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Habitat Relations

Acorn Production Prediction Models for Five Common Oak Species of the Eastern United States

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ABSTRACT Acorn production varies considerably among oak (*Quercus*) species, individual trees, years, and locations, which directly affects oak regeneration and populations of wildlife species that depend on acorns for food. Hard mast indices provide a relative ranking and basis for comparison of within- and between-year acorn crop size at a broad scale, but do not provide an estimate of actual acorn yield—the number of acorns that can potentially be produced on a given land area unit based on the species, number, and diameter at breast height (dbh) of oak trees present. We used 10 years of acorn production data from 475 oak trees to develop predictive models of potential average annual hard mast production by five common eastern oak species, based on tree diameter and estimated crown area. We found a weak ($R^2 = 0.08$–0.28) relationship between tree dbh and acorn production per unit crown area for most species. The relationship between tree dbh and acorn production per tree was stronger ($R^2 = 0.33$–0.57). However, this is because larger-dbh trees generally have larger crowns, not because they have a greater capacity to produce more acorns per unit crown area. Acorn production is highly variable among individual trees. We estimated that dbh of at least 60 dominant or codominant oak trees per species should be randomly sampled to obtain an adequate representation of the range of dbhs ($\geq$12.7 cm dbh) in a given forest area, and achieve precise estimates when using these equations to predict potential acorn production. Our predictive models provide a tool for estimating potential acorn production that land managers and forest planners can apply to oak inventory data to tailor estimates of potential average annual acorn production to different forest management scenarios and multiple spatial scales.

KEY WORDS acorn crop, acorn crop prediction, acorn production, acorns, hard mast, oak.

Acorn crop sizes vary considerably among oak (*Quercus*) species, individual trees, years, and locations (Greenberg 2000), which directly affect oak regeneration (Loftis and McGee 1993) and populations of wildlife species that depend on acorns for food (Martin et al. 1951). Acorns also have far-reaching, indirect effects on ecosystems (Wolff 1996). For example, acorn crop size affects rodent populations; rodents, in turn affect songbird nest success by eating eggs, gypsy moths by eating pupae, and lyme disease by carrying the disease and host ticks that spread it (Wolff 1996, Jones et al. 1998). Acorn crop size also affects deer populations that in turn affect forest structure and tree regeneration by browsing (Feldhamer 2002).

Because of the wide-reaching influence of acorns on wildlife populations and forest ecology, acorn, or hard mast, crop size estimation has long been a focus of land managers and researchers. Numerous quantitative and qualitative methods have been developed for estimating or indexing sizes of acorn crops. Quantitative methods include acorn traps (e.g., Downs and McQuilken 1944, Christisen and Korschgen 1955, Goodrum et al. 1971, Beck 1977, Greenberg and Parresol 2002), visual surveys such as time-constrained acorn counts (Koenig et al. 1994), and scored counts of twigs and acorns on a subsample of oak limbs (Sharp 1958, Whitehead 1969). Qualitative visual survey methods are subjective, categorical rankings of acorn production on trees such as "none" to "bumper crop" (Sharp 1958, Graves 1980, Christisen and Kearby 1984). A hard mast index method for rapid crop size estimation based on the proportion of oaks producing acorns in any given year was recently developed (Greenberg and Warburton 2007). This method could be used to standardize hard mast production surveys among state and federal agencies, thus ensuring that acorn production data are comparable at local, regional, or national scales.

Hard mast indices can provide a relative ranking of within-year acorn crop size at a broad scale, and are useful in

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comparing the relative size of acorn crops among years, species, or locations. However, they do not provide an estimate of actual acorn yield, the number of acorns that can potentially be produced on a given land area unit. Land managers need a tool for tailoring estimates of average acorn production to specific land unit areas and different forest management scenarios.

Clearly, acorn yield will vary according to the number, size, and species of oak trees in any given forest area. Because acorn production varies so dramatically among years and individual trees, long-term data and a large number of sample trees are needed to obtain accurate acorn production averages by oak species.

The influence of tree diameter at breast height (dbh) and crown area on acorn production must also be closely examined in developing accurate acorn yield estimations that can be applied to forest areas. For example, acorn production might be expected to increase with age simply because crown area, the area upon which acorns are produced, expands with dbh (Bechtold 2003).

Crown area, or crown cover area (a two-dimensional measurement that considers only the surface area of the crown), provides a more accurate metric for acorn production than crown volume (a three-dimensional measurement, which includes both the crown surface and full interior) because acorns are produced on the outer branches of oaks (current year growth for the white oak group; prior-year growth for the red oak group). Further, acorn traps are two-dimensional and thus cannot be used to accurately estimate the number of acorns produced per a three-dimensional crown volume. Finally, in contrast to crown area, crown volume generally does not increase with tree dbh in closed canopy conditions, as heavily shaded branches further down on tree boles generally do not persist (Kozlowski et al. 1991).

The relationship between dbh and the number, or density of acorns produced per m^2 crown, must also be carefully examined when developing acorn production models. In other words, assuming that larger trees produce more acorns than smaller trees solely because they have larger crowns could result in underestimates of acorn production if larger trees also produce a greater density of acorns per unit crown area than smaller trees.

We used 10 years (range 7–10 years per study tree) of quantitative acorn production data to develop predictive models of average annual hard mast production by five common oak species in the southern Appalachians of the southeastern United States, based on dbh and estimated crown area of dominant or codominant oak trees $\geq$12.7 cm dbh. Our objective was to provide a tool that land managers and forest planners can apply to forest landscapes with different numbers, sizes, and species of oak trees, to develop potential acorn production estimates at multiple spatial scales.

STUDY AREA

We conducted our study within the Blue Ridge Physiographic province of western North Carolina, throughout the Grandfather and Pisgah districts of the Pisgah National Forest. Average annual precipitation in the region ranged from about 1,000 to 1,500 mm and exceeded 2,500 mm along parts of the southern Blue Ridge escarpment in western North Carolina (McNab 2011).

Winters were short and mild, summers were long and warm. Common tree species on xeric sites included scarlet oak (*Quercus coccinea* Muenchh.), chestnut oak (*Q. prinus* L.), black oak (*Q. velutina* Lam.), blackgum (*Nyssa sylvatica* Marsh.), sourwood (*Oxydendrum arboretum* (L.) DC.), and shortleaf pine (*Pinus echinata* Mill.). Yellow-poplar (*Liriodendron tulipifera* L.), and northern red oak (*Q. rubra* L.) dominated moist slopes and coves. Red maple (*Acer rubrum* L.), hickory (Carya spp.), dogwood (*Cornus florida* L.), and white oak (*Q. alba* L.) were present on all sites (McNab 1996).

METHODS

Acorn Sampling

Trees included in our acorn sampling were from two long-term studies of acorn production by five species of common oaks in the southern Appalachians. The first study (2000–2009) included oak trees ($n = 285$) within the Bent Creek Experimental Forest (BCEF), a 2,500 ha watershed within the Pisgah National Forest. We randomly selected trees to represent a wide range of size classes (12.4–108.0 cm dbh). The second study (2002–2009) included all oak trees ($n = 190$) $\geq$12.7 cm dbh (range = 15.2–69.6 cm dbh) within 30 randomly selected 0.1-ha plots. Plots in the second study included both closed-canopy and 2-aged (harvested ca. 1999 with 15–20% basal area retention) stands of cove hardwood and upland hardwood forest, and were located throughout the Grandfather and Pisgah districts of the Pisgah National Forest, including BCEF. Oak trees within 2-aged stands represented a small proportion (5%) of study trees. We measured dbh of all sample trees (both studies) during winter 2006–2007. We located sample trees (both studies combined) at elevations ranging from 510–1,260 m above sea level and across a wide range of topographic features (i.e., aspect, slope position, and percent slope). Most trees were 80–120 years old and in dominant or codominant (a few were intermediate) crown positions. We did not include trees that showed severe crown dieback (oak decline) or trees that died during the study period. Study species included black oak ($n = 36$), northern red oak ($n = 80$), and scarlet oak ($n = 70$) in the red oak group (subgenus *Quercus* section Lobatae), and chestnut oak ($n = 170$) and white oak ($n = 119$) in the white oak group (subgenus *Quercus* section Quercus).

In both studies, we collected acorns in circular, 0.46-m^2 traps placed randomly beneath the tree crowns. In the BCEF study, the number of traps per tree was approximately proportional to the basal area (2–14 per tree) until 2004, when the number of traps was standardized for consistency between the studies to 3 per tree; in the second study, 3 traps per tree were used beginning at study establishment. Crop size estimates probably were conservative because trap tallies did not account for acorns removed by squirrels or other arboreal consumers. We checked traps at approximately 2-week intervals from mid-August through the completion of acorn drop in the BCEF study, and at approximately 4-week intervals in the second study. We counted acorns and classified them in the lab as aborted (primarily cap material) or well developed. We included well-developed acorns in our analyses, but for purposes of this study we did not distinguish between insect damaged and sound acorns, or acorn size.

Data Analysis

We estimated the number of acorns produced per m^2 crown for each tree based on the average number of acorns per trap. We then estimated the number of acorns produced by each tree's full crown (hereafter whole-tree) by multiplying the average number of acorns per m^2 crown by the estimated crown area (m^2) for that tree. We used individual tree dbh to calculate crown diameter using crown diameter equations developed for each oak species (Table 1; Bechtold 2003). We then used tree diameters to calculate crown areas using the formula for circle area [Area $= \pi(r^2)$] (Table 1).

Regression/Model building

We used linear regression (SAS Institute 2003) to develop two sets of equations relating acorn production of a tree to its dbh for each of the five species. The two response variables were annual average number of acorns produced per m^2 crown and per whole-tree; the independent variable was dbh. A quadratic term (dbh^2) was included as a second independent variable when significant. We used the annual average ($n = 7$–10 years per tree) of acorn production by each tree (per m^2 crown area and per whole-tree) as a single data point because our objective was to estimate overall potential average production per tree, for application to forest landscapes. This value represented the number of acorns each tree would be expected to produce on average relative to its interannual variability. Using the average also addressed the issue of the high number of zero values in the data matrix (29–69% of observations depending on year). High numbers of zero values in tree crop production is not uncommon (Ihalainen et al. 2003, Calama et al. 2008).

To correct for the heavily skewed distribution of both response variables (as indicated by their residuals) in four of the five species and apparent heteroscedasticity for all species, we log transformed [$\log_{10}(Y + 1)$] both response variables for all five species (Zar 1999, Quinn and Keough 2002).

Table 1. Crown diameter equations (in feet) used to calculate crown area (Bechtold 2003). We calculated crown area using the formula for the area of a circle.

Species	Crown diameter (ft)[a] (C_DIAM)
Black oak	C_DIAM = 6.245 + 1.3744(dbh)
Chestnut oak	C_DIAM = 4.6382 + 1.7431(dbh) − 0.0189(dbh^2)
Northern red oak	C_DIAM = 6.2141 + 1.4026(dbh)
Scarlet oak	C_DIAM = 3.971 + 1.6927(dbh)
White oak	C_DIAM = 5.9658 + 1.5212(dbh)

[a] To convert crown diameter to meters, multiply by 0.3048006.

We identified several observations as outliers based on the R-student test in PROC REG in SAS (SAS Institute 2003). Excluding the influential data points did not improve R^2 and resulted in very similar parameter estimates. In addition, when we excluded the influential points, several more data points were identified as influential. Given the variable nature of acorn production over time, and the small change in parameter estimates, we maintained all data points.

These predictive equations can be applied to forest inventory data, assuming those data are unbiased and representative of the diameter distribution present in the sampled area. We estimated the sample size for dbh of dominant or co-dominant oak trees needed to accurately apply our equations to specific land units, based on the effect size (i.e., the strength of the relationship between acorn production and dbh) and the number of predictors in the model (Cohen 1988, Cohen et al. 2003). For multiple linear regression, the effect size (f^2) is estimated as the ratio of the coefficient of determination and the proportion of residual variability not explained by the regression model [$R^2/(1 - R^2)$] (Cohen 1988). The procedure allows power analyses to test the null hypothesis that the proportion of variance of a dependent variable Y explained by a set of predictors is zero (i.e., $R^2 = 0$). To be conservative, we estimated the sample size using an α-value of 0.01 and desired power of 0.99. We calculated sample size estimates using the program G*Power 3.1 (Faul et al. 2009).

RESULTS

Acorn Production Patterns

Average dbh of the trees in our sample ranged from 43.6 to 59.1 cm, and the average estimated crown area of trees in our sample ranged from 61.0 to 119.9 m^2 (Table 2). Average annual number of acorns produced per whole-tree ranged from 246.3 acorns (chestnut oak) to 1,884.0 acorns (white oak; Table 2). During the study period, average annual acorn production per tree ranged from 74 to 2,400 for black oak, 12 to 1,462 for chestnut oak, 49 to 4,745 for northern red oak, 25 to 4,277 for scarlet oak, and 95 to 10,326 for white oak (Fig. 1). Although acorn crop sizes differed substantially among species and years, at least moderate acorn crops (all species combined) were produced in most years. Acorn crop failures, when >50% of the trees did not produce any acorns, occurred 3 times (2003, 2008, and 2009) during our study period (Fig. 1). Individual trees differed in their frequency of acorn production, and in the numbers of acorns produced. Most (78%) of our 475 sample trees did not produce any acorns in ≥25% of years sampled, and nearly 40% of trees did not produce any acorns in ≥50% of years sampled.

Prediction of Acorn Production

The equations relating acorn production to m^2 of crown (acorn density) explained 8–28% of the variation in number of acorns produced. However, 33–57% of the variation in acorn production was explained at the whole-tree level, based on the relationship between dbh and predicted crown area (Tables 3 and 4). For both response variables, coefficients associated with dbh were positive for all five species,

Table 2. Mean (SE) number of acorns (untransformed data), diameter at breast height, and crown area for five common species of southern Appalachian oaks, 2000–2009.

Species	Average annual number of acorn per m^2 of crown	Average annual number of acorn per tree	Dbh (cm)	Crown area (m^2)
Black oak	7.8 (1.0)	742.4 (141.0)	47.4 (2.6)	79.2 (6.7)
Chestnut oak	3.6 (0.4)	246.3 (31.6)	43.6 (1.4)	61.0 (2.3)
Northern red oak	10.6 (1.2)	1464.3 (202.2)	59.1 (2.3)	119.9 (7.7)
Scarlet oak	15.2 (1.5)	1677.6 (276.3)	44.3 (2.2)	93.1 (8.0)
White oak	16.2 (1.7)	1884.0 (292.8)	44.9 (1.9)	89.6 (6.1)
All 5	10.0 (0.6)	1110.2 (97.0)	46.9 (0.9)	84.2 (2.7)

indicating that acorn production increased with increasing tree dbh, primarily in relation to correspondingly greater crown diameter. For species with a significant square term, the associated coefficients were negative, indicating that acorn production tends to decline above a certain diameter threshold (Figs. 2 and 3). At the tree level, acorn production peaked at 77.0, 94.0, 97.0, and 93.0 cm dbh for chestnut oak, northern red oak, scarlet oak, and white oak, respectively.

We estimated that the dbh of at least 60 dominant or codominant oak trees per species should be randomly sampled in order to adequately represent the range of dbhs in a given forest area, when using these equations to predict potential acorn production. We based this estimate on the whole-tree acorn production equation for chestnut oak. This equation had the lowest R^2 value of the five species' equations in spite of a relatively large sample of trees (Table 4). Because we based our sample size estimate in part on the effect size between dbh and acorn production, the chestnut oak equation represents a worst case scenario relative to the other equations and provides a conservative estimate of necessary sample size.

DISCUSSION

Acorn production in our study was extremely variable among individuals, years, and species. Several other studies (as reviewed by Greenberg and Parresol 2002) also indicate that acorn production patterns are erratic. Tree age or size, stand density (Healy, 1997), and weather events such as late spring freezes or heavy precipitation that interferes with oak flower survival or pollen dispersal have been shown to affect acorn production (Sharp and Sprague 1967, Sork et al. 1993, Fearer et al. 2008). Genetics likely plays a large role in an individual tree's production potential as well (Johnson et al. 2002).

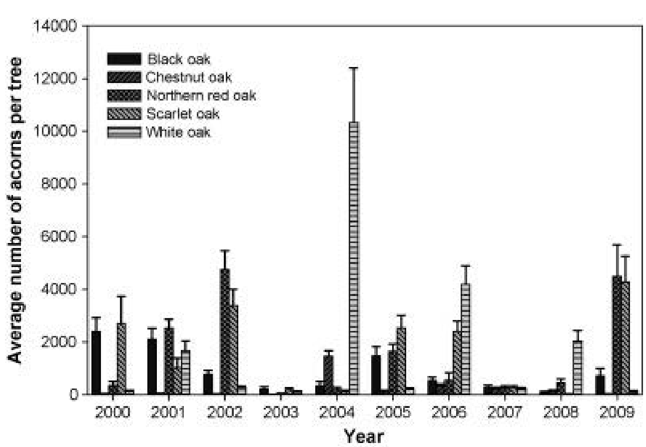

Figure 1. Mean (+SE) annual (2000–2009) number of acorns produced per tree for five common oak species of the southern Appalachians.

The effect of acorn crop size on wildlife populations, oak regeneration, and forest ecology cannot be overlooked. However, our data and other studies suggest that acorn production is difficult to predict from year to year because of high intrinsic variability and difficulty in predicting weather patterns that affect within-year crops. Within-year crop estimation can be obtained by annual hard mast indices (Greenberg and Warburton 2007) and is not the focus of this study. Instead, we provide a simple and efficient planning tool that can be used to estimate average acorn production by five common eastern oak species, at multiple spatial scales and tailored to different forest management scenarios.

Extreme temporal variation in acorn production within oak species highlights the need for long-term data and large sample sizes to obtain accurate estimates of average acorn production. Ours and other studies indicate that the number of acorns produced per tree can range from none to thousands in any given year (Greenberg and Parresol 2002). Crop size estimates differ dramatically among studies and are confounded by the number of trees and years sampled (both very small in most studies), which years are sampled, and the geographic area sampled (Greenberg and Parresol 2002). Although our 10-year data clearly demonstrate years of relatively higher and lower acorn production by each species, we were not able to ascertain whether our sample period included bumper crops, since crop-size is relative to other sampled years (e.g., Healy et al. 1999). However, because bumper crops are relatively infrequent, inconsistent, and lie far outside the typical range of production variability (e.g., outlier data), it is unlikely that inclusion or omission of a bumper year would greatly affect our long-term averages of acorn production. Our goal was not to attempt to predict temporal patterns of acorn production. Instead, we used long-term data to develop models that can be used by land managers and forest planners to predict average annual acorn production potential at broad spatial and temporal scales.

The structure and site characteristics of oak-dominated forest areas vary considerably across the southern

Table 3. Regression equations for predicting the average number of acorns produced per m^2 of crown based on tree diameter at breast height (cm).

Species	n	R^2	P-value	RMSE[a]	Equation[b]
Black oak	36	0.26	0.0015	0.3	$\text{Log}_{10}(Y + 1) = 0.27900 + 0.01152(\text{dbh})$
Chestnut oak	170	0.08	$\leq$0.001	0.3	$\text{Log}_{10}(Y + 1) = 0.01248 + 0.01822(\text{dbh}) - 0.00013455(\text{dbh}^2)$
Northern red oak	80	0.28	$\leq$0.001	0.4	$\text{Log}_{10}(Y + 1) = -0.47938 + 0.03915(\text{dbh}) - 0.00024304(\text{dbh}^2)$
Scarlet oak	70	0.10	0.0076	0.4	$\text{Log}_{10}(Y + 1) = 0.77772 + 0.00656(\text{dbh})$
White oak	119	0.18	$\leq$0.001	0.4	$\text{Log}_{10}(Y + 1) = 0.55275 + 0.00996(\text{dbh})$

[a] Root mean square error

[b] To convert to actual (rather than $\log_{10}$) number of acorns per m^2, take the antilog of equation result and subtract 1, that is, acorns per m^2 crown = $(10^{(\text{equation result})}) - 1$.

Appalachians. Our data represent dominant or codominant oak trees across a wide range of size classes and sites. We did not include topographic variables such as landform (McNab 1996) or elevation in our models in order to provide a straightforward predictive tool for land managers requiring minimal data. However, these variables can be largely inferred by the associations between occurrence of different oak species and site characteristics. For example, northern red oak generally occurs on productive sites, whereas scarlet, black, and chestnut oak generally occur on xeric, low quality sites (McNab 1996).

Oak decline, a combination of stress factors including low site quality site, drought, defoliating insects, frost and stand disturbance, and pathogens such as the shoe string fungus (*Armillaria mellea*) or bark beetles (*Dendroctonus frontalis* Zimmerman; Starkey and Oak 1989), causes progressive oak crown dieback and mortality and affects large areas across much of the southern United States (Starkey et al. 2004, Heitzman et al. 2007). Mature black oak and scarlet oak, growing on xeric, low quality sites are especially susceptible to oak decline (Starkey and Oak 1989). At BCEF, oak decline affected 0.5% of dominant or codominant oak annually (1991–2006), with highest decline-related mortality in scarlet and black oak (Greenberg et al. 2011). Widespread oak mortality also can occur from defoliation by gypsy moths (*Lymantria dispar*; Elkinton et al. 1996). Changes in abundance of dominant and codominant oak trees can also be caused by natural disturbances such as wind, or the gradual replacement of oak by other more shade-tolerant species (Greenberg et al. 2011). Thus, re-inventories of dominant and codominant oak should be undertaken at regular intervals to adjust long-term predictive estimates of acorn production based on severe decline and mortality associated with oak decline or other factors. Further, land managers should consider the relatively greater vulnerability of black oak and scarlet oak to oak decline when planning for sustainable acorn production over the long term.

Few studies have evaluated the effects of stand density on mast production by oaks. However, some research suggests that residual oaks and hickories may increase their production of nuts after thinning or timber harvests, likely a result of decreased competition, increased light to tree crowns, and possible increases in crown size over time (Perry and Thill 2003, Perry et al. 2004). The crown diameter equations used in our models were developed from stand-grown trees (Bechtold 2003). Acorn production estimates using our models may be less accurate for open-grown trees, or those in low-stocked stands where dbh:crown area relationships may be altered. However, estimates would likely err on the conservative side, as crown areas in low-density stands are more likely to increase in relation to dbh than decrease.

Because of the high variability in acorn production among individual trees, our averages and (or) models cannot be validly applied to a small number of oaks. The precision of our models is dependent on the presence of an adequate number of oak trees (sample size) per species to achieve precise estimates of acorn production for a given land unit. Our recommended minimum sample size of 60 dominant or codominant oak trees ($\geq$12.7 cm dbh) should be randomly sampled within any given inventory when applying these acorn production equations. We stress the importance of a random sample to ensure that the range of diameters sampled is truly representative of what is present in the forest area of interest. We determined this sample size using the effect size estimated from the chestnut oak equation, as it had lowest R^2 value and therefore represents a conservative estimate. However, because estimates of acorn production will likely be highly inaccurate if they are applied to 1 or a few trees, the specified minimum number of individuals should

Table 4. Regression equations for predicting the average number of acorns produced annually per tree based on tree diameter at breast height (cm).

Species	n	R^2	P-value	RMSE[a]	Equation[b]
Black oak	36	0.57	$\leq$0.001	0.4	$\text{Log}_{10}(Y + 1) = 1.06367 + 0.03123(\text{dbh})$
Chestnut oak	170	0.33	$\leq$0.001	0.6	$\text{Log}_{10}(Y + 1) = 0.20984 + 0.06029 (\text{dbh}) - 0.00039431(\text{dbh}^2)$
Northern red oak	80	0.53	$\leq$0.001	0.6	$\text{Log}_{10}(Y + 1) = -0.14836 + 0.07539(\text{dbh}) - 0.00039950(\text{dbh}^2)$
Scarlet oak	70	0.49	$\leq$0.001	0.5	$\text{Log}_{10}(Y + 1) = 1.16744 + 0.05158(\text{dbh}) - 0.00026797(\text{dbh}^2)$
White oak	119	0.54	$\leq$0.001	0.6	$\text{Log}_{10}(Y + 1) = 0.71155 + 0.06346(\text{dbh}) - 0.00034290(\text{dbh}^2)$

[a] Root mean square error.

[b] To convert to actual (rather than $\log_{10}$) number of acorns take the antilog of equation result and subtract 1, that is, acorns = $(10^{(\text{equation result})}) - 1$.

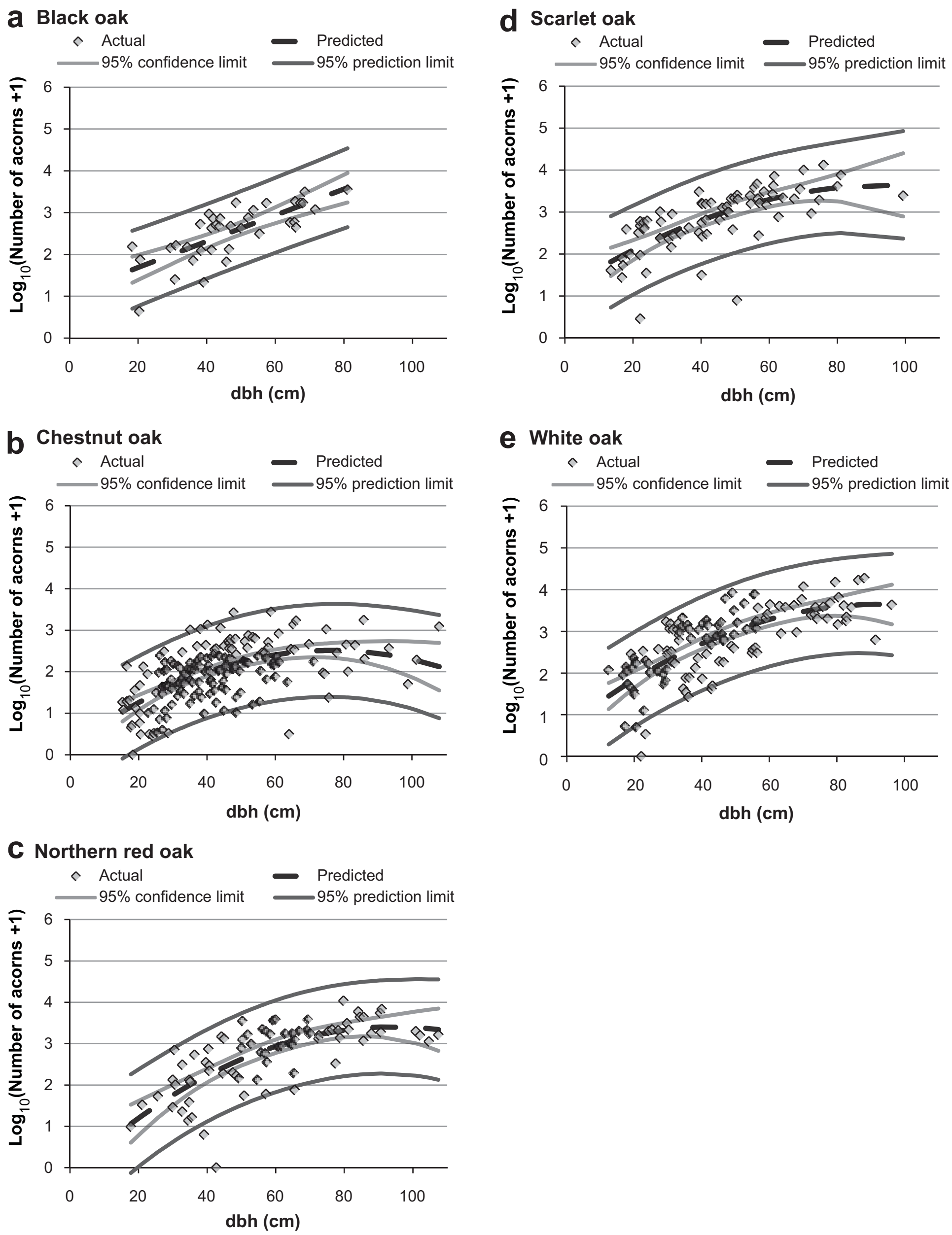

Figure 2. Predicted and actual (2000–2009) number of acorns produced per tree by diameter at breast height with 95% confidence intervals for five common oak species of the southern Appalachians. Species are (a) black oak, (b) chestnut oak, (c) northern red oak, (d) scarlet oak, and (e) white oak.

be sampled for using our models to predict average annual production at scales ranging from stand-level to large landscapes.

Our models indicate that increased acorn production with tree dbh is largely a function of the relationship between dbh and crown diameter (Fig. 4). Although we found a relationship between tree dbh and acorn density per unit crown area for most species, the relationship was weak and explained little (8–28%) of the variation in acorn production by trees of different dbh classes. Other studies (as reviewed by Greenberg and Parresol 2002) also have noted that tree dbh has a minor effect, if any, on the number of acorns produced per unit crown area although some, like ours, reported a slight decrease in acorn production by very large oaks (Downs and McQuilken 1944, Goodrum et al. 1971). Thus, we suggest that crown area is the biggest determinant of acorn production. The apparent decline in acorn production for larger diameter trees may be a function of the competition for limited space in the canopy. This results in trees that continue to increase in dbh without a corresponding increase in crown area, thus changing the relationship between diameter and crown area, and creating the negative (but very small) quadratic term in the equations. This could help explain the large variance in acorn production estimates at the larger dbh range. A greater sample size of large-dbh oaks would help explain this relationship.

Our models applied acorn production per unit (m^2) crown area to crown areas that were predicted from tree dbh. Because the crown diameter equations used the independent variable (dbh) to calculate crown area (Bechtold 2003), this

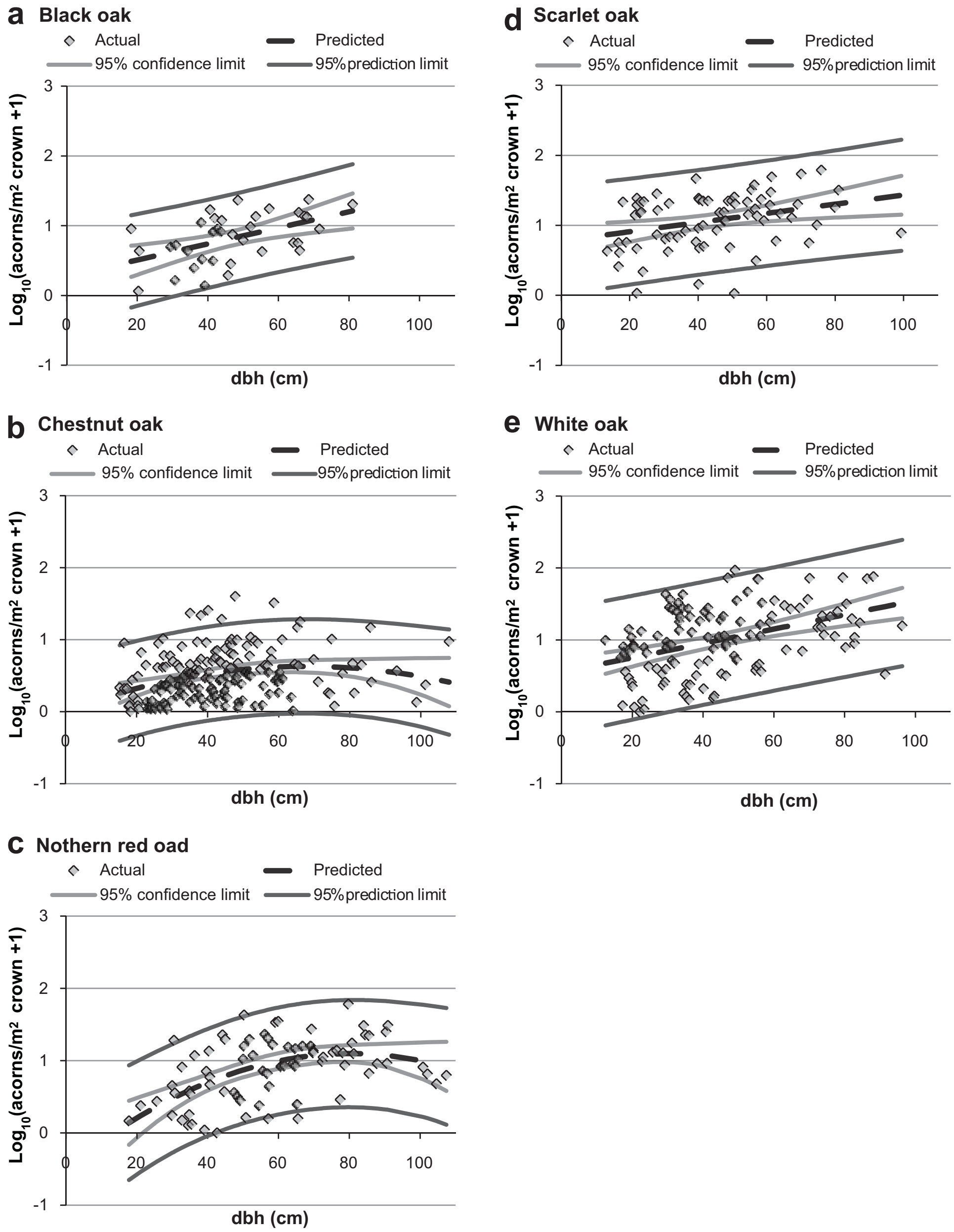

Figure 3. Predicted and actual (2000–2009) number of acorns produced per m^2 crown with 95% confidence intervals for five common oak species of the southern Appalachians. Species are (a) black oak, (b) chestnut oak, (c) northern red oak, (d) scarlet oak, and (e) white oak.

appears to create additional multicollinearity. In other words, we modeled 1 relationship (crown area) in order to model a different relationship (acorn production) based on the same x-variable (dbh). We recognize this, but believe it was appropriate because crown area is the limiting factor for the number of acorns an individual tree can produce. In addition, individual crown area measurements introduce yet a different source of error, as they are irregularly shaped and difficult to measure with accuracy. Finally, land managers are unlikely to obtain actual crown measurements because of the time and effort required, especially where measurements of multiple trees per species are required. Our approach provides a standardized method for estimating crown area and thus acorn production, based on an easily obtained metric (dbh) and provides the simplest and most time-efficient tool for land managers to estimate acorn production at a large scale.

Because acorn production is largely a function of crown area, land managers may wish to maximize oak crown area when selecting residual oak trees for silvicultural prescriptions. Crown area-dbh curves (Bechtold 2003) indicate that the same total crown area can be achieved either by selecting fewer large-dbh oak trees or more, smaller-dbh dominant or codominant oak trees. For example, 1.6 60-cm dbh northern red oak trees would (on average) provide the same crown area as 1.0 80-cm dbh tree, and 2.4 60-cm dbh trees would provide the same crown area as 1.0 100-cm tree (Fig. 4). The number of smaller trees needed to provide the same crown area as fewer larger trees differs among oak species with the crown area–dbh relationship (Fig. 4). Retention of

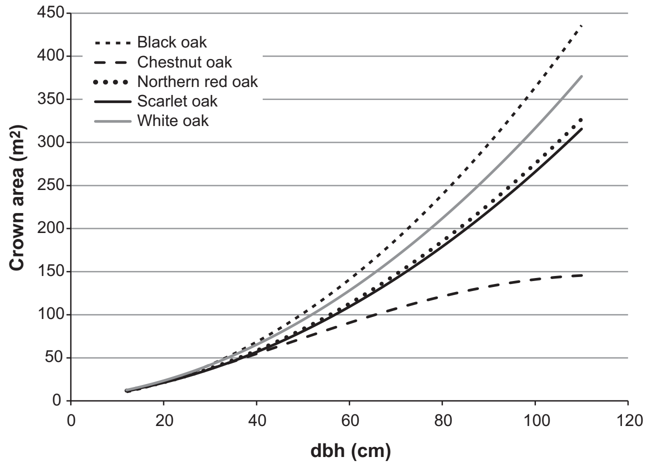

Figure 4. Predicted crown area by diameter at breast height (based on equations in Bechtold 2003) for five common oak species of the southern Appalachians.

more, smaller-diameter oaks rather than fewer large-diameter oaks increases the probability that at least some of the trees will produce acorns in any given year, and permits a wider spatial distribution of acorn production potential across the forest landscape. In addition, large-dbh oak trees may have a greater probability of dying than smaller-dbh trees, and acorn production could be impacted more if those (fewer) trees died. Further, smaller-dbh trees will eventually grow into larger-dbh trees with larger crowns, and likely produce acorns over a longer time span. Given the high variability in acorn production among individual trees, maximizing total crown area of oaks will maximize acorn production per total basal area only if trees that reliably produce acorns are selected for retention (Healy et al. 1999).

We developed our equations based on oak trees sampled within the Pisgah National Forest in the southern Appalachian Mountains of western North Carolina. The extent to which models are spatially transferable is an important consideration in their applicability. Previous studies demonstrate broad synchrony in acorn production patterns in the central and southern Appalachians (Fearer et al. 2008). Climatic patterns that influence acorn production (e.g., April temperature, July precipitation) also have similar spatial patterns in this region (Fearer et al. 2008), and other studies have noted such consistency in climatic patterns across very broad geographic regions (Koenig 2002). Given these similar patterns in both acorn production and climate, we suggest that these models are applicable to the central and southern Appalachian Mountains (West Virginia and western Maryland south through northern Georgia), and possibly throughout the eastern United States where these species occur. However, we acknowledge that their transferability needs to be quantitatively assessed to provide more precise guidance on applicability beyond the southern Appalachians.

MANAGEMENT IMPLICATIONS

Our potential acorn production models provide a simple and efficient planning tool that can be used to estimate potential average annual acorn production by five common eastern oak species at multiple spatial scales, and tailored to different forest management scenarios. Our predictive equations, based on long-term data, can be applied to forest inventory data that includes estimates of oak densities by species and the dbh of $\geq$60 randomly selected oaks per species to ensure accuracy and precision. These models can be applied at the stand- or landscape-level where a sufficient number ($\geq$60 per species) of oaks occur; accuracy will likely improve with larger areas containing a greater number of oak trees. The influence of within-year acorn crops on wildlife populations, oak regeneration, and forest ecology cannot be overlooked, but are difficult to predict for future years because of the irregularity of acorn production and the influence of weather variables. Within-year acorn crop estimation can be obtained by annual hard mast indices (Greenberg and Warburton 2007), but are not addressed in our models. Instead, our models predict potential average annual (over the long-term) acorn production by several oak species, in unharvested forests or under various levels of oak tree retention. Land managers can also use these models to predict changes in average acorn production in relation to stand dynamics over broad temporal scales, as densities of dominant or codominant oaks decrease, dbh increases, and the dbh-crown area ratios change with maturation.

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