		HMI[d]				
Site	Year	acorns/m^{2}[a]	kg/ha[b]	%CROWN	%TWA	Whitehead	Koenig	Graves
Delta	2010-2111	7.9	198.0	22.1	0.28	2.1	7.7	0.70
Chickasaw	2009-2010	7.1	130.0	23.4	0.26	2.3	5.9	0.82
Mingo	2009-2010	5.7	100.0	28.0	0.55	3.6	6.8	1.00
White River	2010-2111	7.6	286.0	33.9	0.44	2.9	14.6	0.89
Tensas River	2010-2111	21.5	211.0	36.7	0.56	3.0	10.0	0.94
Tensas River	2009-2010	20.5	190.0	37.8	0.60	3.5	7.8	0.80
Delta	2009-2010	41.3	743.0	51.1	0.67	4.1	13.5	1.34
White River	2009-2010	30.9	1355.0	51.8	0.68	4.4	17.6	1.53
Chickasaw	2011-2012	59.8	1672.0	52.3	[c]		26.0	
Chickasaw	2010-2111	94.2	1790.0	57.8	0.89	5.2	26.5	1.50
Noxubee	2010-2111	78.9	651.4	58.6	0.76	5.3	30.8	1.81
Mingo	2011-2012	81.1	657.0	61.5			26.0	
Monsanto	2009-2010	98.7	704.7	71.1	0.91	5.7	25.8	1.79
Noxubee	2009-2010	117.8	890.2	71.9	0.83	6.1	36.2	1.89

[a] The sum of all sound and not sound acorns collected from seed traps

[b] Value derived for sound acorns only

[c] blank denotes no trees surveyed.

[d] Procedures for hard mast indices (HMI) include percent crowns with acorns (%CROWN), percent of trees with acorns (%TWA), and other methods following, Whitehead (1969), Koenig et al. (K et al.; 1994) and Graves (1980).

Table 3.4 Pearson product moment correlation coefficients between mean hard mast indices and mean annual number and biomass of acorns from seed traps under red oaks at 7 study area in the Mississippi Alluvial Valley, 2009-2011.

		acorns/m^2			kg/ha		
HMI[a]	df	*F*-statistic	*r*	*P*	*F*- statistic	*r*	*P*
%CROWN	12	71.6	0.937	<0.001	8.6	0.680	0.015
Whitehead	12	67.7	0.933	<0.001	8.3	0.674	0.016
Graves	12	42.6	0.900	<0.001	8.4	0.677	0.016
Koenig et al.	14	83.6	0.935	<0.001	8.7	0.647	0.012
%TWA	12	30.1	0.866	<0.001	8.2	0.670	0.009

[a] The HMIs represent percent crowns with acorns (%CROWN), percent of trees with acorns (%TWA) and others described in the methods (Whitehead 1969, Graves 1980, and Koenig et al. 1994).

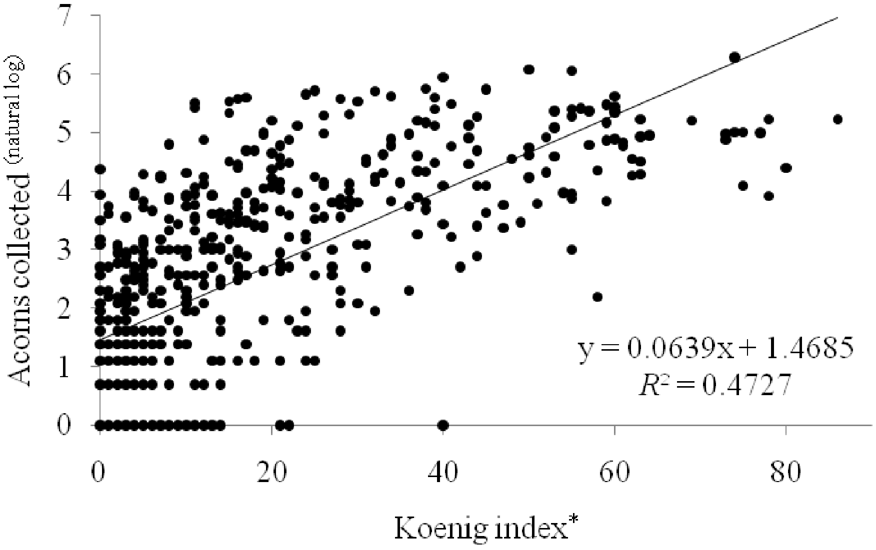

Figure 3.1 Relationship between number of red oak acorns collected from seed traps and number of acorns counted from tree canopies in 30 seconds using field binoculars from 7 study area in the Mississippi Alluvial Valley, 2009-2011.

* From Koenig et al. (1994)

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CHAPTER IV

SYNTHESIS

A principle of the North American Waterfowl Management Plan (NAWMP) is that population growth rate is linked to abundance of wetland habitats (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986). Empirical evidence supports this claim as researchers have linked wetland habitat conditions with survival, body mass, and population recruitment of ducks (Reinecke et al. 1987, Delnicki and Reinecke 1986, Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987). Conservation planners that implement the NAWMP, such as Joint Ventures, have called for large-scale and multi-year studies of foraging carrying capacity of habitats used by wintering and migrating ducks. A unifying approach of JVs is use of a bioenergetics (i.e., daily ration) model (Reinecke et al. 1989). A bioenergetics model requires knowledge of how much food is available and is consumed daily by ducks. To this end, a sundry of studies were undertaken specifically aimed at estimating the amount of waterfowl forage (i.e., kg[dry]/ha) in various habitat types (Stafford et al. 2006, Kross et al. 2008, Foster et al. 2010, Straub et al. 2012). Specific to the Mississippi Alluvial Valley, there are landscape scale estimates of rice (Stafford et al. 2006) and moist-soil wetlands (Kross et al. 2008). Landscape scale multi-year estimates of forage for ducks in hardwood bottomlands of the MAV are non-existent, although this habitat type supports many critical life-history functions of ducks (Heitmeyer and Fredrickson 1990, Heitmeyer 2006)

Ducks consume acorns of bottomland red oaks (*Quercus* spp. Section *Erythrobalanus*) for important sources of energy, protein, and other nutrients (Kaminski et al. 2003). Acorns provide high levels of metabolizable energy and important fatty acids (Heitmeyer and Fredrickson 1990). Fatty acids from acorns are essential for wintering mallards (*Anas platyrhynchos*), wood ducks (*Aix sponsa*), and other birds building lipid reserves for spring migration and reproduction (Heitmeyer et al. 2005). Aquatic macro-invertebrates are an additional source of protein that is consumed by ducks in hardwood bottomlands (Wehrle et al. 1995, Foth 2011). Compared to other available duck foods in the MAV, maximal availability of acorn abundance is temporally delayed. For example, parent plants of agricultural and moist-soil plants mature and drop their seeds during summer-fall (Kross et al. 2008, Foster et al. 2010, Hagy and Kaminski 2012). After these seeds dehisce, they gradually decline in abundance due to granivory (Stafford et al. 2006, Hagy and Kaminski 2012) and decomposition (Nelms and Twedt 1996, Greer et al. 2009). In comparison, red oaks drop their seeds from fall-early spring (Chapter 1). Further, these oak acorns retain their energy over winter, whether inundated or not, and their energy content of acorns is consistent among years (Leach 2011, Leach et al. 2012). However, exact timing of peak acorn abundance within and among sites and years is unknown. Cleary, having better understanding of when acorn abundance is greatest, its relationship with acorn yield, and how many acorns survive winter will further our knowledge and management capabilities of bottomland hardwood forests.

In addition to their importance as wildlife forage, oaks and their acorns have been the focus of countless researchers interested in the evolutionary ecology of seed production (Janzen 1971, Kelly 1994, Kelly and Sork 2002). Ecologists study patterns and processes of masting, defined as the intermittent synchronous production of large seed crops. Oaks have garnered particular interest given their inherent links with other species, especially humans (Ostfeld et al. 1996, Ostfeld and Keesing 2000). Indeed, oaks are known for their variability in acorn production among individuals, sites, years, and species. Numerous hypotheses have been proposed to elucidate the causative mechanisms that trigger masting (for a review see Kelly 1994). Yet, there remains a dearth of information regarding species that inhabit hardwood bottomland forests, such as in the MAV. Therefore, I sampled over 400 individual red oaks in 4 autumn-winters (2008-2012) at up to 7 study areas in 5 states in the MAV. I sampled acorns from 5 species in the MAV including cherrybark (*Q. pagoda*), Nuttall (*Q. texana*), pin (*Q. palustris*), water (*Q. nigra*), and willow oaks (*Q. phellos*). I estimated red oak acorn 1) yield (i.e., acorns collected in seed traps), 2) synchronicity of intra- and inter-species yield of acorns within and among sites and 3) abundance of acorns on the ground or in the water at canopy and forest scales. Additionally, I evaluated 5 visual surveys designed to index yield from counts of acorns attached to branches in early autumn. I also recommend new estimates of red oak acorn abundance for use by the Lower Mississippi Valley JV (Table 2.5).

Study site was the most influential factor explaining variation in red oak acorn yield, and no other explanatory variable showed consistent patterns. Factors explaining variation in acorn yield were complex (i.e., many and interacting parameters) and generally unrelated to tree size or density and volume of conspecifics. I suggest researchers target factors, such as age (Goodrum et al. 1971), weather (Koenig et al. 1996, Pons and Pausas 2012), hydrology, soil (Wolgast and Stout 1977), and other site-specific covariates. There is a considerable knowledge gap in site productivity, soil nutrients, and hydrology for bottomland red oaks. Given annual fluctuations and importance of these variables in hardwood bottomland, I suggest researchers design studies to explore the aforementioned relationships.

My study indicated peak forest-scale acorn abundance is linearly related to percentage of red oak trees in the overstory and varies up to 2 orders of magnitude during a masting and non-masting years (Table 2.5). Because waterfowl are mobile and all sites never failed in mast production in any year, acorn forage likely exists somewhere in the MAV every year, although its availability is related to hydrology and flooding of hardwood bottomlands. Nevertheless, I suggest conservation planners adopt my values that are represented by mast years and summarized in Chapter 1 (Table 1.5).

I was not able to sample all 5 red oaks species at each site, because they did not occur at all sites. For example, pin oak only occurs at Mingo and Chickasaw National Wildlife Refuges in the northern MAV. Also, cherrybark and water oaks were scarce, whereas Nuttall oak occurred relatively frequently. I sampled all red oaks randomly with no species-specific restrictions (i.e.; n = 40 trees/site). Although this approach allowed me to gather data from the most abundant red oaks at each study area, I sacrificed precision at the species-specific level. However, from the perspective of estimating duck or other wildlife forage, sampling all red oaks collectively has a minimal effect on estimating carrying capacity, because all red oak acorns are palatable and do not differ among species in metabolizable energy derived from them by ducks (Barras et al. 1996, Kaminski et al. 2003). Therefore, I suggest future researchers should attempt acquiring precise, species-specific estimates of acorn yield and abundance.

There remains a critical need for further research in hardwood bottomlands. Research has demonstrated the importance of bottomland hardwoods to ducks during winter in the MAV, especially mallards (Heitmeyer et al. 2005, Davis et al. 2009, Davis and Afton 2010, Davis et al. 2011, Pearse et al. 2012). These studies complement others showing importance of hardwood bottomland to wood ducks (Fredrickson and Hansen 1983, Delnicki and Reinecke 1986, Hepp et al. 1989, Barras et al. 1996, Davis et al. 2001, Davis et al. 2007). Thus, I encourage researchers to address the micro- and macro-scale movements, abundance, and distribution of wintering wood ducks and mallards in relation to acorn and aquatic invertebrate abundances in the MAV. In the MAV, there has been research documenting use of rice fields and moist-soil wetlands by mallards and other dabbling ducks (Manley et al. 2004, Pearse et al. 2008, Havens et al. 2009, Hagy and Kaminski 2012). However, there is little known about use and distribution of mallards and wood ducks in forested wetlands across the MAV and southeastern United States (Kaminski et al. 1993, Davis et al. 2009, Davis and Afton 2010). Research that links annual fluctuations in food resource abundance, waterfowl movements and survival, and other biological outcomes possibly linked to population demographics are valuable and needed for waterfowl conservation.

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APPENDIX A

HISTOGRAM OF RED OAK ACORN MASS AND NUMBER COLLECTED FROM SEED TRAPS IN THE MISSISSIPPI ALLUVIAL VALLEY 2009-2012

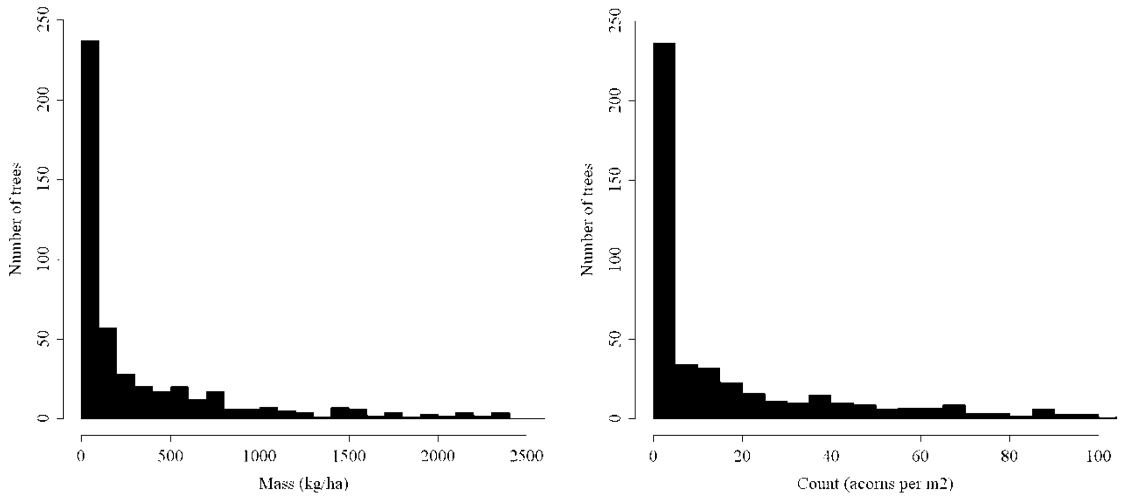

Figure A.1 Distribution of acorns mass and number from red oak trees in bottomland hardwood sites in the Mississippi Alluvial Valley, autumns-winters 2009-2012.

APPENDIX B

PARAMETER ESTIMATES EXPLAINING VARIATION IN SOUND RED OAK ACORN YIELD IN BOTTOMLAND HARDWOOD FOREST IN THE MISSISSIPPI ALLUVIAL VALLEY DURING AUTUMN-WINTERS 2009-2012.

Table B.1 Parameter estimates and 95% confidence intervals from a generalized linear model explaining variation in sound red oak acorn yield in bottomland hardwood forest at 5 sites in the Mississippi Alluvial Valley during autumn-winters 2009-2012.

		2009-2010		2010-2011		2011-2012	
Parameter [b]		β	95% CIs[j]	β	95% CIs[j]	β	95% CIs[j]
Intercept [c]		-0.848	-2.110 – 0.476	0.443	-1.284 – 2.240	1.511	-0.167 – 3.183
DBH [d]		0.026	0.011 – 0.041	0.037	0.016 – 0.059	0.029	0.008 – 0.051
Basal Area [d]		[b]		0.329	0.023 – 0.645		
Site							
	Delta	2.773[e]	1.935 – 3.601	-0.330[f]	-2.483 – 1.780	1.275[f]	-0.813 – 3.347
	Mingo	1.134[e]	0.282 – 1.981	3.319[f]	1.211 – 5.404	2.342[f]	0.118 – 4.515
	Tensas River	1.982[e]	1.066 – 2.936	0.322[f]	-2.037 – 2.643	0.979[f]	-1.340 – 3.308
	White River	2.644[e]	1.675 – 3.660	1.752[f]	-0.686 – 4.140	1.286[f]	-1.207 – 3.820
Crown class [g]							
	Dominant	0.630	-0.003 – 1.274	0.495	-0.062 – 1.067	0.656	0.090 – 1.239
	Suppressed	-0.701	-1.472 – 0.134	-0.604	-1.331 – 0.158	-1.213	-1.919 – -0.463
Species [h]							
	cherrybark and water			1.990	1.266 – 2.775	0.692	-0.057 – 1.523
	Pin			-0.121	-0.836 – 0.597	0.057	-0.646 – 0.787
	Willow			0.381	-0.326 – 1.111	1.258	0.614 – 1.932
Site * DBH [i]							
	Delta			-0.027	-0.058 – 0.005	-0.044	-0.076 – -0.011
	Mingo			-0.049	-0.080 – -0.019	-0.034	-0.062 – -0.003
	Tensas River	...	...	-0.037	-0.071 – -0.002	-0.029	-0.065 – 0.008

Table A.2 (continued)

White River	...	...	-0.058	-0.091 – -0.022	-0.026	-0.064 – 0.013

[a] Sites include Delta National Forest and Chickasaw, Mingo, Tensas River and White River NWRs.

[b] Blanks denote parameter was not included in the optimal model.

[c] The intercept is the mean number of acorns produced when all of the explanatory variables take on the value 0.

[d] Continuous covariate; interpretation = for every one-unit change in the covariate the expected log count of acorns changes by β.

[e] β is difference in acorn production among sites in relation to the arbitrary reference site, Chickasaw NWR holding all other variables constant.

[f] β is the difference in intercepts relative to the arbitrary reference cite (Chickasaw NWR) holding all other variables constant

[g] β is difference in acorn production among crown classes in relation to the arbitrary reference crown class (co-dominant) holding all other variables constant.

[h] β is difference in acorn production among red oak species in relation to the arbitrary reference species (Nuttall) holding all other variables constant.

[i] β is the difference in slopes of acorn production in relation to DBH between the arbitrary reference site (Chickasaw NWR) and the other sites holding all other variables constant.

[j] When confidence intervals do not include zero there is a statistically significant ($\acute{\alpha} = 0.05$) difference from the reference group.

APPENDIX C

. VARIANCE STRUCTURES USED TO MODEL THE RESIDUAL VARIANCE OF LINEAR MODELS PREDICTING THE ABUNDANCE OF RED OAK ACORNS RELATIVE TO THE COMPOSITION OF RED OAK TREES

Table C.1 Variance structures used to model the residual variance of linear models predicting the abundance of red oak acorns relative to the composition of red oak trees in the overstory and sampling month in a good and poor masting year.

Masting Class	Notation[a]	Explanation of variance structure	AIC_c[b]	K[c]
Poor	varComb	Different variances per SITE *and* residual variance of %RO multiplied by an exponential function	1857.1	13
	varComb	Different variances per SITE *and* Variances increases as %RO increases	1862.0	12
	varComb	Different variances per YEAR *and* Variances increases as %RO increases	1890.2	10
	varFixed	Variances increases as %RO increases	1900.4	9
	varComb	Different variances per YEAR *and* residual variance of %RO multiplied by an exponential function	1901.1	11
	varIdent	Different t variances per SITE	1903.5	12
	varExp	residual variance of %RO multiplied by an exponential function	1910.9	10
	varIdent	Different variances per YEAR	1941.8	10
	none	variances constant for each residual	1949.5	9
Good	varComb	Different variances per SITE *and* residual variance of %RO multiplied by an exponential function	2859.8	12
	varComb	Different variances per SITE *and* Variances increases as %RO increases	2896.2	11
	varIdent	Different variances per SITE	2966.0	11
	varComb	Different variances per YEAR *and* Variances increases as %RO increases	2998.1	10
	varComb	Different variances per YEAR *and* residual variance of %RO multiplied by an exponential function	3005.6	11
	varIdent	Different variances per YEAR	3011.6	10
	none	Variances constant for each residual	3033.6	9
	varExp	Residual variance of %RO multiplied by an exponential function	3035.6	10
	varFixed	Variances increases as %RO increases	3045.0	9

[a] Notation follows Zuur et al (2007) and was implemented in Program R 2.13.1.

[b] Akaikie's information criteria corrected for sample size.

[c] Number of estimable parameters.

APPENDIX D

EQUATION USED TO CALCULATE AN EXPONENTIAL FUNCTION (Δ) USED TO NORMALIZE THE NON-LINEAR RESIDUALS OF A LINEAR REGRESSION MODEL ESTIMATING RED OAK ACORN ABUNDANCE

Equation used to calculate an exponential function (δ) used to normalize the non-linear residuals of a linear regression model estimating red oak acorn abundance (Zuur et al. 2009).

$$Variance\ (\varepsilon_i) = (\sigma^2\ x\ e^{\,2\delta\ X\ \%ROi})$$

Where ε_i are the residuals, σ^2 = sum of the variance of all residuals' e = the constant 2.718282, δ = the estimated exponential parameter, and $\%RO_i$ = the percentage of canopy comprised of red oaks for observation i.