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Red Oak Acorn Production, Mass, and Gross Energy Dynamics in the Mississippi Alluvial Valley

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RED OAK ACORN PRODUCTION, MASS, AND GROSS ENERGY DYNAMICS IN THE MISSISSIPPI ALLUVIAL VALLEY

By

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Acorns of red oaks (*Quercus* spp; Subgenus *Erythrobalanus*) are important forage for wildlife and seed for oak regeneration. I estimated production of viable acorns by red oaks in 5 forests in the Mississippi Alluvial Valley (MAV) and 2 greentree reservoirs (GTRs) in Mississippi. Mean acorn production in the MAV was 439 kg(dry)/ha of red oak crown (CV = 29%) during autumn-winter 2009-2010 and 794 kg/ha (CV = 19%) in GTRs during autumn-winters 2008-2010. I recommend researchers sample acorn production in the MAV for ≥5 years to improve precision of estimates (i.e., CV ≤ 15%).

I estimated mass and gross energy (GE) of viable red oak acorns after 90 days in unflooded and flooded hardwood bottomlands in Mississippi. Within species, mass loss of acorns was <8.4% and variation in GE ≤0.08 kcal(dry)/g. Winter decomposition of intact viable red oak acorns would have minimal effect on wildlife carrying capacity of hardwood bottomlands.

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CHAPTER I

ESTIMATING AND MODELING RED OAK ACORN PRODUCTION IN THE MISSISSIPPI ALLUVIAL VALLEY

The Mississippi Alluvial Valley (MAV) contains most of the large tracts of bottomland hardwood forests in the United States (Schoenholtz et al. 2005). These lowland forests are among the most productive ecosystems in North America (Heitmeyer et al. 2005). Great primary production in these systems is maintained by fertile alluvial soils, a nearly subtropical climate, frequent rainfall, and hydrologically induced nutrient inputs (Heitmeyer et al. 2005). Ecological processes in these systems are driven largely by winter-spring flooding from adjacent rivers, precipitation runoff resulting in ponding, and other seasonal climatic events including ice storms (Fredrickson and Heitmeyer 1988, Connor and Sharitz 2005).

Availability of earth and vegetation moving equipment in the early 20th century facilitated extensive drainage and clearing of hardwood bottomlands in the MAV, hastening conversion to agricultural lands (Fredrickson 2005*a*). About 2.8 million ha of an original 10 million ha of seasonally flooded bottomland hardwood forests remain in the MAV (Reinecke et al. 1989, King et al. 2005). Despite losses of bottomland hardwood forests, remaining tracts are important for sustaining for many silvicolous wildlife populations (Fredrickson et al. 2005).

Efforts to suppress natural flooding have resulted in decreased seasonal inundation of lowland forests in the MAV (Reinecke et al. 1988, King et al. 2005). Accordingly, wildlife managers developed greentree reservoirs (GTRs) in the late-1930s to provide consistent winter flooding in bottomland hardwood forests for waterfowl and hunters. A GTR is a hardwood bottomland area impounded by levees and flooded naturally or artificially by pumping or gravity flowing water (Reinecke et al. 1989, Fredrickson 2005*b*). Subsequently, >100 GTRs have been developed in the MAV (Wigley and Filer 1989). While GTRs provide consistent winter flooding of hardwood bottomland, increased duration and depth of impounded waters in GTRs may affect forest community composition (Young et al. 1995), red oak (*Quercus* spp; Subgenus *Erythrobalanus*) regeneration (Gray and Kaminski 2005, Guttery 2006, Thornton 2009), and production of acorns by red oaks (Francis et al. 1983).

Within bottomland hardwood forests in the MAV, cherrybark oak (*Q. pagoda*), Nuttall oak (*Q. texana*), pin oak (*Q. palustris*), water oak (*Q. nigra*), and willow oak (*Q. phellos*) are ecologically and economically valuable red oaks (Fredrickson and Heitmeyer 1988, Kaminski et al. 2003, Denman and Karnuth 2005). Acorns of red oaks are a seasonally abundant and nutritious food source for ducks and other wildlife using hardwood bottomlands (Allen 1980, Delnicki and Reinecke 1986, Fredrickson and Heitmeyer 1988, Barras et al. 1996, Dabbert and Martin 2000, Heitmeyer 2006).

Information regarding red oak acorn production in the MAV originates from studies conducted in southeast Missouri (McQuilkin and Musbach 1977), west-central Mississippi (Francis 1983), and east-central Arkansas (Guttery 2006, Thornton 2009).

Although investigators reported cumulative acorn crops through winter, studies were limited to a single oak species and site in the MAV.

Realizing the ecological importance of bottomland hardwood forests in the MAV, the Lower Mississippi Valley Joint Venture (LMVJV) of the North American Waterfowl Management has established an 800,000 ha reforestation objective (Twedt et al. 2006). The LMVJV uses science-based estimates of duck population carrying capacity (i.e., duck-energy days [DED]) to estimate numbers of wintering waterfowl potentially supported by wetland habitats in the MAV (Loesch et al. 1994). Conservation planners and waterfowl biologists assume ample forage availability during winter is critical to sustaining continental waterfowl populations (Weller and Batt 1988, Reinecke et al. 1989, Loesch et al. 1994). Seeds and tubers of moist-soil plants, agricultural seeds, and acorns of red oaks are important foods of waterfowl wintering in the MAV (Delnicki and Reinecke 1986, Fredrickson and Heitmeyer 1988, Reinecke et al. 1989, Heitmeyer 2006, Kross et al. 2008). Abundance of rice and other agricultural and moist-soil seeds have been estimated in recent MAV and other regional studies (Stafford et al. 2006, Kross et al. 2008, Foster et al. 2010, Wiseman et al. 2010). In contrast, production of acorns by red oak trees in bottomland hardwood forests has not been estimated at the scale of the MAV.

Precise MAV-wide estimates (i.e., CV $\leq$ 15%; Stafford et al. 2006, Kross et al. 2008) of annual, cumulative red oak acorn production during autumn-winter in non-impounded, naturally flooded bottomland hardwood forests (NFF), and GTRs are currently lacking. This information is needed to estimate carrying capacity and aid restoration, management, and conservation planning of bottomland hardwood forests for waterfowl, other wildlife, and forest products (Reinecke et al. 1989, Loesch et al. 1994, Kaminski et al. 2003). Therefore, my primary objective was to estimate red oak acorn production at sites in the MAV (CV ≤ 15%). I define acorn production as quantity of sound acorns (i.e., those sinking in water; Allen 1989, Barras et al. 1996) falling from crowns of red oak trees and recovered by sampling (see METHODS section). Secondarily, my objective was to model variation in red oak acorn production as a function of relevant biotic and abiotic parameters including study site, density of red oak trees (i.e., basal area), hydrologic regime (i.e., GTR vs. NFF), species of red oak, and bole diameter.

Study Area

I sampled in 5 bottomland hardwood forests in the MAV including: Mingo National Wildlife Refuge (NWR), Missouri; Chickasaw NWR, Tennessee; southern unit of White River NWR, Arkansas; Delta National Forest, Mississippi; and Tensas NWR, Louisiana (Table 1.1). I selected these sites to achieve a geographically representative sample of publically owned, naturally flooded (not GTR) bottomland hardwood forests in the MAV.

To assess possible effects of GTR management on acorn production by red oaks, I sampled in Sunflower GTR and GTR 1 at Delta National Forest in the alluvial valley of west-central Mississippi and Noxubee NWR in the Interior Flatwoods of east-central Mississippi, respectively.

Methods

MAV-Wide Survey

I constructed acorn traps having a 1-m^2 sampling frame fabricated from treated lumber (2.5 cm x 10 cm) mounted atop 4 1.5 m lengths of electrical conduit. At each sampling site, I pushed conduit 20-25 cm into the ground, giving traps stability during periods of flooding, yet keeping them elevated to deter seed predators. I constructed funnels of fiberglass window screening which tapered from inside the sampling frame to a small opening where a wide mouthed plastic container was attached to collect acorns (Guttery 2006). I installed traps from 1 August-27 September 2009. This installation period was before sound acorns began falling from the crowns of sampled red oaks in response to gravity during autumn-winter 2009-2010 (A. G. Leach, Mississippi State University, personal observation; Guttery 2006). I visited all traps monthly from 1 October 2009-16 March 2010 to collect acorns, remove debris from traps, and repair traps destroyed or impaired by black bear (*Ursus americana*), felled trees, or flooding events. During each collection period, I stored all whole, partially depredated, and underdeveloped acorns from each trap in an individually labeled plastic bag.

I used a multi-stage sampling design to estimate red oak acorn production within and among study sites in the MAV (Stafford et al. 2006, Kross et al. 2008, Straub 2008). In each study site, I created a sampling frame including all non-impounded, naturally flooded bottomland hardwood forest within 0.08-0.32 km from roads accessible via automobile. This sampling frame facilitated researcher accessibility of sample plots and assumedly alleviated any possible effects of increased light exposure to red oaks attributable to road grades (Guariguata and Sáenz 2002). I designated sample plots (0.2 ha) as primary sampling units, sampled red oak trees within each plot as secondary units, and each sampled 1-m^2 area of red oak crown as tertiary units (Stafford et al. 2006, Kross et al. 2008, Straub 2008).

Within the sampling frame at each study site, I established 20 primary and 40 alternate 0.2-ha circular plots using a generalized random tessellation stratified spatial design (Stevens and Olsen 2004). If a primary plot contained <2 red oak trees ≥25 cm diameter at breast height (DBH), I surveyed the nearest alternate plot and ultimately sampled 20 0.2-ha plots per study site. Within each sampled plot, I recorded species and DBH of any present cherrybark, Nuttall, pin, water, or willow oak of bole diameter likely productive of acorns (i.e., ≥25 cm DBH; Sharp and Chisman 1961, Greenberg 2000). Next, I randomly selected two red oaks within each sampled plot (n = 40 red oaks/study site). For each sampled red oak, I calculated the mean of four radii (r; m) measured in the cardinal directions extending from outer edge of bole to canopy drip line and estimated crown area with the following equation: crown area = πr^2. Next, I randomly selected a cardinal direction and installed a 1-m^2 acorn trap mid-way between bole and canopy drip line of each selected red oak (Stelzer et al. 2004, Guttery 2006). If a randomly selected cardinal direction resulted in overlapping crown from an adjacent conspecific, I randomly selected a remaining cardinal direction.

GTR and NFF Survey

To investigate possible influence of GTR impoundments and hydrological management on production of acorns by red oaks, I sampled Sunflower GTR and GTR 1 at Delta National Forest and Noxubee NWR, respectively. Sunflower GTR and GTR 1 have been managed as GTRs since 1959 and 1955, respectively (Francis et al. 1983, Ervin et al. 2006). Within Delta National Forest and Noxubee NWR, I also selected a nearby (<18 km) NFF area (~250 ha) and sampled acorn production of red oaks in these areas (Francis 1983, Wehrle et al. 1995).

I used a multi-stage sampling design to estimate red oak acorn production within GTR and NFF areas at each study site. My sampling units and methods replicated those described for the MAV-wide survey. Specifically, I used a generalized random tessellation stratified spatial design to establish 20 0.2-ha circular plots within each GTR and NFF area (n = 80 plots; Stevens and Olsen 2004). I inventoried red oaks within plots as described for the MAV-wide survey, however I only sampled acorn production of 1 red oak tree per plot. If a plot contained <1 red oak tree ≥25 cm DBH, I randomly selected a previously sampled plot containing ≥2 red oaks ≥25 cm dbh and sampled a second red oak within that plot. At Noxubee NWR, I sampled acorn production from red oaks in 15 and 19 plots in GTR 1 and the NFF area, respectively (n = 40 sampled red oaks), because other plots did not contain a red oak meeting sample criteria. All primary plots in the Sunflower GTR and NFF at Delta National Forest contained ≥1 red oak meeting the sampling criteria. I installed acorn traps during 25-27 October and 30 October-5 November 2008 at Delta National Forest and Noxubee NWR, respectively. All other methodology replicated that described for the MAV-wide survey.

Laboratory Methods

I stored collected acorns in a freezer at -10˚C at Mississippi State University for <2 months before processing. During sample processing, I first thawed acorns, then separated acorns that sunk in water (i.e., sound acorns; Allen 1989, Barras et al. 1996) from those that floated (i.e., unsound). Next, I halved acorns with shears and classified them as follows: 1) wholly intact, 2) either > or <50% consumed by insects (e.g., weevil [*Curculio* spp.]), 3) either > or < 50% consumed by wildlife, and 4) underdeveloped (Young 1990). I dried all sound acorns (including pericarp) which were wholly intact, or <50% consumed by insects or wildlife in each sample to constant mass in a mechanical convection oven at 60°C for 5 days. I then weighed sound acorns with pericarps and recorded mass to the nearest 0.001 g.

Statistical Analyses

Estimating Red Oak Acorn Production in the MAV

I used the survey package in R version 2.11.1 (R Development Core Team 2009) to estimate sound acorn production. This procedure incorporated appropriate sampling weights for the 3 stages (i.e., plots, red oak trees, and sampled crown area; Stafford et al. 2006, Kross et al. 2008, Straub 2008). I calculated probability of selecting a plot within each study site by dividing 1.0 by the total area of the sampling frame within a respective study site. Next, within each plot, I calculated the probability of selecting a red oak tree by dividing 2.0 by total number of red oaks in a respective plot. Lastly, I calculated probability of placing an acorn trap under a 1-m^2 area of red oak crown by dividing 1.0

by total estimated crown area of a sampled tree. I calculated individual sample weights as inverse of the product of the three probabilities (Stafford et al. 2006, Kross et al. 2008, Straub 2008). I extrapolated mean cumulative (i.e., autumn-winter) mass (i.e., kg[dry]) of acorns produced per m^2 red oak crown to production per hectare of red oak crown (hereafter kg/ha) which enabled objective comparisons of relative acorn production among study sites (Cañellas et al. 2007).

Modeling Red Oak Acorn Production in the MAV

I used the GLM package in R version 2.11.1 (R Development Core Team 2009) to model relationships between sound acorn production per m^2 red oak crown (i.e., cumulative *n* collected/trap), study site, DBH of sampled trees, basal area (m^2) of red oaks (≥25 cm dbh) per plot, and red oak species. I modeled acorn production as cumulative number of sound acorns produced per m^2 red oak crown rather than mass, because these metrics were strongly correlated ($r = 0.85$), and discrete counts allowed more appropriate modeling techniques given strongly right skewed distribution of my data (Zuur et al. 2009). I used cumulative number of sound red oak acorns collected per trap from 27 September 2009 until 16 March 2010, as my dependent variable. I selected study site (SITE; i.e., Chickasaw NWR [1], Delta National Forest [2], Mingo NWR [3], Tensas NWR [4], or White River NWR [5]), diameter at breast height (DBH), total basal area (m^2) of red oaks per plot (BA), and red oak species (SPECIES; i.e., cherrybark oak [1], Nuttall oak [2], pin oak [3], water oak [4], or willow oak [5]) as measured or recorded explanatory variables.

I used histograms and box plots to perform exploratory data analyses (Quinn and Keough 2002). These analyses revealed a strongly right-skewed distribution in my dependent variable characterized by a large number of zero values resulting from trees that did not produce a sound acorn during autumn-winter 2009-2010 (i.e., 57 [35%] of 161). Thus, I log transformed (base 10) the dependent variable in an attempt to achieve normality in my data set and model error terms (Quinn and Keough 2002:65). However, residual and fitted values obtained from a linear regression model applied to transformed data were funnel shaped and non-randomly distributed indicating poor model fit (Zuur et al. 2009). Therefore, I modeled the untransformed data with a generalized linear model (GLM) using the negative binomial distribution and log link. The negative binomial distribution is useful for modeling discrete count data characterized by right skewed distributions, numerous zero values, and overdispersion (i.e., variance exceeding mean; Zuur et al. 2009).

Scatterplots indicated a potential quadratic relationship between acorn production and DBH. Therefore, I used the anova command in R version 2.11.1 (R Development Core Team 2009) to compare the log likelihood ratio of nested GLMs with and without a quadratic term for DBH (i.e., DBH + DBH^2). Results indicated inclusion of a quadratic DBH term did not significantly improve model likelihood ($L = 0.37$; $df = 1$, $P = 0.541$). Thus, I did not include a quadratic term for DBH in my analysis. Similarly, I tested for improved log likelihood of a model with a quadratic term for BA (i.e., BA + BA^2); however, inclusion did not significantly improve model likelihood ($L = 0.55$; $df = 1$, $P = 0.457$). Thus, I did not include a quadratic term for BA in my analysis.

To test for correlation among my explanatory variables, I used the corvif function in the AED package (Zuur et al. 2009) in R version 2.11.1 (R Development Core Team 2009) to calculate variance inflation factors (VIF). I considered explanatory variables with a VIF ≥ 3 correlated and removed these variables until all VIFs were <3 (Zuur et al. 2009). I then formulated a priori 10 seemingly biologically important candidate models for possible explanation of variation in red oak acorn production and used Akaike's Second Order Information Criteria (AIC*c*) to identify the most parsimonious model (hereafter best model; Burnham and Anderson 2002). I calculated model-averaged parameter estimates ($\hat{\beta}$), unconditional standard errors (SE), and 95% confidence intervals from a confidence set of best models with an evidence ratio (i.e., w_i / w_{min}) ≥0.05, where w_{min} was Akaike weight for model with lowest ΔAIC*c* (Burnham and Anderson 2002:171). Evidence ratios are considered relative likelihood a given model is more plausible than the model having the lowest AIC*c* (Burnham and Anderson 2002).

Generalized linear models do not produce R^2 values; therefore, I used null and residual deviance from the best model to calculate explained deviance (i.e., pseudo R^2; Zuur et al. 2009). Null and residual deviances are similar to total and residual sums of squares produced from a linear regression model (Zuur et al. 2009). I calculated explained deviance using the following equation: $100 \text{ X } \frac{\text{null deviance} - \text{residual deviance}}{\text{null deviance}}$ (Zuur et al. 2009:218).

Estimating Red Oak Acorn Production in GTRs and NFFs

I used the same methods described for the MAV-wide survey to estimate red oak acorn production in GTRs and NFFs, while using appropriate values to calculate sample weights (i.e., 1 or 2 red oaks sampled/plot). I extrapolated estimates to mean cumulative (i.e., autumn-winter) mass (kg[dry]) of sound acorns produced per hectare of red oak crown (kg/ha).

Modeling Red Oak Acorn Production in GTRs and NFFs

I used the GLM package in R version 2.11.1 (R Development Core Team 2009) to model relationships between acorn production per m^2 red oak crown (i.e., cumulative *n* acorns/trap), study site, DBH of sampled trees, basal area (m^2) of red oaks (≥25 cm DBH) per plot, hydrologic regime, red oak species, and year of study. I used cumulative number of sound red oak acorns collected annually per m^2 red oak crown during autumn-winters 2008-2010 as my dependent variable. I selected study site (SITE; i.e., Delta National Forest [1] or Noxubee NWR [2]), diameter at breast height (DBH), total basal area (m^2) of red oaks per plot (BA), hydrologic regime (REGIME; i.e., GTR [1] or NFF [2]), red oak species (SPECIES; i.e., cherrybark oak [1], Nuttall oak [2], water oak [3], or willow oak [4]), and year of study (YEAR; i.e., autumn-winter 2008-2009 [1] or autumn-winter 2009-2010 [2]) as measured or recorded explanatory variables.

Scatterplots indicated a potential quadratic relationship between acorn production and DBH. Therefore, I used the anova command in R version 2.11.1 (R Development Core Team 2009) to compare the log likelihood ratio of nested GLMs with and without a quadratic term for DBH (i.e., $DBH + DBH^2$). Results indicated inclusion of a quadratic DBH term improved model likelihood ($L = 14.67$, $df = 1$, $P < 0.001$); therefore, I included a quadratic term for DBH in my analysis. Similarly, I tested for improved log likelihood of a model with a quadratic term for BA (i.e., $BA + BA^2$). Results indicated inclusion of the quadratic term improved model likelihood ($L = 4.12$, $df = 1$, $P = 0.042$) therefore, I included a quadratic term for BA in my analysis.

To test for correlation among explanatory variables, I used the corvif function in the AED package (Zuur et al. 2009) in R version 2.11.1 (R Development Core Team 2009) to calculate variance inflation factors (VIF). I considered explanatory variables with a VIF ≥ 3 to be correlated and removed these variables until all VIFs were <3 (Zuur et al. 2009). I then formulated a priori 10 seemingly biologically important candidate models for possible explanation of variation in red oak acorn production and used Akaike's Second Order Information Criteria (AIC*c*) to identify the best model (Burnham and Anderson 2002). I calculated model-averaged parameter estimates ($\hat{\beta}$), unconditional standard errors (SE), and 95% confidence intervals from a confidence set of best models with an evidence ratio (i.e., w_i / w_{min}) ≥0.05 (Burnham and Anderson 2002:171).

Results

Estimating Red Oak Acorn Production in the MAV

Based on presence of black bear sign on acorn traps (e.g., hair, tooth marks), I concluded that bears molested or destroyed 12 traps at Tensas NWR and 17 traps at White River NWR during autumn-winter 2009-2010. Additionally, 3 acorn traps at White River NWR were not accessible from December 2009-June 2010 due to bottomland flooding. Also, I lost a sample from 7 acorn traps at Tensas NWR. If acorn production data for any red oak tree were not available for ≥1 sampling period, I excluded tree and corresponding acorn data from analysis. Thus, results from Tensas and

White River NWRs represent cumulative acorn production data from 21 and 20 red oak trees, respectively (Table 1.2). The 40 acorn traps at Chickasaw and Mingo NWRs and Delta National Forest yielded complete acorn production data (Table 1.2).

Mean acorn production was variable across study sites ranging from 60.46-1,234.65 kg/ha (Table 1.2). Among study sites in the MAV, mean red oak acorn production was 439.98 kg/ha with a CV = 28.68%, which was greater than my a priori goal of ≤15% (Table 1.2).

Modeling Red Oak Acorn Production in the MAV

None of my explanatory variables were correlated (VIFs < 1.5), so I included all variables in my analysis. Plots of residual and fitted values of the best model did not indicate significant non-random patterns in the residuals; therefore, I concluded appropriate model fit. The best model explaining variation in red oak acorn production included additive effects of SITE and DBH and had model weight of 0.495 (Table 1.3). Explained deviance of the best model was 32.5%. However, model selection indicated a competitive model (i.e., ΔAIC < 2) including additive effects of SITE, DBH, and SPECIES (Table 1.3). Model selection favored inclusion of SITE and DBH; all 5 top models contained these variables and collectively accounted for all Akaike model weight (Table 1.3). Model-averaged parameter estimates indicated red oaks at Delta National Forest ($\hat{\beta}$ = 3.740, SE = 0.467, 95% CI: 2.820, 4.660), Tensas NWR ($\hat{\beta}$ = 2.760, SE = 0.533, 95% CI: 1.710, 3.800), and White River NWR ($\hat{\beta}$ = 3.560, SE = 0.524, 95% CI: 2.540, 4.590; Table 1.4) produced more sound acorns per m^2 crown than those at Chickasaw NWR (i.e., arbitrary reference study site; Table 1.4), while the 95%

confidence interval for the parameter estimating acorn production by red oaks at Mingo NWR included zero ($\hat{\beta}$ = 1.320, SE = 0.737, 95% CI: -0.122, 2.770; Table 1.4). Number of acorns produced per m^2 red oak crown was related positively to DBH ($\hat{\beta}$ = 0.040, SE = 0.007, 95% CI: 0.027, 0.053; Table 1.4). In comparison to cherrybark oak, the arbitrary reference species, 95% confidence intervals for parameters estimating number of acorns produced per m^2 crown by Nuttall oak, pin oak, water oak, and willow oak included zero (Table 1.4).

Estimating Red Oak Acorn Production in GTRs and NFFs

Installation of acorn traps at Delta National Forest and Noxubee NWR was post initiation of sound acorn abscission in autumn 2008 (A. G. Leach, Mississippi State University, personal observation). For comparative purposes, 4.7% and 19.6% of the total cumulative sound acorn production by sampled red oaks during autumn-winter 2009-2010 was collected by 25 October 2009 at Delta National Forest and Noxubee NWR, respectively. Thus, estimates of cumulative acorn production by red oaks at these study sites may be conservative for autumn-winter 2008-2009.

During autumn-winter 2008-2009, one acorn trap in the Noxubee NWR NFF area was nonfunctional during a period of overbank flooding from the Noxubee River. Additionally, in summer 2009, one previously sampled red oak at the Noxubee NWR NFF was wind thrown. Thus, sample size for the Noxubee NWR NFF area for each year of study was 19 red oaks.

Among study sites, mean red oak acorn production in NFF areas was 373.20 (CV = 26.57%) and 1,130.38 kg/ha (CV = 24.05%) during autumn-winters 2008-2009 and

2009-2010, respectively (Table 1.5). Among study sites mean red oak acorn production in GTRs was 374.62 (CV = 26.67%) and 1,214.16 kg/ha (CV = 19.81%), during autumn-winter 2008-2009 and 2009-2010, respectively (Table 1.5). Among years mean red oak acorn production was 771.83 (CV = 23.00%), and 794.39 kg/ha (CV = 19.38%), in NFFs and GTRs, respectively. Among study sites and hydrologic regimes, estimates of mean acorn production by red oak species ranged from 36.32-458.02 and 619.15-1,525.15 kg/ha during autumn-winter 2008-2009 and 2009-2010, respectively (Table 1.6).

Modeling Red Oak Acorn Production in GTRs and NFFs

None of my explanatory variables were correlated (VIFs < 1.5), so I included all variables in analysis. Plots of residual and fitted values of the best model did not indicate significant non-random patterns in the residuals; therefore, I concluded appropriate model fit. The best model included additive effects of REGIME, DBH + DBH^2, SPECIES, BA + BA^2, and YEAR and had model weight of 0.781 (Table 1.7). Explained deviance for the best model was 41.68%. Number of acorns produced per m^2 red oak crown was related positively to DBH ($\hat{\beta}$ = 0.0850, SE = 0.0187, 95% CI: 0.0486, 0.1220) until a threshold DBH of ~85 cm; thereafter, the relationship was negative ($\hat{\beta}$ = -0.0005, SE = 0.0001, 95% CI: -0.0008, -0.0003). Similarly, number of acorns produced per m^2 red oak crown was related positively to basal area (BA) of red oaks within a plot ($\hat{\beta}$ = 1.2800, SE = 0.3140, 95% CI: 0.6700, 1.9000) until a threshold BA of ~2.35 m^2/plot (i.e., ~11.75 m^2/ha); thereafter, the relationship was negative ($\hat{\beta}$ = -0.2740, SE = 0.0770, 95% CI: -0.4250,-0.1230). Willow oaks produced greatest number of acorns per m^2 crown in comparison to the arbitrary reference species, cherrybark oak ($\hat{\beta}$ = 0.7870, SE = 0.2960, 95% CI: 0.2070, 1.3700). Number of acorns produced per m^2 red oak crown in NFF areas was slightly less than in GTRs ($\hat{\beta}$ = -0.4640, SE = 0.2190, 95% CI:-0.8930, -0.0347). In comparison to the arbitrary reference study site, Delta National Forest, 95% confidence interval for the parameter estimating number of acorns produced per m^2 red oak crown at Noxubee NWR included zero ($\hat{\beta}$ = 0.0344, SE = 0.1470, 95% CI: -0.2530, 0.3220). Among sites, flooding regimes, and red oak species, number of acorns produced per m^2 red oak crown was greater in autumn-winter 2009-2010 than 2008-2009 ($\hat{\beta}$ = 1.1500, SE = 0.1780, 95% CI: 0.8040, 1.5000; Table 1.8).

Discussion

Red Oak Acorn Production in the MAV

My study was the first attempt at generating unbiased estimates of red oak acorn production in non-impounded, naturally flooded bottomland hardwood forests across a major extent of the MAV. However, my estimates of red oak acorn production may be conservative, because I could neither account for acorns that fell beyond the canopy perimeter of sample trees because of wind dispersal nor arboreal predation by birds and mammals (McQuilkin and Musbach 1977). Nonetheless, these inherent possible biases were unavoidable and would plague any investigator attempting to collect acorns falling from red oak crowns in response to gravity.

I did not achieve my a priori goal of estimating mean red oak acorn production in the MAV with CV ≤ 15%. However, previous MAV-wide estimates of seed abundance also reported CVs > 15% (Stafford et al. 2006, Kross et al. 2008). Kross et al. (2008)

reported annual (n = 3) CVs of moist-soil seed abundance in the MAV ranging from 18.6-29.3%; however, their among year estimate of 556 kg/ha had a CV = 12.5%. Likewise, Stafford et al. (2006) reported annual estimates (n = 3) of late-autumn abundance of waste rice in the MAV with CVs ranging from 22.7-31.2%, but their among year estimate of 78.4 kg/ha had a CV = 15%. Sampling of red oak acorn production in the MAV will continue through autumn-winter 2011-2012, thus an increasingly precise multi-year estimate of red oak acorn production in the MAV is possible.

My estimate of mean acorn production per hectare of red oak crown in the MAV was ~5.6 times greater than late-autumn waste rice abundance in rice fields of the MAV (Stafford et al. 2006) and ~80% autumn seed abundance in managed moist-soil wetlands in the MAV(Kross et al. 2008). In addition, my estimate of mean red oak acorn production was 2.6 times greater than the current forage (i.e., red oak acorns, moist-soil seeds, and aquatic macro-invertebrates) abundance estimate of 166 kg/ha in bottomland hardwood forests with 100% red oak basal area used by LMVJV conservation planners (Reinecke and Kaminski 2007). Thus, current LMVJV conservation planning may underestimate red oak acorn abundance and carrying capacity of bottomland hardwood forests in the MAV, warranting continued sampling of acorn production to derive a more long-term estimate.

Also of interest to ecologists and managers are spatio-temporal patterns in red oak mast seeding. Mast seeding is the intermittent synchronous production of large seed crops by a population of plants (Sork et al. 1993, Kelly and Sork 2002, Koenig and Knops 2005). Ecologists and wildlife managers are interested in understanding oak mast seeding cycles, because these events affect behavior, movements, survival, and fecundity of acorn consumers and their predators and prey, thereby influencing holistic forest community ecology (Jones et al. 1998, McShea 2000, Ostfeld and Keesing 2000, McShea and Healy 2002, Kelly et al. 2008). Acorn production by oak populations is typically normally distributed, with years of poor, intermediate, and good production rather than strictly bimodal with years of good or poor production (Koeinig and Knops 2000, Koenig and Knops 2002, Abrahamson and Layne 2003). White oak species (*Quercus* spp; Subgenus *Lepidobalanus*) typically have shorter intervals between mast seeding events (i.e., 2-3 years) than red oaks (i.e., 3-6 years); moreover, mast seeding is relatively synchronous within but not among subgenera (Sork et al. 1993, Koenig and Knops 2002, Abrahamson and Layne 2003, Kelly et al. 2008). Asynchrony of mast seeding events between oak subgenera is related to one versus two growing seasons required for maturation of white and red oak acorns, respectively, resulting in exposure of these acorns to different year-specific environmental conditions (Sork et al. 1993, Koenig and Knops 2002).

Mast seeding behavior is hypothesized to result from proximate cues such as weather (e.g., temperature, precipitation), and resource availability (e.g., light, soil moisture), and ultimate causes potentially resulting from adaptations to increase residual seed available for oak regeneration through seed-predator satiation, and maximization of pollination efficiency (Sork et al. 1993, Kelly and Sork 2002, Koenig and Knops 2002, Koenig and Knops 2005; but see Abrahamson and Layne 2003). Furthermore, oaks on sites with poor soil fertility exhibit more pronounced mast seeding due to longer time necessary to recover reserves after a large mast crop (Kelly and Sork 2002, Abrahamson and Layne 2003).

Spatio-temporal patterns in red and white oak mast seeding across the MAV are unknown, but previous studies suggest variable patterns in mast seeding among sites and species. Hereafter, I will use criteria outlined in Greenberg and Parresol (2002) to describe relative acorn production: 1) poor (i.e., <60% of study mean), 2) moderate (i.e., >60% and equal to study mean), and 3) good acorn production (i.e., >study mean). During a 14-year study of pin oak production in southeastern Missouri, McQuilkin and Musbach (1977) reported good pin oak acorn production every 2-3 years. A five year study of Nuttall oak acorn production at Delta National Forest revealed 2 consecutive years of poor and 3 years of good acorn production (Francis 1983). Willow oaks in an Arkansas GTR yielded 1 year of poor, 2 years of moderate, and 1 year of good acorn production over four years of study (Thornton 2009).

Across my study sites in the MAV, estimates of red oak acorn production varied >20 fold. In comparison to mean red oak acorn production in the MAV (439.39 kg/ha), acorn production at Chickasaw NWR (60.46 kg/ha), Mingo NWR (73.41 kg/ha), and Tensas NWR (185.05 kg/ha) was poor, while production at Delta National Forest (851.33 kg/ha) and White River NWR (1,234.65 kg/ha) was good during autumn-winter 2009-2010. Additionally, among study sites with complete data sets, those having poor acorn production had fewer sampled trees bearing sound acorns (i.e., Mingo NWR [52.5%], Chickasaw NWR [37.5%]) compared to Delta National Forest (80.0%) which had good acorn production in autumn-winter 2009-2010. Relative to effect of SITE on production of acorns by red oaks, model-averaged parameter estimates indicated other explanatory variables explained comparatively little variation in red oak acorn production (Table 1.4).

However, given the current temporally limited data set, I can only speculate regarding causation of great among study site variation in production of acorns by red oaks. For instance, poor acorn production at Mingo and Chickasaw NWRs during autumn-winter 2009-2010 may have been caused by a frost in late-spring 2008 (i.e., minimum daily temperature 0°C on 15 April 2008; Poplar Bluff, Missouri and Ripley, Tennessee; National Climatic Data Center [NCDC] 2010) which potentially killed red oak flowers otherwise resulting in sound acorns in autumn 2009 (Goodrum et al. 1971, Sork et al. 1993, Kelly and Sork 2002, Koenig and Knops 2002). Similarity in estimates of acorn production and exposure to a critical weather variable (i.e., late-spring frost) by red oaks at Mingo and Chickasaw NWRs suggests certain weather variables may explain some variation in acorn production by red oaks in the MAV. However, Delta National Forest and Tensas NWR are ~73 km linear distant and likewise predictably should experience similar weather patterns; however, mean acorn production by red oaks at the former (851.33 kg/ha) was 4.6 times greater than the latter (185.05 kg/ha) during autumn-winter 2009-2010. Thus, variation in red oak acorn production in the MAV is likely not simply a function of weather tracking (Kelly and Sork 2002, Koenig and Knops 2005).

Significant variation in intensity of production of red oak acorns among study sites <500 km apart during autumn-winter 2009-2010 suggests red oaks in the MAV may synchronize mast seeding events at smaller geographic scales than other oak populations (Koenig and Knops 2002, Koenig and Knops 2005). Among year variation in relative intensity of acorn production by red oaks in the MAV is likely great, thus, observing the full range of production intensity may necessitate ≥5 years of monitoring (Healy et al. 1999, Koenig and Knops 2002, Abrahamson and Layne 2003). Documenting spatio-temporal patterns of oak mast seeding in the MAV is likely important to management of oak and wildlife populations and understanding community ecology in bottomland hardwood forests (McShea 2000, Ostfeld and Keesing 2000, McShea and Healy 2002, Kelly et al. 2008).

Red Oak Acorn Production in GTRs and NFFs

Forest managers are interested in effects of GTR management on red oak acorn production. However, prior studies of red oak acorn production in GTR and NFF areas have produced ambiguous results. For example, McQuilkin and Musbach (1977) reported similar pin oak acorn production on GTR and NFF areas at Mingo NWR. In contrast, Francis (1983) reported Nuttall oaks in the Sunflower GTR in Delta National Forest produced 34% fewer acorns per unit crown area than those in a NFF area within the same forest. Alternatively, Young (1990) reported acorn production by cherrybark oaks was ≤6 times greater in GTRs than in NFF in Noxubee NWR.

My results indicated red oaks in NFFs produced fewer acorns than trees in GTRs. However, relative to other explanatory variables, REGIME explained little variation in production of red oak acorns (Table 1.8). Furthermore, given great variability in acorn production capabilities among conspecific oaks, small unexplained variation in acorn production among flooding regimes potentially resulted from unintentional selection of unequal numbers of superior acorn producers among areas (Healy et al. 1999, Greenberg and Parresol 2002). In comparison to mean red oak acorn production in the MAV

(439.39 kg/ha) during autumn winter 2009-2010, acorn production by red oaks in sampled GTRs was moderate (374.62 kg/ha) during autumn-winter 2008-2009 and good (1,214.16 kg/ha) during autumn 2009-2010. During autumn-winter 2009-2010 mean acorn production (range = 619.15-1,525.15 kg/ha; Table 1.6) by all red oak species sampled at Noxubee NWR and Delta National Forest for my GTR and NFF survey was good compared to mean acorn production (439.39 kg/ha) by red oaks in the MAV survey and suggested relatively synchronous mast seeding by red oak species across my Mississippi study sites.

The quadratic relationship detected between number of acorns produced per m^2 red oak crown and bole diameter may be related to greater allocation of moisture and nutrients resources to root and shoot growth by oaks in small diameter classes, while oaks in large diameter classes may experience declining vigor and increased crown die back, thereby reducing acorn production (Lockhart et al. 2005). Furthermore, detected quadratic relationship of basal area of red oaks per plot (BA) and number of acorns produced per m^2 red oak crown could result from a slightly more complex relationship. Though monoecious, red oaks depend on flower pollination from neighboring conspecifics, but effective pollination distance is relatively short (i.e., 17-65 meters; Smouse et al. 2001, Sork et al. 2002), thus red oaks with relatively few nearby conspecifics could experience reduced flower pollination and acorn production. Alternatively, red oaks with a great many nearby conspecifics could suffer from increased competition for light and soil nutrients, thereby reducing acorn production (Healy 1997, Guariguata and Sáenz 2002). Though my results suggest number of acorns produced per m^2 red oak crown decreased after bole diameter and local (0.2 ha) basal area of red oaks reached 85 cm and ~11.75 m^2 per ha, respectively, further study is required to determine if these relationships are similar across years and study sites in the MAV and Interior Flatwoods of Mississippi.

Management and Research Implications

My results suggest red oaks subjected to GTR hydrology for >50 years can produce acorn crops similar to conspecifics in NFFs. However, my study was short-term and unable to completely document patterns of acorn production by red oaks subjected to GTR hydrology. Furthermore, water management regimes vary among GTRs; hence my results may not apply to other GTRs (Covington and Laubhan 2005). Additionally, unnatural winter flooding regimes typical of GTRs are associated with increased red oak mortality, reduced red oak seedling survival, and transition of red oak forests to those dominated by more water-tolerant species such as overcup oak (*Quercus lyrata*; Young et al. 1995, Fredrickson 2005*b*, Gray and Kaminski 2005, Guttery 2006, Thornton 2009). Therefore, managers committed to ensuring long-term productive red oak bottomlands in GTRs should consider developing monitoring strategies which record parameters such as red oak survival, crown health, and advanced regeneration and understand silvicultural treatments to increase red oak regeneration from mast crops. Managers of GTRs should also be prepared to reduce flooding frequency and duration in GTRs at the expense of waterfowl hunting opportunity (Reinecke et al. 1989, Covington and Laubhan 2005).

Black bear molestation of acorn traps resulted in considerable loss of data at Tensas and White River NWRs. Researchers are currently evaluating performance of acorn traps constructed of material potentially less attractive to bears (e.g., PVC).

Furthermore, visual surveys might reduce sampling effort and costs, but still facilitate reliable long-term monitoring of acorn production, unaffected by arboreal predation or trap disturbance (Koenig et al. 1994). Researchers may consider concurrent studies of wildlife population and foraging ecology and acorn production by red and white oaks to investigate potential linkages between oak mast seeding and community ecology of bottomland hardwood forests (Jones et al. 1998, McShea 2000, Ostfeld and Keesing 2000).

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Table 1.1 Study sites on National Wildlife Refuges (NWR) and a National Forest in the Mississippi Alluvial Valley and Interior Flatwoods of east-central Mississippi.

Site	Latitude/longitude	Nearest city
Mingo NWR[b]	36°59'54" N/90°09'50" W	Puxico, Missouri
Chickasaw NWR[b]	35°50'00" N/89°39'30" W	Ripley, Tennessee
White River NWR[b]	34°10'27" N/91°07'19" W	St. Charles, Arkansas
Noxubee NWR[a]	33°16'55" N/88°45'52" W	Starkville, Mississippi
Delta National Forest[a]	32°43'55" N/90°47'20" W	Rolling Fork, Mississippi
Tensas NWR[b]	32°12'40" N/91°23'45" W	Tallulah, Louisiana

[a]Study site in autumn-winters 2008-2010
[b]Study site in autumn-winter 2009-2010

Table 1.2 Mean ($\bar{x}$) sound acorn (i.e., those sinking in water) production (kg[dry]) per hectare of red oak (*Quercus* spp; Subgenus *Erythrobalanus*) crown (n = number of red oak trees sampled), standard errors (SE), and coefficient of variation (CV)[a] in non-impounded, naturally flooded bottomland hardwood forests in National Wildlife Refuges (NWR) and a National Forest in the Mississippi Alluvial Valley (MAV), autumn-winter 2009-2010.

Site (state)	n	$\bar{x}$	SE	CV(%)
Mingo NWR (Missouri)	40	73.41	48.33	65.83
Chickasaw NWR (Tennessee)	40	60.46	21.09	34.88
White River NWR (Arkansas)	20	1,234.65	618.61	50.10
Delta National Forest	40	851.33	226.36	26.59
Tensas NWR (Louisiana)	21	185.05	43.02	23.25
MAV	161	439.98	126.20	28.68

[a]CV = (SE/ $\bar{x}$)*100

Table 1.3 Models examining effects of explanatory variables study site (SITE), basal area (BA; m^2) of red oaks (*Quercus* spp; Subgenus *Erythrobalanus*) ≥25 cm diameter at breast height (DBH) per sample plot (0.2 ha), red oak species (SPECIES), red oak DBH, and an intercept only model (NULL) on sound red oak acorn (i.e., those sinking in water) production (*n* acorns abscised/m^2 red oak crown) in non-impounded, naturally flooded bottomland hardwood forests in National Wildlife Refuges (NWR) and a National Forest in the Mississippi Alluvial Valley, autumn-winter 2009-2010. For each model, estimated parameters (K), Akaike's Second Order Information Criteria (AIC*c*, ΔAIC*c*), and model weights (w_i) are presented.

Model	K	AIC*c*	ΔAIC*c*	w_i
SITE+DBH	7	969.7	0.0	0.495
SITE+DBH+SPECIES	11	971.1	1.4	0.249
SITE+DBH+BA	8	971.9	2.2	0.165
SITE+DBH+SPECIES+BA	12	973.4	3.7	0.080
SITE*DBH	11	977.3	7.6	0.011
SITE+SPECIES	10	993.8	24.1	0.000
SITE	6	998.0	28.3	0.000
SPECIES+DBH	7	1017.0	47.3	0.000
SPECIES	6	1020.0	50.3	0.000
NULL	2	1023.3	53.6	0.000

Table 1.4 Model-averaged effect estimates ($\hat{\beta}$), unconditional standard errors (SE), and 95% confidence intervals (CI) for parameters in a priori negative binomial regression models in a confidence set of best models (evidence ratio >0.05; Table 1.3) explaining variation in sound red oak (*Quercus* spp; Subgenus *Erythrobalanus*) acorn (i.e., those sinking in water) production (*n* acorns abscised/m^2 red oak crown) in non-impounded, naturally flooded bottomland hardwood forests in Mingo National Wildlife Refuge (NWR), Missouri; Chickasaw NWR, Tennessee; White River NWR, Arkansas; Delta National Forest, Mississippi; and Tensas NWR, Louisiana; autumn-winter 2009-2010.

Parameter	$\hat{\beta}$	SE	95% CI
INTERCEPT	-2.340	0.767	-3.840 − -0.836
BA	0.007	0.037	-0.066 − 0.079
DBH	0.040	0.007	0.027 − 0.053
SITE(DELTA NATIONAL FOREST)[a]	3.740	0.467	2.820 – 4.660
SITE(MINGO NWR)[a]	1.320	0.737	-0.122 – 2.770
SITE(TENSAS NWR)[a]	2.760	0.533	1.710 − 3.800
SITE(WHITE RIVER NWR)[a]	3.560	0.524	2.540 – 4.590
SPECIES(NUTTALL OAK)[b]	-0.154	0.400	-0.937 − 0.630
SPECIES(PIN OAK)[b]	0.341	0.599	-0.833 – 1.520
SPECIES(WATER OAK)[b]	0.203	0.477	-0.733 – 1.140
SPECIES(WILLOW OAK)[b]	0.038	0.306	-0.562 – 0.638

[a]Levels of categorical variable SITE report parameter estimates of mean acorn production relative to arbitrary reference study site, Chickasaw NWR.
[b]Levels of categorical variable SPECIES report parameter estimates of mean acorn production relative to arbitrary reference species, cherrybark oak.

Table 1.5 Mean ($\bar{x}$) sound acorn (i.e., those sinking in water) production (kg[dry]) per hectare of red oak (*Quercus* spp; Subgenus *Erythrobalanus*) crown, standard errors (SE), and coefficient of variation (CV)[a] in non-impounded, naturally flooded bottomland hardwood forest (NFF) and greentree reservoir (GTR) areas at Delta National Forest and Noxubee National Wildlife Refuge, Mississippi, autumn-winters 2008-2010. Areas are number of NFF and GTR areas sampled and trees are number of red oaks sampled.

Site	Autumn-winter(s)	*n* areas	*n* trees	$\bar{x}$	SE	CV(%)
NFF	2008-2009	2	39	373.20	99.17	26.57
	2009-2010	2	39	1,130.38	271.81	24.05
GTR	2008-2009	2	40	374.62	99.92	26.67
	2009-2010	2	40	1,214.16	240.54	19.81
NFF	2008-2010	2	39	771.83	177.53	23.00
GTR	2008-2010	2	40	794.39	153.98	19.38

[a]CV = (SE/ $\bar{x}$)*100

Table 1.6 Mean ($\bar{x}$) sound acorn (i.e., those sinking in water) production (kg[dry]) per hectare of crown, standard errors (SE), and coefficient of variation (CV)[a] of cherrybark oak (*Quercus pagoda*), Nuttall oak (*Q. texana*), water oak (*Q. nigra*), and willow oak (*Q.* phellos) in greentree reservoir and non-impounded, naturally flooded bottomland hardwood forest areas at Delta National Forest and Noxubee National Wildlife Refuge, Mississippi. Trees are total number of trees of each species sampled.

Species	Autumn-winter	*n* trees	$\bar{x}$	SE	CV(%)
Cherrybark oak	2008-2009	13	292.94	58.60	20.00
	2009-2010	14	794.64	396.54	50.00
Nuttall oak	2008-2009	39	458.02	131.19	28.64
	2009-2010	39	1,168.54	270.96	23.19
Water oak	2008-2009	6	36.32	16.79	46.23
	2009-2010	6	619.15	256.44	41.42
Willow oak	2008-2009	21	289.92	53.40	18.42
	2009-2010	20	1,525.15	353.16	23.16

[a]CV = (SE/ $\bar{x}$)*100

Table 1.7 Models examining effects of explanatory variables study site (SITE), basal area (BA; m^2) of red oaks (*Quercus* spp; Subgenus *Erythrobalanus*) ≥25 cm diameter at breast height (DBH) per sample plot (0.2 ha), hydrologic regime (i.e., greentree reservoir (GTR), or non-impounded, naturally flooded bottomland hardwood forest (NFF)), red oak species (SPECIES), red oak DBH, autumn-winter of study (YEAR) and an intercept only model (NULL) on sound red oak acorn (i.e., those sinking in water) production (*n* abscised/m^2 crown) in NFF and GTR areas in Delta National Forest and Noxubee National Wildlife Refuge, Mississippi, during autumn-winters 2008-2010. For each model, estimated parameters (K), Akaike's Second Order Information Criteria (AIC*c*, ΔAIC*c*), and model weights (*w*i) are presented.

Model	K	AIC*c*	ΔAIC*c*	w_i
REGIME+DBH+DBH^2+SPECIES+BA+BA^2+YEAR	11	1382.6	0.0	0.781
SITE*REGIME+DBH+DBH^2+SPECIES+BA+BA^2+ YEAR	13	1386.2	3.6	0.126
DBH+DBH^2+SPECIES+BA+BA^2+YEAR	10	1388.2	5.6	0.048
SITE+DBH+DBH^2+SPECIES+BA+BA^2+YEAR	11	1390.3	7.7	0.016
SITE*REGIME+DBH+DBH^2+SPECIES+YEAR	11	1390.4	7.8	0.015
REGIME+DBH+DBH^2+SPECIES+YEAR	9	1390.8	8.2	0.013
SPECIES	5	1435.0	52.4	0.000
SITE	3	1445.5	62.9	0.000
REGIME	3	1456.8	74.2	0.000
NULL	2	1461.5	78.9	0.000

Table 1.8 Model-averaged effect estimates ($\hat{\beta}$), unconditional standard errors (SE), and 95% confidence intervals (CI) for parameters in a priori negative binomial regression models in a confidence set of best models (evidence ratio >0.05; Table 1.7) explaining variation in sound red oak (*Quercus* spp; Subgenus *Erythrobalanus*) acorn (i.e., those sinking in water) production (*n* acorns abscised/m^2 crown) in greentree reservoir (GTR) and non-impounded, naturally flooded bottomland hardwood forest (NFF) areas at Delta National Forest and Noxubee National Wildlife Refuge, Mississippi, during autumn-winters 2008-2010.

Parameter	$\hat{\beta}$	SE	95% CI
INTERCEPT	-1.1400	0.7930	-2.7000 – 0.4100
DBH	0.0850	0.0187	0.0486 – 0.1220
DBH^2	-0.0005	0.0001	-0.0008 − -0.0003
BA	1.2800	0.3140	0.6700 − 1.9000
BA^2	-0.2740	0.0770	-0.4250 − -0.1230
REGIME(NFF)[a]	-0.4640	0.2190	-0.8930 − -0.0347
SITE(NOXUBEE NWR)[b]	0.0344	0.1470	-0.2530 – 0.3220
SPECIES(NUTTALL OAK)[c]	-0.4960	0.3480	-1.1800 – 0.1870
SPECIES(WATER OAK)[c]	0.5950	0.4380	-0.2630 − 1.4500
SPECIES(WILLOW OAK)[c]	0.7870	0.2960	0.2070 – 1.3700
YEAR(AUTUMN-WINTER 2009-2010)[d]	1.1500	0.1780	0.8040 – 1.5000

[a]Levels of categorical variable REGIME report parameter estimates of mean acorn production relative to arbitrary reference hydrologic regime, GTR.
[b]Levels of categorical variable SITE report parameter estimates of mean acorn production relative to arbitrary reference study site, Delta National Forest.
[c]Levels of categorical variable SPECIES report parameter estimates of mean acorn production relative to arbitrary reference species, cherrybark oak.
[d]Levels of categorical variable YEAR report parameter estimates of mean acorn production relative to arbitrary reference study year, autumn-winter 2008-2009.

CHAPTER II

MASS AND GROSS-ENERGY OF RED OAK ACORNS IN MISSISSIPPI HARDWOOD BOTTOMLANDS DURING WINTER

The North American Waterfowl Management Plan (NAWMP) identified the Mississippi Alluvial Valley (MAV) as a continentally important region for wintering and migrating waterfowl (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986, Reinecke et al. 1989, Baldassarre and Bolen 2006). Conservation planners and waterfowl biologists assume adequate winter forage is critical to sustaining continental duck populations (Weller and Batt 1988, Reinecke et al. 1989, Loesch et al. 1994). Ducks wintering in the MAV forage in flooded agricultural fields, moist-soil wetlands, and bottomland hardwood forests (Reinecke et al. 1989, Loesch et al. 1994). The Lower Mississippi Valley Joint Venture (LMVJV) of NAWMP seeks precise estimates of food abundance in waterfowl habitats in the MAV to calculate carrying capacity of this ecoregion for wintering ducks (i.e., duck-energy days [DED]; Loesch et al. 1994).

Accordingly, early-winter abundance of waste rice and other agricultural and moist-soil seeds have been estimated recently in the MAV and across Tennessee (Stafford et al. 2006, Kross et al. 2008, Foster et al. 2010*b*, Wiseman et al. 2010). In addition, research estimating abundance of red oak acorns (*Quercus* spp; Subgenus *Erythrobalanus*) and aquatic macroinvertebrates during winter in bottomland hardwood forests in the MAV was initiated in autumn 2008 and continues (R. M. Kaminski, Mississippi State University, personal communication, Chapter I).

Within bottomland hardwood forests in the MAV, red oak acorns (e.g., cherrybark oak [*Q. pagoda*], Nuttall oak [*Q. texana*], pin oak [*Q. palustris*], water oak [*Q. nigra*], and willow oak [*Q. phellos*]) occur commonly and provide nutritious forage for ducks (Allen 1980, Delnicki and Reinecke 1986, Fredrickson and Heitmeyer 1988, Dabbert and Martin 2000, Heitmeyer 2006). True metabolizable energy (TME; Miller and Reinecke 1984) of red oak acorns fed to mallards (*Anas platyrhynchos*) and wood ducks (*Aix sponsa*) was estimated at 2.67 kcal/g (dry mass; Kaminski et al. 2003). The TME of red oak acorns is similar to moist-soil seeds and raw soybeans (~2.5-2.7 kcal/g) but less than cereal grains (>3.0 kcal/g; Kaminski et al. 2003). However, decomposition of red oak acorns in hardwood bottomlands during winter may reduce mass, gross energy (GE), and ultimately TME available to ducks from acorns. Likewise, annual variation in GE of red oak acorns could alter TME acquired by ducks. Thus, winter decomposition and annual variation in mass and GE of red oak acorns have potential to reduce wintering duck carrying capacity of bottomland hardwood forests (Kaminski et al. 2003).

Winter decomposition of agricultural and moist-soil seeds have been investigated (Neely 1956, Nelms and Twedt 1996, Greer et al. 2009, Foster et al. 2010*a*, Hagy 2010). However, to my knowledge, neither decomposition of red oak acorns within bottomland hardwood forests nor annual variation in red oak acorn GE has been studied. Determining TME requires complex methodology compared to GE (Kaminski et al. 2003). If GE of intact red acorns does not vary among years, then neither would TME be expected to vary because TME is determined by feeding foods of known GE to animals, such as acorns to ducks (Kaminski et al. 2003). Therefore, my objectives were to estimate: (1) winter mass loss and GE dynamics of red oak acorns in unflooded and flooded areas within bottomland hardwood forests, and (2) between year variability in GE of red oak acorns.

Study Area

I studied decomposition of red oak acorns during winter at Noxubee National Wildlife Refuge (NWR; 33°16’55” N/88°45’52” W) in the Interior Flatwoods of east-central Mississippi and Delta National Forest (32°43’55” N/90°47’20” W) in the alluvial valley of west-central Mississippi. I studied effects of submergence on decomposition of red oak acorns within greentree reservoirs (GTRs), because these sites offered consistent winter flooding. A GTR is a hardwood bottomland area impounded by levees and flooded naturally or artificially by pumping or gravity flowing water (Reinecke et al. 1989, Fredrickson 2005).

During winter 2008-2009, I studied GE dynamics of red oak acorns in flooded bottomland hardwood forests at GTR 1 in Noxubee NWR. During winter 2009-2010, I studied dynamics of mass loss and GE of red oak acorns in GTR 1 and in the Sunflower GTR at Delta National Forest. Additionally, during winter 2009-2010, I studied dynamics of mass loss and GE of red oak acorns in unflooded bottomland hardwood forest areas at Noxubee NWR and Delta National Forest.

Methods

Acorn Collection and Preservation for Mass Loss and GE Experiments

During autumn 2008, I collected whole sound acorns (i.e., those sinking in water; Allen 1989, Barras et al. 1996) of cherrybark oak, pin oak, Nuttall oak, Shumard oak (*Q. Shumardii*), water oak, and willow oak (*n* = 500 acorns/species) from the campus of Mississippi State University (MSU), Delta National Forest, Noxubee NWR, and the city of Starkville, Mississippi. I used these acorns to study effects of submergence on GE of red oak acorns during winter 2008-2009.

During winter 2009-2010, I compared mass and GE of red oak acorns in unflooded and flooded bottomland hardwoods at Noxubee NWR and Delta National Forest, necessitating laboratory processing of 1,500 sound acorns per species. Because of increased sample size and cost of GE assays, I restricted my winter 2008-2009 experiment to Nuttall oak, pin oak, and willow oak acorns. I selected these species because they comprised the majority of red oak trees sampled during my study of red oak acorn production in the MAV (Chapter1). I stored collected acorns in a freezer at -10˚C at MSU for <2 months for preservation before subsequent mass loss and GE experiments (Barras et al. 1996).

Mass Loss of Red Oak Acorns, Winter 2009-2010

Before exposure of acorns to hardwood bottomland areas in winter 2009-2010, I thawed and inspected acorns ensuring pericarps were intact, then air dried them for 72 hours at room temperature (~21˚C) in an indoor laboratory at MSU. I then separated these air dried acorns into 140 samples of 10 acorns each for pin oak, Nuttall oak, and willow oak (Baker et al. 2001). I then weighed each air dried acorn sample to nearest 0.001 g and placed 120 samples of each species into separate, porous (300 μm) packets constructed of fiberglass window screening. Before sealing each packet with stainless steel staples, I enclosed an aluminum tag to identify it uniquely. I oven dried remaining 20 samples of each species to constant mass at 60˚C for 5 days to determine mean air dried moisture content. I then subtracted the species specific moisture percentage from each air dried acorn sample used in the mass loss experiment to estimate dry mass of samples before experimental exposure to unflooded or flooded sites (Baker et al. 2001).

I separated the 120 packets of each species into 12 groups of 10 packets each and assigned 3 groups each to unflooded and flooded treatments per study site. Before exposure, I strung packets within each flooding group together with plastic cable ties leaving 10-15 cm between packets. Upon exposure of flooded packets, I secured each group with two iron reinforcing rods to ensure submergence to a consistent depth of ~28 cm and to aid retrieval of packets.

To prevent mammalian predation of acorn samples in unflooded hardwood bottomland areas, I placed packets within 1-m^2 enclosures constructed of a 5 cm x 10 cm treated lumber frame with a hinged hardware cloth top allowing access by investigators to samples during winter. At each of the two study sites, I placed one enclosure containing all unflooded red oak acorn packets in a hardwood bottomland area that did not flood during winter, these areas were ≤5 km from the GTRs containing my flooded packets. Within each enclosure, I segregated packets (*n* = 90/enclosure) by species, ensuring no packets were stacked and covered them with 5-10 cm of nearby leaf litter, approximating local forest floor detritus conditions. Unflooded samples were periodically saturated by rain but never submersed in standing water during study.

I placed acorn samples in unflooded and flooded areas on 19 November 2009 and 21 November 2009 at Noxubee NWR and Delta National Forest, respectively. Thereafter, I removed 1 group of unflooded and flooded packets of each species at 30, 60, and 90 days from each study site. I completed retrieval of all packets on 17 February 2010 and 19 February 2010 at Noxubee NWR and Delta National Forest, respectively.

GE of Red Oak Acorns, Winter 2008-2009

I prepared 10 individually labeled plastic bags each for cherrybark oak, pin oak, Nuttall oak, Shumard oak, water oak, and willow oak. Next, I thawed and placed 10 randomly selected acorns of a respective species into each bag and submitted these samples to Department of Animal and Dairy Sciences, MSU, for GE analyses of fresh acorns (i.e., 0 days of experimental exposure; Kaminski et al. 2003). I also prepared 30 porous (300 μm) packets constructed of fiberglass window screening for each of the 6 species (n = 180 packets) and placed 10 randomly selected acorns in each packet. I then replicated flooding methodology described for winter 2009-2010 mass-loss experiment.

On 5 December 2008, I submerged all packets in GTR 1 at Noxubee NWR. An unexpected drawdown of GTR 1 on 15 February 2009 led to mammalian predation of >80% of 90 day treatment group of pin oak, Shumard oak, and water oak acorns; however, remaining cherrybark oak, Nuttall oak, and willow oak packets were unmolested. Within 3 days of drawdown, I moved remaining acorn packets to a flooded ditch in GTR 1 and submersed packets until retrieval on 5 March 2009. However, I did not include pin oak, Shumard oak, or water oak in analysis because of small sample size ($n \leq 3$ packets) for 90 day treatment of these species.

GE of Red Oak Acorns, Winter 2009-2010

I prepared and submitted fresh (i.e., 0 days of experimental exposure) acorns of Nuttall oak, pin oak, and willow oak for GE assays as described for the 2008-2009 GE study. Thereafter, pre-exposure handling, treatment groups, and exposure durations were identical to those described for the winter 2009-2010 mass-loss study because acorn samples from that study were analyzed for GE content after dry mass determinations.

Between-Year Variation in GE of Red Oak Acorns

During autumns 2008-2009, I collected 10 whole sound acorns from each of 10 cherrybark, Nuttall, pin, Shumard, water, and willow oak trees on the MSU campus, Delta National Forest, Noxubee NWR, and cities of Stoneville and Starkville, Mississippi. After collection, I submitted acorn samples for GE analysis to Department of Animal and Dairy Sciences, MSU.

Laboratory Methods

Mass Loss and GE of Red Oak Acorns

After retrieval of acorn samples from study sites, I removed acorns from packets and rinsed them with tap water, removing debris and algae. I then placed acorn samples into individually labeled plastic bags and submitted them to Department of Animal and Dairy Sciences, MSU, for dry mass and GE assays (Kaminski et al. 2003). Laboratory staff processed samples in following manner: 1) dried acorns from each sample to constant mass; 2) ground dried acorns, including pericarps, into a homogenous mixture; and 3) determined mean GE values using a Parr adiabatic oxygen bomb calorimeter (Kaminski et al. 2003).

Statistical Analyses

Mass Loss of Red Oak Acorns, Winter 2009-2010

I analyzed red oak acorn mass loss data using a mixed model analysis of variance (ANOVA) in R version 2.11.1 (R Development Core Team 2009), designating $\alpha = 0.05$ a priori. My dependent variable was percentage of dry mass of each acorn sample remaining after exposure. I designated flooded or not, red oak species, and duration of exposure as fixed effects and study site as a random effect for each species. I used Tukey's Honestly Significant Difference Test to determine pair-wise differences within significant main effects with ≥2 levels (Quinn and Keough 2002).

GE of Red Oak Acorns, Winter 2008-2009

I analyzed 2008-2009 GE data using a one-way ANOVA in R version 2.11.1 (R Development Core Team 2009), designating $\alpha = 0.05$ a priori. My dependent variable was mean GE of each acorn sample post exposure. I designated duration of submergence as a fixed effect for each species.

GE of Red Oak Acorns, Winter 2009-2010

I analyzed 2009-2010 GE data using a mixed model ANOVA in R version 2.11.1 (R Development Core Team 2009), designating $\alpha = 0.05$ a priori. My dependent variable was mean GE of each acorn sample after exposure. Fixed and random effects were identical to those described in the study of mass loss of red oak acorns.

Between-Year Variation in GE of Red Oak Acorns

I used a two-way ANOVA in R version 2.11.1 to test for a possible effect of year and species on GE of red oak acorns (R Development Core Team 2009), designating $\alpha = 0.05$ a priori. My dependent variable was mean GE of acorns collected from each red oak tree. I designated year and red oak species as fixed effects.

Results

Mass Loss of Red Oak Acorns, Winter 2009-2010

Data collection for estimation of red oak acorn production in the MAV (Chapter 1) delayed retrieval of acorns from the 30-day exposure treatment until 40 days elapsed for unflooded and flooded acorns at Noxubee NWR and Delta National Forest. Therefore, mass loss and GE data are reported for 40, 60, and 90 days of exposure during winter 2009-2010.

Mean mass of unflooded willow oak acorns was significantly greater (~1.1%) than flooded samples across exposure durations ($F_{1, 154} = 19.60$, $P < 0.001$), and mass of acorns decreased with exposure duration ($F_{3, 154} = 145.40$, $P < 0.001$; Table 2.1). Mean mass of unflooded Nuttall oak and pin oak acorns did not differ significantly from those flooded across exposure durations ($F_{1, 154} \leq 3.45$, $P \geq 0.065$), but mass of acorns decreased with exposure duration ($F_{3, 154} \geq 8.98$, $P < 0.001$; Table 2.1). When data was combined across unflooded and flooded acorn samples, mean mass loss of Nuttall, pin, and willow oak acorns after 90 days of exposure was 4.7%, 8.1%, and 6.6%, respectively.

GE of Red Oak Acorns, Winter 2008-2009

Mean GE of flooded willow oak acorn samples did not differ significantly across 30, 60, and 90 day exposure durations during winter 2008-2009 ($F_{3, 36} = 1.62$, $P = 0.202$; Table 2.2). However, mean GE of flooded cherrybark and Nuttall oak acorns did differ significantly across exposure duration ($F_{3, 36} \geq 17.97$, $P < 0.001$; Table 2.2). However, variation in mean GE of fresh cherrybark oak and Nuttall oak acorns and those exposed to flooded hardwood bottomlands for 90 days were only 0.01 and 0.08 kcal/g, respectively.

GE of Red Oak Acorns, Winter 2009-2010

Mean GE of unflooded Nuttall, pin, and willow oak acorns did not differ significantly from flooded samples across exposure durations ($F_{1, 154} \leq 1.20$, $P \geq 0.272$; Table 2.3). However, GE Nuttall, pin, and willow oak acorns differed significantly across exposure durations ($F_{3, 151} \geq 29.4$, $P \leq 0.001$; Table 2.3). However, differences in mean GE of fresh Nuttall, pin, and willow oak acorns and those exposed to unflooded or flooded hardwood bottomlands for 90 days were only 0.05, 0.03 and 0.03 kcal/g, respectively.

Between-Year Variation in GE of Red Oak Acorns

Mean GE of acorns differed among species ($F_{5, 108}$ = 98.09, P < 0.001), ranging from 4.80-5.38 kcal/g (Table 2.4). Within species, however, GE of red oak acorns varied ≤0.09 kcal/g between years and did not differ significantly ($F_{1, 108}$ = 0.65, P = 0.423).

Discussion

My results indicated mass of red oak acorns declined 5.3-8.4% after 90 days of submergence, which is slightly greater than 4% mass loss by water oak acorns in South Carolina wetlands (Neely 1956). However, mass loss of red oak acorns was less than many other seeds consumed by waterfowl post submersion, including: Japanese millet (57%; *Echinochloa frumentacea*; Neely 1956, Hagy 2010), panic grass (33%; *Panicum* sp.; Nelm and Twedt 1996), rice (18%), corn (50%), and soybeans (86%; Neely 1956).

Variation in mass loss between unflooded and flooded Nuttall, pin, and willow oak acorns after 90 days was ≤1.4%. In contrast, Foster et al. (2010*a*) estimated mass loss of flooded corn, soybean, and grain sorghum seeds to be 40-300% greater than unflooded samples after 12 weeks of submergence. Foster et al. (2010*a*) observed submersed agricultural seeds swell and soften quickly and hypothesized these traits hastened decomposition. Conversely, acorn pericarps remained firm and lacked macro-scopic fractures post submersion, slowing microbe colonization and decomposition (Winston 1956).

In addition to mass loss, variation in GE of red oak acorns might alter TME and ultimately estimates of habitat carrying capacity for waterfowl (Kaminski et al. 2003). However, within species variation in GE of red oak acorns produced between years or after 90 days winter exposure in bottomland hardwood forests was ≤0.09 kcal/g, which is <1.7% of mean GE of fresh acorns of red oak species commonly consumed by waterfowl ($\bar{x}$ = 5.49 kcal/g; Kaminski et al 2003). These small variations in GE of red oak acorns would not significantly affect TME estimates of acorns consumed by waterfowl.

Resistance of red oak acorns to mass loss and GE alteration during winter likely results from a pericarp which regulates water uptake (Bonner 1968) and deters microbial colonization (Winston 1956); thereby, maintaining viability of acorns during winter dormancy (Briscoe 1961, Larsen 1963). Barras et al. (1996) reported pericarp thickness declined among water oak ($\bar{x}$ = 0.55 mm), Nuttall oak ($\bar{x}$ = 0.44 mm), and willow oak acorns ($\bar{x}$ = 0.37 mm); thus, winter mass loss of water oak ($\bar{x}$ = 4%; Neely 1956), Nuttall ($\bar{x}$ = 5.3%) and willow oak ($\bar{x}$ = 7.1%) acorns post 90 days submergence may be inversely related to pericarp thickness. While fresh agricultural and moist-soil seeds have greater or comparable TME to red oak acorns after consumption by waterfowl (Kaminski et al. 2003), acorns may have a greater propensity to retain mass and nutrient quality during winter because of their pericarp.

Research Implications

Consistent small variation (i.e., <0.09 kcal/g) in GE of red oak acorns produced between years and post 90 days of winter exposure suggests determination of TME from these acorns by ducks is not warranted (Kaminski et al. 2003). However, regional variation in production of red oak acorns in the MAV (i.e., 60-1,234 kg/ha; Chapter I) has great consequences to estimates of carrying capacity of bottomland hardwood forests for wintering waterfowl. Thus, I recommend researchers focus on improving understanding of red oak acorn production dynamics and waterfowl foraging ecology in bottomland hardwood forests of the MAV.

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Table 2.1 Mean ($\bar{x} \pm$ SE) percent dry mass (g) of sound acorns (i.e., those sinking in water) of Nuttall oak (*Quercus texana*), pin oak (*Q. palustris*), and willow oak (*Q. phellos*) remaining post exposure for 40, 60, and 90 days in unflooded and flooded bottomland hardwood forest areas at Noxubee National Wildlife Refuge and Delta National Forest, Mississippi, winter 2009-2010.

		40 days	60 days	90 days
Species	Treatment	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE
Nuttall oak	Unflooded	99.56±0.83A[a]	99.54±1.36A	96.01±1.27A
	Flooded	97.21±1.21A	98.29±1.10A	94.66±0.94B
Pin oak	Unflooded	94.72±0.53A	96.42±0.44B	92.10±0.46C
	Flooded	96.05±0.35A	95.76±0.40A	91.65±0.34B
Willow oak	Unflooded	96.28±0.48A	97.29±0.43A	93.89±0.40B
	Flooded	95.01±0.28A	95.52±0.25A	92.90±0.28B

[a]Means within rows with unlike letters differ ($P < 0.05$) by Tukey pairwise multiple comparison test.

Table 2.2 Mean ($\bar{x} \pm$ SE) gross energy (kcal/g) of sound acorns (i.e., those sinking in water) of cherrybark oak (*Quercus pagoda*), Nuttall oak (*Q. texana*), and willow oak (*Q. phellos*) post submergence for 0 (fresh), 30, 60, and 90 days in greentree reservoir 1 at Noxubee National Wildlife Refuge, Mississippi, winter 2008-2009.

	0 days	30 days	60 days	90 days
Species	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE
Cherrybark oak	5.37±0.02A[a]	5.51±0.02B	5.41±0.01A	5.38±0.01A
Nuttall oak	4.88±0.01AC	4.91±0.01A	5.00±0.01B	4.80±0.01C
Willow oak	5.37±0.01A	5.34±0.01A	5.36±0.01A	5.35±0.01A

[a]Means within rows with unlike letters differ ($P < 0.05$) by Tukey pairwise multiple comparison test.

Table 2.3 Mean ($\bar{x}$ ± SE) gross energy (kcal/g) of sound acorns (i.e., those sinking in water) of Nuttall oak (*Quercus texana*), pin oak (*Q. palustris*), and willow oak (*Q. phellos*) post exposure for 0 (fresh), 40, 60, and 90 days in unflooded and flooded bottomland hardwood forest areas at Noxubee National Wildlife Refuge and Delta National Forest, Mississippi, winter 2009-2010.

		0 days	40 days	60 days	90 days
Species	Treatment	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE
Nuttall oak	Unflooded	4.97±0.02A[a]	4.93±0.01A	4.88±0.01B	4.95±0.01A
	Flooded	4.97±0.02A	4.89±0.01B	4.91±0.01A	5.00±0.02A
Pin oak	Unflooded	5.10±0.01A	5.05±0.01B	5.01±0.01B	5.10±0.01A
	Flooded	5.10±0.01A	5.02±0.01B	4.99±0.01B	5.13±0.02A
Willow oak	Unflooded	5.41±0.03A	5.29±0.01B	5.28±0.02B	5.38±0.01A
	Flooded	5.41±0.03A	5.28±0.01B	5.29±0.01B	5.38±0.01A

[a]Means within rows with unlike letters differ ($P < 0.05$) by Tukey pairwise multiple comparison test.

Table 2.4 Mean ($\bar{x}$ ± SE) gross energy (kcal/g) of 10 fresh, whole, and sound (i.e., those sinking in water) acorns from 10 trees of each of six red oak species (*Quercus* spp; Subgenus *Erythrobalanus*) collected from the campus of Mississippi State University, Delta National Forest, Noxubee National Wildlife Refuge, and cities of Stoneville and Starkville, Mississippi, during autumns 2008-2009.

		2008	2009
Common Name	Scientific Name	$\bar{x}$ ± SE	$\bar{x}$ ± SE
Cherrybark oak	*Q. pagoda*	5.39±0.04	5.38±0.03
Nuttall oak	*Q. texana*	4.89±0.03	4.80±0.05
Pin oak	*Q. palustris*	5.07±0.02	5.14±0.03
Shumard oak	*Q. shumardii*	4.90±0.03	4.84±0.03
Water oak	*Q. nigra*	5.29±0.01	5.30±0.03
Willow oak	*Q. phellos*	5.34±0.03	5.33±0.05

CHAPTER III

SYNTHESIS

Bottomland hardwood forests provide numerous ecological services to society, including wildlife habitat, carbon storage, timber products, and water quality improvement (King et al. 2009). Additionally, bottomland hardwood forests are an important component of wintering waterfowl habitat complexes consisting of forested, moist-soil, and agricultural wetlands in the Mississippi Alluvial Valley (MAV; Pearse 2007). Within bottomland hardwood forests, hard mast from red oaks (*Quercus* spp; Subgenus *Erythrobalanus*) provides seasonally abundant forage for wintering waterfowl and other wildlife, particularly in late winter as forage availability in other habitats wanes (e.g., agricultural wetlands; Fredrickson and Heitmeyer 1988, Stafford et al. 2006, Davis and Afton 2010). However, flooding of forested wetlands in the MAV is unpredictable; thus, to provide consistent winter flooding, waterfowl habitat managers created greentree reservoirs (GTRs). A GTR is a hardwood bottomland area impounded by levees and flooded naturally or artificially by pumping or gravity flowing water (Reinecke et al. 1989, Fredrickson 2005). Although GTRs provide consistently flooded habitat for wintering waterfowl, unnatural flooding regimes in GTRs affect many aspects of bottomland and red oak ecology and may negatively impact red oak acorn production (Francis 1983, Young et al. 1995, Fredrickson 2005, Guttery 2006, Thornton 2009).

The Lower Mississippi Valley Joint Venture (LMVJV) of the North American Waterfowl Management Plan uses science-based estimates of duck population carrying capacity (i.e., duck-energy days [DED]) to estimate numbers of wintering waterfowl potentially supported by wetland habitats in the MAV (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986, Loesch et al. 1994). However, no study has estimated spatio-temporal variation in red oak acorn production through an MAV-wide survey. Furthermore, mass, gross energy (GE), and ultimately true metabolizable energy (TME; Miller and Reinecke 1984) of red oak acorns consumed by waterfowl could be altered by winter decomposition of these seeds. Thus, understanding dynamics of production and decomposition of red oak acorns is essential to estimating carrying capacity in bottomland hardwood forests of the MAV.

In Chapter 1, I initiated studies to estimate mean acorn production by cherrybark oak (*Q. pagoda*), Nuttall oak (*Q. texana*), pin oak (*Q. palustris*), water oak (*Q. nigra*), and willow oak (*Q. phellos*) in 5 non-impounded, naturally flooded bottomland hardwood forests (NFF) in the MAV and 2 GTRs in Mississippi. Among study sites in the MAV, mean cumulative (i.e., autumn-winter) mass (kg[dry]) of acorns produced per hectare of red oak crown (hereafter kg/ha) was 439 kg/ha (CV = 28.68%) during autumn-winter 2009-2010. This estimate was ~5.6 times greater than late-autumn waste rice abundance in rice fields (Stafford et al. 2006) and ~80% of the autumn seed abundance in managed moist-soil wetlands in the MAV(Kross et al. 2008). In addition, my estimate of mean red oak acorn production in bottomland hardwood forests in the MAV was 2.6 times greater than the current forage abundance estimate of 166 kg/ha in bottomland hardwood forests with 100% red oak basal area (i.e., red oak acorns, moist-soil seeds, and aquatic macroinvertebrates) used by LMVJV conservation planners (Reinecke and Kaminski 2007). Additionally, during autumn-winter 2009-2010, production of red oak acorns varied >20 fold across study sites in the MAV. I used criteria described in Greenberg and Parresol (2002) to rate relative acorn production intensity by red oaks in MAV study sites, and concluded mean acorn production by red oaks at three study sites was poor (i.e., <60% MAV mean; range = 60.46-185.05 kg/ha), while red oaks at two other study sites had good acorn production (i.e., >MAV mean; 851.33 and 1,234.65 kg/ha).

Red oak acorn production in sampled GTRs was moderate (i.e., >60% and equal to 2009-2010 MAV mean; $\bar{x}$ = 374.62 kg/ha; CV = 26.67%) and good (i.e., >2009-2010 MAV mean; $\bar{x}$ = 1,214.16 kg/ha; CV = 19.81%) during autumn-winters 2008-2009 and 2009-2010, respectively. Across years, mean red oak acorn production was 771.83 (CV = 23.00%) and 794.39 kg/ha (CV = 19.38%) in NFFs and GTRs, respectively. Based on my results, acorn production by red oaks in sampled NFFs and GTRs was similar in autumns-winters 2008-2010.

In Chapter II, I quantified mass loss and GE dynamics of cherrybark oak, Nuttall oak, water oak, and willow oak acorns during winter in unflooded and flooded bottomland hardwood forests in the Interior Flatwoods and alluvial valley of Mississippi. Mass loss of red oak acorns was similar among unflooded and flooded treatments and ranged from 5.3-8.4% post 90 days of exposure. Within red oak species, variation in GE of acorns produced between years or after 90 days of winter exposure in bottomland hardwood forests was ≤0.09 kcal/g, which is <1.7% of the mean GE of fresh acorns of red oak species commonly consumed by waterfowl ($\bar{x}$ = 5.49 kcal/g; Kaminski et al 2003). Resistance of red oak acorns to loss of mass and apparently TME during winter likely results from a pericarp which regulates water uptake (Bonner 1968) and deters microbial colonization (Winston 1956); thereby, maintaining viability of acorns during winter dormancy (Briscoe 1961, Larsen 1963)

Conservation planners need not be concerned winter decomposition of red oak acorns will significantly affect estimates of waterfowl carrying capacity in bottomland hardwood forests. However, my study suggests production of acorns by red oaks varies greatly across the MAV within and among years. Spatio-temporal dynamics in red oak acorn production and possible influences on wildlife behavior, survival, movements, reproduction, and ultimately bottomland hardwood forest community ecology in the MAV is unknown and should be studied in the future. Furthermore, the greatly fragmented mosaic of bottomland hardwood forests now present in the MAV may impede dispersal of wildlife (e.g., Louisiana black bear [*Ursus americanus luteolus*]; Vaughan 2002, King et al. 2006), thereby exacerbating effects of variable acorn crops on population dynamics of acorn consumers.

My study suggests red oaks subjected to GTR hydrology for >50 years can produce acorn crops similar to those of conspecifics in NFFs. However, water management regimes vary among GTRs; hence my results may not apply to other GTRs (Covington and Laubhan 2005). Managers committed to ensuring long-term productive red oak bottomlands in GTRs should consider developing monitoring strategies which record parameters such as red oak survival, crown health, advanced regeneration and understand silvicultural treatments to increase red oak regeneration from mast crops. Managers of GTRs should also be prepared to reduce flooding frequency and duration in

GTRs at the expense of waterfowl hunting opportunity (Reinecke et al. 1989, Covington and Laubhan 2005).

Long-term sampling (i.e., ≥5 years) is likely needed to document and potentially predict spatio-temporal dynamics of acorn production by red oaks in bottomland hardwood forests in the MAV. Furthermore, researchers and conservation planners should consider not only mean acorn production by red oaks in the MAV but also consequences of spatio-temporal variation in acorn production on population dynamics of wildlife using bottomland hardwood forests (Jones et al. 1998, McShea 2000, Ostfeld and Keesing 2000, Kelly et al. 2008).

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