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ecology

Forecasting Long-Term Acorn Production with and without Oak Decline Using Forest Inventory Data

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Acorns are important as wildlife food and for oak regeneration, but production is highly variable, posing a challenge to forest managers targeting acorn production levels. Forest managers need tools to predict acorn production capability tailored to individual landscapes and forest management scenarios, adjusting for oak mortality and stand development over time. We implemented published predictive models of average annual acorn production by five oak species common to the eastern United States in the Forest Vegetation Simulator (FVS) and used forest inventory data to estimate long-term acorn production on the Bent Creek Experimental Forest watershed, with and without oak decline. Under a no-management scenario, simulations forecasted a 58% increase in average annual acorn production by 2062 without oak decline but a 17% decrease with oak decline. Forecasts were influenced by the initial abundance and basal area of different oak species on the landscape and stand dynamics over time. Simulations indicated that heavy oak mortality with regeneration failure could substantially affect acorn production over the long term by reducing the proportion of mature canopy oaks and relative abundance of oak species. FVS ACORN provides a powerful tool for long-term acorn production planning that can be tailored to individual landscapes and forest management scenarios to predict average annual number and mass of acorns.

Keywords: acorn, Forest Vegetation Simulator, hard mast, oak decline, upland hardwood forest

Acorn production concerns land managers and researchers because of the far-reaching influence of acorns on wildlife species and forest ecology. Acorns are the primary source of oak (*Quercus*) regeneration (Loftis and McGee 1993), and crop size has been linked to survival and recruitment of wildlife populations ranging from migratory birds to black bear (*Ursus americanus* Pallas) (Rodewald 2003, Clark et al. 2005). Acorns are considered a keystone to biological diversity (Wolff 1996) because of their influence on populations of rodents, an important prey base for raptors and carnivores, and on populations of white-tailed deer (*Odocoileus virginianus* Zimmermann) that in turn alter forest structure and composition through browsing (Feldhamer 2002).

Acorn production is highly variable among years, oak species, locations, and individual trees, posing a challenge to forest managers targeting specific acorn production levels (Greenberg and Parresol 2002, Fearer et al. 2008, Lashley et al. 2009). Numerous methods have been developed to index or rank acorn crop size (e.g., Greenberg and Warburton 2007). Hard mast indices based on annual visual surveys of acorn production (e.g., Whitehead 1969, Koenig et al. 1994) can provide a ranking of within-year acorn crop size at a broad scale and are useful for comparing relative crop size among years, species, and locations. Some studies report correlations of acorn crop size to spring oak flower abundance (Feret et al. 1982) or spring temperature and summer drought (Sork et al. 1993). Each of these methods is time-consuming and limited to within-year estimates of acorn production (Greenberg and Warburton 2007).

Methods to predict within-year crop sizes are further limited by their inability to provide an estimate of the actual number or mass of acorns that can potentially be produced on a landscape. Regardless of crop size in any given year, potential or average annual acorn production on a given unit of forestland is dictated by the number, species, and size of oak trees occurring within that specific area. Clearly, planning for sustained acorn production must focus on landscape-level estimates of long-term average acorn production potential rather than on amounts produced in a particular year or location.

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Long-term estimates of acorn production are influenced by forest dynamics that include establishment, growth, and mortality of oaks and, consequently, continuous change in acorn production potential. Complex, mountainous topography ranging from moist north-facing slopes or coves to subxeric south-facing slopes or ridgetops influence distribution and abundance of different oak species and site quality that affects growth and recruitment patterns (McNab 2010). Over time, active forest management such as timber harvest or intermediate stand management creates complex landscapes with stands of different age classes, tree sizes, and abundance of different oak species (Loftis et al. 2011).

Oak decline is a particular concern for land managers or forest planners when planning for a sustained oak component and acorn production levels. Drought is the most common inciting factor in oak decline, whereas advanced tree age and low site quality are considered predisposing factors. Opportunistic organisms such as armillaria root fungi (*Armillaria mellea*) or bark beetles (Starkey et al. 1989, 2004, Oak et al. 2004) are believed to contribute to already-declining trees. Declining trees first show foliage wilt and browning followed by progressive branch dieback in the middle and upper crown. Trees eventually die if crown dieback continues. Greenberg et al. (2011) reported a 0.5% annual oak decline mortality rate of mature, tagged oak trees within the Bent Creek Experimental Forest (BCEF) watershed, with disproportionately higher mortality rates in scarlet oak. The dominance of mature oaks, the prevalence of low-quality sites, and other stress factors across much of the southern United States have caused large areas to be affected by oak decline (Heitzman et al. 2007) and others to remain vulnerable (Oak et al. 2004).

Forest managers would benefit from tools to predict acorn production capability that can be tailored to individual landscapes and forest management scenarios and include adjustments for oak recruitment, tree growth, and mortality over time. We implemented published predictive models of potential average annual acorn production by five common eastern oak trees (Rose et al. 2012) into the Forest Vegetation Simulator (FVS), and used forest inventory data from the Bent Creek Experimental Forest watershed to estimate production at the landscape level over 50 years, with and without oak decline. We hypothesized that average annual acorn production would differ among oak species due to differences in their relative abundance and rates of growth, recruitment, and mortality and that oak decline would result in decreasing acorn production over time.

Methods

Study Area

The BCEF encompasses a 2,250-ha watershed in western North Carolina (35.5°N, 82.6°W) within the Pisgah Ranger district of the Pisgah National Forest. It is one of 79 experimental forests and ranges nationwide, maintained by the USDA Forest Service for conducting research (Adams et al. 2004). The BCEF was established in 1925 to investigate silvicultural methods for managing and regenerating exploited and unproductive forests of the southern Appalachians. Since its establishment, the majority of the BCEF forest has undergone managed disturbances for research studies in forestry. In addition, severe wind disturbance events, such as the remnants of Hurricane Opal in 1995 (Greenberg and McNab 1998, McNab et al. 2004) and Hurricanes Ivan and Frances in 2004 (Greenberg et al. 2011) have periodically caused substantial tree blowdowns throughout the BCEF.

Annual precipitation averages 800 mm and is evenly distributed year-round. Winters are short and mild; summers are long and warm. Elevation ranges from 650 to 1,070 m. Species composition is typical of the upland hardwood forests of the southern Appalachian Mountains. Common tree species on subxeric sites include scarlet oak (*Quercus coccinea* Meunchh.), chestnut oak (*Quercus prinus* L.), black oak (*Quercus velutina* Lam.), blackgum (*Nyssa sylvatica* Marsh.), sourwood (*Oxydendrum arboreum* [L.] DC.), and occasional shortleaf pine (*Pinus echinata* Miller) and pitch pine (*Pinus rigida* Miller). Tulip poplar (*Liriodendron tulipifera* L.) and northern red oak (*Quercus rubra* L.) dominate moist slopes and coves. Red maple (*Acer rubrum* L.), hickory (*Carya* spp.), dogwood (*Cornus florida* L.), and white oak (*Quercus alba* L.) are present on all sites (McNab et al. 2004).

Oak Inventory Data

From 2003 to 2007 we established a grid of 44 permanent, 12.6-m radius (0.05 ha) vegetation inventory and monitoring plots. The grid was placed using a random starting point, and plots were spaced at 800 $\times$ 800 m throughout the BCEF (Figure 1). Two plots were identified as nonforested and omitted from analyses. For each plot, species and dbh were recorded for all trees $\geq$10 cm dbh and $\geq$1.3 m tall in the 12.6-m radius plot. In addition, we established two 3.6-m radius (0.004 ha) subplots nested within the larger plot (Figure 2) to quantify tree regeneration, including seedlings, saplings, and stump sprouts. Trees $<$10 cm dbh were tallied by species in five size classes ($<$0.3 m height, 0.3–$<$0.6 m height, 0.6–$<$0.9 m height, 0.9–$<$1.2 m height, and 1.2 m height and $<$3.8 cm dbh). We measured dbh for trees of 3.8–$<$10.0 cm dbh. Only the dominant stem for each cluster of stump sprouts was tallied. At each plot center we measured slope, aspect, and elevation using a digital elevation model with global positioning system (GPS) coordinates. Upland oak site index, base age 50 (Carmean et al. 1989), was estimated from species composition using a moisture regime index (McNab 2010); stand age was estimated using top height (average height of the largest 98.8 trees/ha as defined by dbh) and the estimated site index. Summary BCEF stand inventory data used in FVS are presented in Table 1.

Acorn Prediction Models

We used acorn production prediction models developed by Rose et al. (2012). These models used 10 years of acorn trapping data from 475 dominant and codominant oak trees in the southern Appalachians to develop predictive models of average annual hard mast production for five common eastern oak species: black oak, scarlet oak, chestnut oak, northern red oak, and white oak. Acorns were collected in three or more 0.46 m^2 traps placed beneath each tree crown. The number of acorns produced per m^2 crown was estimated each year based on the average number of acorns per trap for each tree. Individual tree crown areas were calculated from dbh using crown-diameter equations developed for each oak species (Bechtold 2003) and calculating circular crown areas. They developed the following linear regression equations for predicting the average annual number of acorns produced per tree using dbh as the independent variable and a quadratic term (dbh^2) as a second independent variable when significant (Rose et al. 2012):

1. Black oak: $\log_{10}(Y + 1) = 1.06367 + 0.03123(\text{dbh})$.

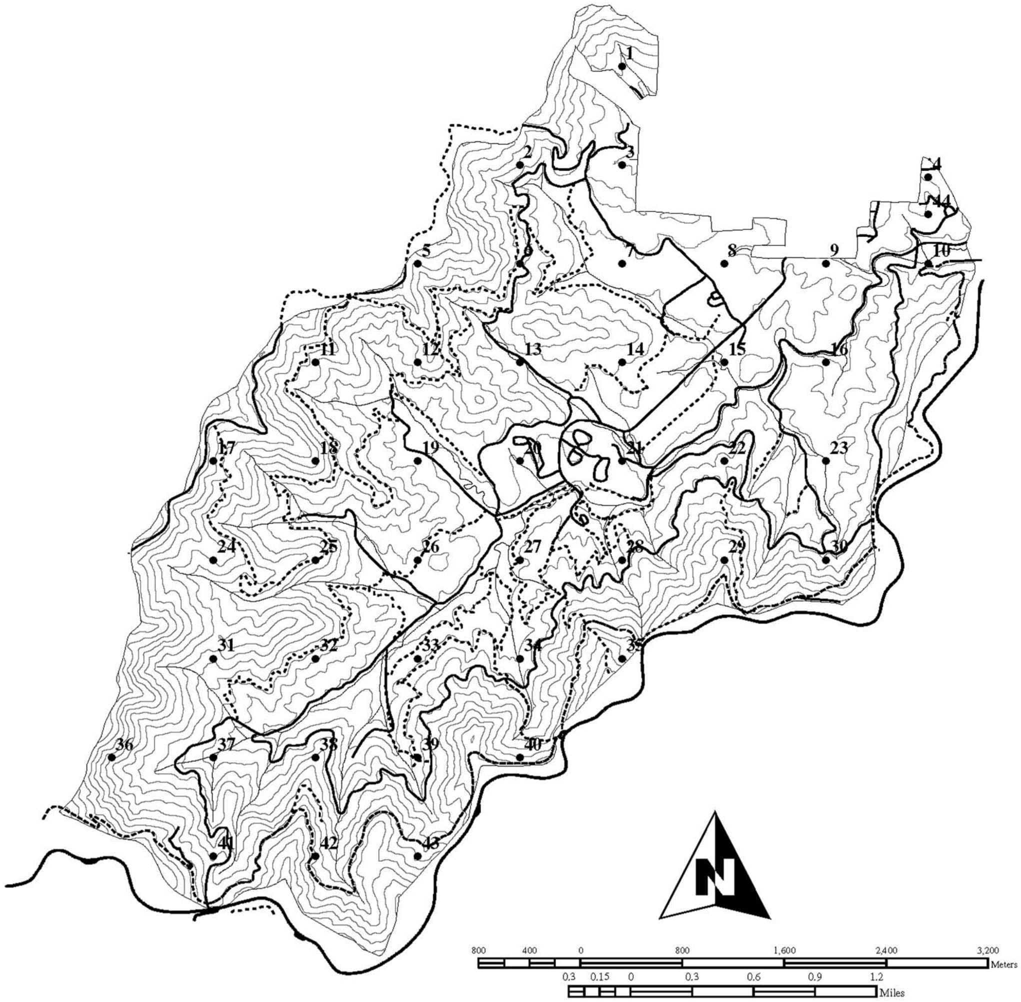

Figure 1. Location of forest inventory and monitoring plots spaced in an 800 × 800-m grid in the Bent Creek Experimental Forest, North Carolina, USA.

2. Chestnut oak: $\log_{10}(Y + 1) = 0.20984 + 0.06029(\text{dbh}) - 0.00039431(\text{dbh}^2)$.
3. Northern red oak: $\log_{10}(Y + 1) = -0.14836 + 0.07539(\text{dbh}) - 0.00039950(\text{dbh}^2)$.
4. Scarlet oak: $\log_{10}(Y + 1) = 1.16744 + 0.05158(\text{dbh}) - 0.00026797(\text{dbh}^2)$.
5. White oak: $\log_{10}(Y + 1) = 0.71155 + 0.06346(\text{dbh}) - 0.00034290(\text{dbh}^2)$.

where Y is the acorn production in number of acorns per tree.

FVS Modeling

The FVS is the nationally supported growth-and-yield modeling system of the USDA Forest Service. FVS is a semi-distance-independent, individual tree growth model with geographically specific variants containing localized growth, mortality, and regeneration models (Dixon 2002, Crookston and Dixon 2005). Forest stand inventories are input into FVS and projected forward for up to 40 growth cycles. Random growth variation is added to simulations through the addition of a random deviate based on the distribution of errors associated with the diameter increment model and is explained in detail in Dixon (2002). Probabilistic disturbance events (abiotic and biotic) that affect growth and survival of trees may also be added to FVS through the use of model modifiers and a random number generator in the Event Monitor (EM). The EM may also be used to conditionally schedule events and compute complex structural statistics not found in standard FVS output files.

When upland hardwood stands in the southern Appalachians are simulated, it is important to include the potential loss of oaks due to oak decline. An oak decline probability/risk system is simulated in FVS via the Oak Decline EM, mountain version (Courter 2005). This add-on to FVS estimates the probability of an oak decline event, and if a random number draw is less than the probability, the effects of oak decline are simulated. Oak decline risk is based on stand age, site quality, condition, slope, and species composition.

We added acorn production prediction models (Rose et al. 2012) to FVS as an EM function (April 2012 software release). The function, called ACORNS, returns the average number or mass of acorns per ha per year for any or all of the five oak species mentioned above (FVS computes values in English empirical units; we converted the outputs to metric for these analyses). Acorn production is computed for dominant and codominant trees, defined in FVS as trees greater than the 60th percentile tree for the height distribution, and having dbh ≥12.7 cm (Rose et al. 2012). The number of acorns is adjusted for logarithmic back transformation bias (Beauchamp and Olson

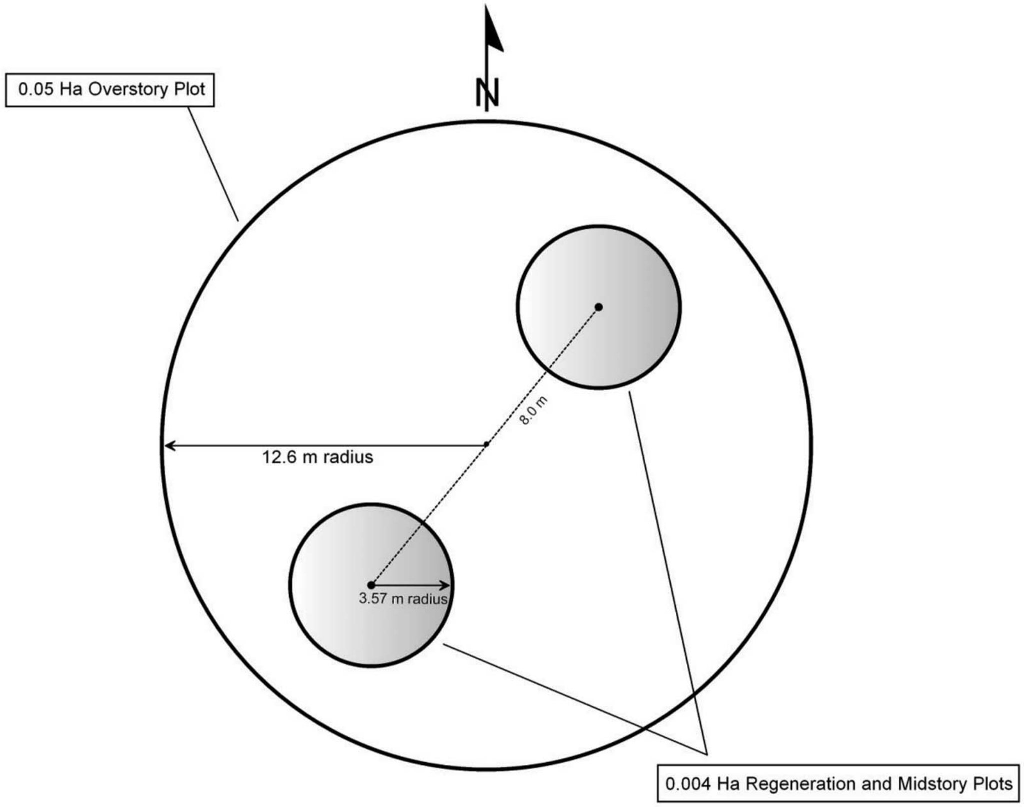

Figure 2. Plot design for tree and regeneration inventory and monitoring used in FVS to forecast average annual acorn production on the Bent Creek Experimental Forest, North Carolina, USA.

Table 1. Density for total oak, five oak species, and nonoak tree regeneration (seedlings and saplings <12.7 cm dbh), density and basal area of pole-size (12.7–<30.5 cm dbh) and mature trees (≥30.5 cm dbh), stand age, and site index from 2007 plot inventory of Bent Creek Experimental Forest, used in FVS ACORN to forecast long-term acorn production with and without oak decline.

	Regeneration		Pole-size trees		Mature tree	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Density (trees/ha)						
Total oak	747.6 ± 204.7	0.0–6,490.1	66.8 ± 10.8	0.0–320.5	50.1 ± 6.3	0.0–160.3
Chestnut oak	77.6 ± 34.0	0.0–1,018.5	25.8 ± 5.8	0.0–180.3	21.0 ± 5.0	0.0–120.2
Scarlet oak	75.2 ± 24.4	0.0–624.0	8.6 ± 3.0	0.0–80.1	10.5 ± 2.8	0.0–60.1
Northern red oak	300.6 ± 100.1	0.0–2,995.4	5.7 ± 2.1	0.0–60.1	7.6 ± 2.2	0.0–60.1
Black oak	140.1 ± 44.4	0.0–1,123.3	5.2 ± 1.8	0.0–60.1	3.3 ± 1.4	0.0–40.1
White oak	153.9 ± 88.1	0.0–3,619.5	21.5 ± 6.4	0.0–220.3	7.6 ± 2.2	0.0–60.1
Nonoak	2,832.0 ± 518.3	0.0–12,271.4	244.2 ± 19.9	40.1–580.9	57.2 ± 8.7	0.0–260.4
Total trees	3,579.6 ± 651.1	0.0–15,346.9	311 ± 21.6	40.1–641.0	107.3 ± 8.2	0.0–260.4
Basal area (m^2/ha)						
Total oak			2.7 ± 0.4	0.0–12.4	8.3 ± 1.1	0.0–26.9
Chestnut oak			1.1 ± 0.3	0.0–8.2	3.4 ± 0.9	0.0–21.7
Scarlet oak			0.3 ± 0.1	0.0–2.3	1.5 ± 0.4	0.0–9.6
Northern red oak			0.2 ± 0.1	0.0–2.3	1.5 ± 0.5	0.0–15.1
Black oak			0.2 ± 0.1	0.0–2.6	0.5 ± 0.2	0.0–6.5
White oak			0.9 ± 0.2	0.0–7.7	1.4 ± 0.4	0.0–8.9
Nonoak			7.4 ± 0.7	1.4–19.3	7.5 ± 1.3	0.0–37.5
Total trees			10.0 ± 0.7	1.7–20.6	15.8 ± 1.4	0.0–38.1
Stand age (yr)					72.8 ± 3.9	23.0–138.0
Stand site index (m height at age 50)					20.6 ± 0.6	14.9–32.3

1973). FVS calculates acorn mass by multiplying the number of acorns by the average mass of acorns as listed in the seed catalog by the F.W. Schumacher Company, Inc. (2013).

We used the Southern variant of FVS (Keyser 2008) to grow the 2007 BCEF inventory data to 2012 and project stand development (growth and mortality) for the next 50 years (2012–2062) without active management (for details on FVS models, see Dixon 2002). We simulated each plot 60 times; 30 without and 30 with oak decline and computed average oak density and basal area per ha across all simulations and all plots. In addition, average annual acorn numbers and weight were computed for each of the five species found in Equations 1–5.

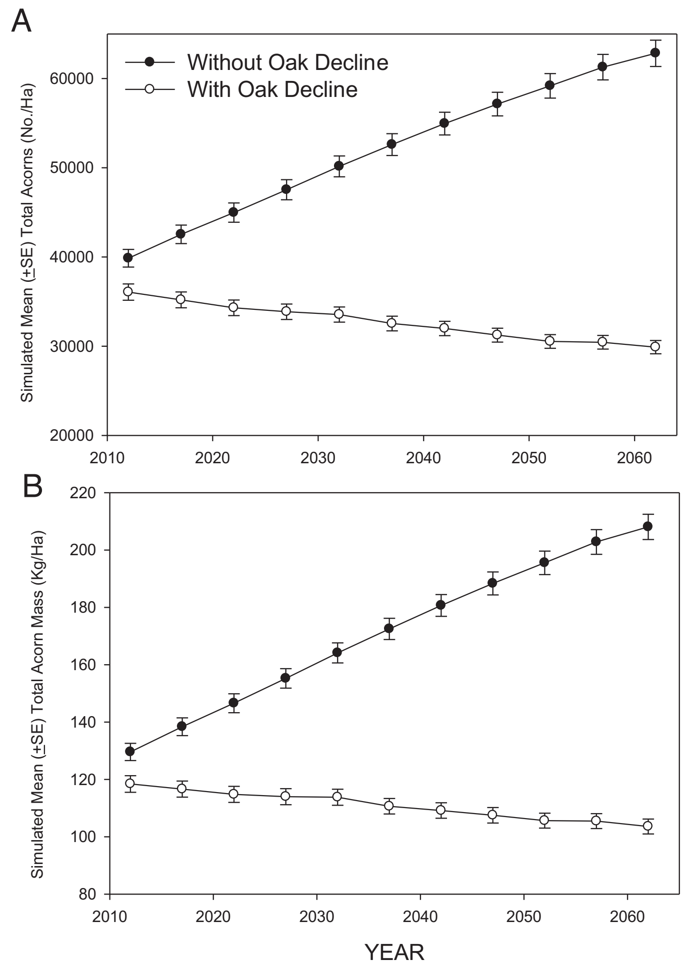

Figure 3. Forecasted (2012–2062) average (±SE) annual (A) total number of acorns/ha and (B) total acorn mass (kg/ha), generated by FVS with and without oak decline events using forest inventory and monitoring plots from the Bent Creek Experimental Forest, North Carolina, USA.

Results

Simulations without Oak Decline

Under a no-management scenario, FVS simulations without oak decline forecasted a substantial, steady increase of 58% (from 39,859 to 62,829 acorns/ha) in average total annual number of acorns (Figure 3A) and 61% in average total annual acorn mass (130–208 kg/ha) (Figure 3B) between 2012 and 2062 in the BCEF watershed. Initially, white oak and scarlet oak showed the highest average annual number (14,510 and 13,373 acorns/ha, respectively) and mass (43 and 29 kg/ha, respectively) compared with northern red oak (5,791 acorns/ha and 26 kg/ha) or chestnut oak (4,578 acorns/ha and 17 kg/ha); black oak showed the lowest production (1,608 acorns/ha and 4 kg/ha) (Figure 4A and B). Simulated average annual number and mass of acorns by all five species increased from 2012 to 2062, with the steepest increases in northern red oak (115%) and black oak (169%) and more gradual increases in chestnut oak (24%), scarlet oak (44%), and white oak (46%) (Figure 4A). Because of the heavier weight of northern red oak acorns, the northern red oak mass surpassed that of scarlet oak (Figure 4B). Despite a large increase in total acorn production over the 50-year simulation period, the relative contribution of each oak species to total average annual number and mass of acorns produced remained relatively constant (Figure 4A and B).

The initial (2012) simulated average density and average basal area of acorn-producing size oak trees (defined in FVS as trees more than the 60th percentile tree for the height distribution and dbh ≥12.7 cm; see Methods) without oak decline was 109 trees/ha and 12 m^2/ha, respectively, and included chestnut oak (42 trees/ha and 5 m^2/ha), white oak (29 trees/ha and 2 m^2/ha), scarlet oak (18 trees/ha and 2 m^2/ha), northern red oak (12 trees/ha and 2 m^2/ha), and black oak (8 trees/ha and 1 m^2/ha). Total oak density decreased steadily for the first 25 years, followed by a steep increase for the next 20 years, resulting in a negligible net change in total density between 2012 and 2062 (Figure 5A). In contrast, total oak basal area increased steadily each decade, resulting in a 29% increase between 2012 and 2062 (Figure 5B). Simulated density of chestnut oak, scarlet oak, and white oak trees decreased steadily over the 50-year period, ending with 32, 55, and 36%, respectively, fewer trees in 2062 than in 2012 (Figure 6A). In contrast, density of northern red oak and black oak remained relatively steady for the first 25 years, followed by a sharp increase over the next 20 years, resulting in a net increase of 172 and 151%, respectively, between 2012 and 2062 (Figure 6A). Basal area of each species increased slowly but steadily over the 50-year period, with smaller increases by chestnut oak (19%), scarlet oak (13%), and white oak (15%) and relatively greater increases by northern red oak (72%) and black oak (76%) between 2012 and 2062 (Figure 6B). These changes resulted in decreased relative abundance (proportion of total oak) of chestnut oak (29%), scarlet oak (8%), and white oak (18%) and greater relative abundance of northern red oak (34%) and black oak (20%) in 2062 than in 2012. Despite a large increase in total oak basal area, the relative contribution of each species to total basal area remained similar from 2012 to 2062.

Simulations with Oak Decline

Under a no-management scenario FVS simulations with oak decline forecasted a slow decrease of 17% (36,067 to 29,892 acorns/ha) in total number of acorns (Figure 3A) and 13% decrease in average annual mass (118 to 104 kg/ha) between 2012 and 2062 (Figure 3B) in the BCEF watershed. Initially, white oak and scarlet oak showed the highest average annual number (13,135 and 11,470 acorns/ha, respectively) and mass (43 and 17 kg/ha, respectively) compared with northern red oak (5,674/ha and 26 kg/ha) or chestnut oak (4,353 acorns/ha and 17 kg/ha) and black oak produced the least (1,435 acorns/ha and 4 kg/ha) (Figure 4C and D). Simulated average annual number and mass of acorns produced by all five species decreased from 2012 to 2062 for chestnut oak (27%), scarlet oak (49%), and white oak (12%) but increased for northern red oak (29%) and black oak (37%) (Figure 4C and D). Forecasted change in total and northern red oak average annual acorn production was most evident during the first 20 years and then leveled off. In contrast, forecasted decline in acorn production by scarlet oak was relatively steep for the 50 years simulated. Despite some decrease in total acorn production over the 50-year simulation period, the relative contribution of chestnut oak, black oak, and white oak to total average annual number or mass of acorns remained relatively constant. In contrast, the relative contribution of scarlet oak dropped from 32% of total acorns produced in 2012 to 19% of total in 2062 and from 24 to 14% of total mass, whereas the relative contribution of northern red oak to total acorns produced increased from 16% in 2012 to 25% in 2062 and from 22 to 32% of total mass (Figure 4C). Increased production of heavier northern red oak acorns partially

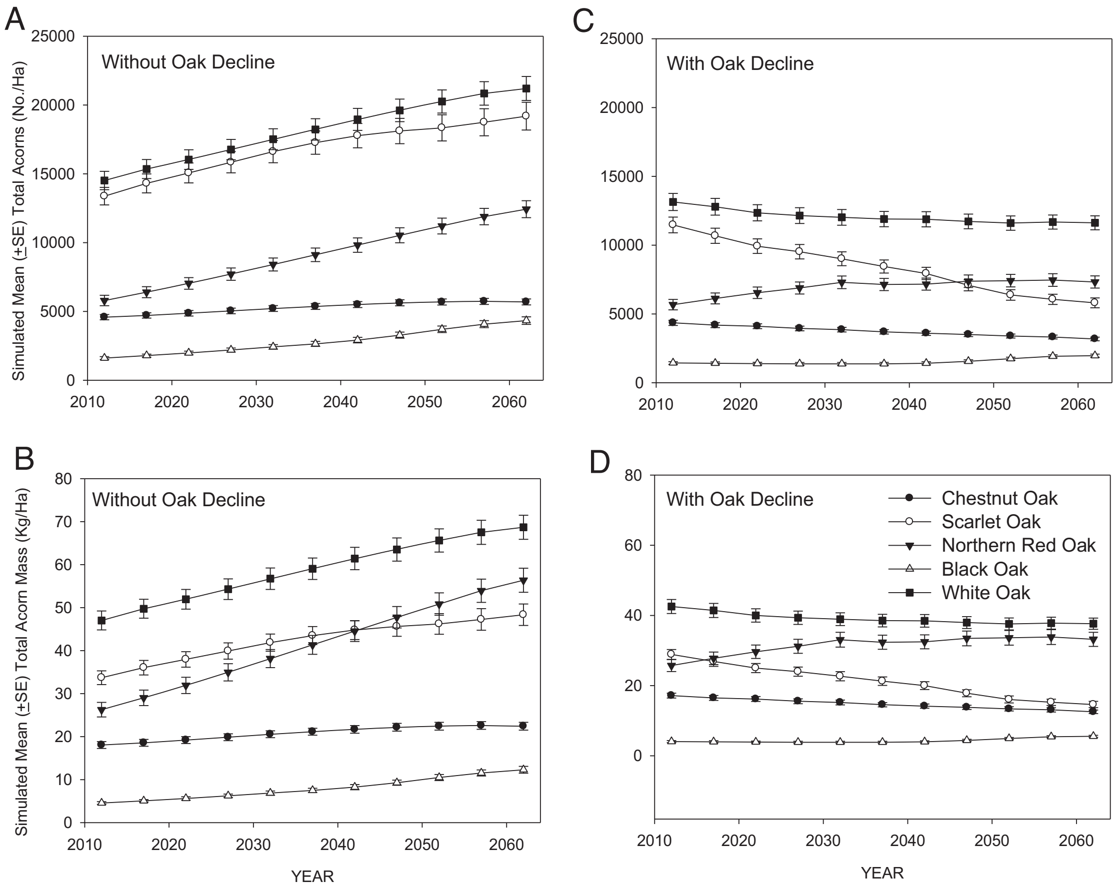

Figure 4. Forecasted (2012–2062) average (±SE) annual total (A) number of acorns/ha and (B) acorn mass (kg/ha) produced without oak decline and (C) number of acorns and (D) acorn mass produced with oak decline for chestnut oak, scarlet oak, northern red oak, black oak, and white oak, generated by FVS using forest inventory and monitoring plots from the Bent Creek Experimental Forest, North Carolina, USA.

compensated for reduced production of (lighter) scarlet oak acorns (Figure 4D).

The initial (2012) simulated average density and average basal area of acorn-producing size oak trees (defined in FVS as trees more than the 60th percentile tree for the height distribution and dbh ≥12.7 cm; see Methods) with oak decline was 101 trees/ha and 11 m^2/ha, respectively and included chestnut oak (40 trees/ha and 4 m^2/ha of total density and basal area, respectively), white oak (26 trees/ha and 2 m^2/ha), scarlet oak (16 trees/ha and 2 m^2/ha), northern red oak (12 trees/ha and 2 m^2/ha), and black oak (7 trees/ha and 1 m^2/ha) (Figure 5A and B). Total oak density decreased steadily for the first 25 years, reaching a low of 57 trees/ha, followed by an increase and ending with 72 trees/ha, about 30% fewer than in 2012 (Figure 5A). Total oak basal area decreased steadily each decade, ending in 2062 with 8 m^2/ha, about 26% less than in 2012 (Figure 5B). Simulated density of chestnut oak, scarlet oak, and white oak trees decreased over the 50-year period, ending with 53, 83, and 56%, respectively, fewer trees in 2062 than in 2012 (Figure 6C). In contrast, the density of northern red oak and black oak increased sharply beginning in about 2042 and ending with 100 and 98% higher tree densities in 2062 than in 2012, respectively (Figure 6C). The basal area of chestnut oak, scarlet oak, and white oak decreased by 30, 60, and 29%, respectively, whereas the basal area of northern red oak increased 11%, and black oak basal area did not change between 2012 and 2062 (Figure 6D). Uneven changes in the density and basal area of the five species resulted in changes to relative abundance from 2012 to 2062. Chestnut oak, scarlet oak, and white oak decreased from 40 to 26%, 16 to 4%, and 26 to 16% of total oak abundance, respectively, whereas northern red oak and black oak increased from 12 to 34% and 7 to 20% of total oak abundance, respectively, between 2012 and 2062. The proportion of chestnut oak, white oak, and black oak basal area to total basal area remained relatively constant (±2% or less) but decreased from 16 to 9% for scarlet oak and increased from 17 to 25% northern red oak between 2012 and 2062.

Discussion

Our acorn production forecasts for the BCEF watershed emphasized the importance of incorporating temporal stand dynamics including growth, mortality, and recruitment of oaks into long-term planning for acorn production. Our simulations under a no-management scenario indicated that in the absence of oak decline, total acorn production increased substantially over 50 years, but changes in acorn production were not uniform among the five oak species. Forecasts of total acorn production were heavily influenced by the initial relative abundance and basal area of different oak species on the landscape and differences in growth and mortality rates among them. Sharp increases in the density of total acorn-producing oak trees and especially of northern red oak and black oak after 2040 may also be an artifact of our size and (or) height criteria used to define an oak of acorn-producing size, as FVS projected growth over time. Forecasted increases in the density and basal area of northern

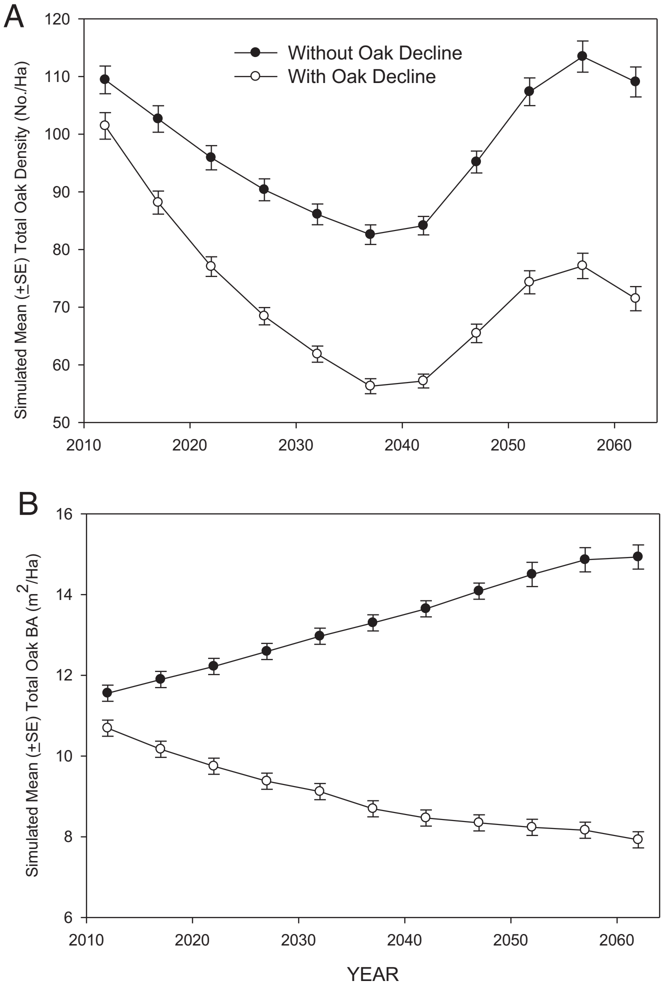

Figure 5. Forecasted (2012–2062) average (±SE) annual total (A) density (trees/ha) and (B) basal area (m^2/ha) of acorn-producing size oak trees (defined in FVS as trees more than the 60th percentile tree for the height distribution and dbh ≥12.7 cm), including chestnut oak, scarlet oak, northern red oak, black oak, and white oak species combined, generated by FVS with and without oak decline events using forest inventory plots from the Bent Creek Experimental Forest, North Carolina, USA.

red oak resulted in increased northern red oak acorn production between 2012 and 2062. The heavier mass of northern red oak acorns further amplified its importance over time relative to that of other species, such as scarlet oak, which produced more, but lighter, acorns.

Abundance, distribution, size, growth, and mortality rates of different oak species are heavily influenced by topography and forest management (McNab 2010, Loftis et al. 2011), resulting in acorn production potentials that are unique to each landscape and changing continuously over time. The contribution of each oak species to total acorn production based on initial and forecasted changes in relative abundance and size and differences in their production capability indicates the importance of including forest inventory data and species-specific models in long-term planning for acorn production targets.

Contrasting results between simulations with and without oak decline further illustrate how acorn production is likely to be affected by heavy oak mortality that is unevenly distributed among the five species. Whereas simulations under a no-management scenario without oak decline forecasted a 58% increase in average annual acorn production by 2062, simulations with oak decline forecasted a 17% decrease. The steepest declines were seen in scarlet oak, which is most vulnerable to oak decline-related mortality (Oak et al. 2004), but production also declined for white oak and chestnut oak, and corresponded with decreasing density and basal area of those species. The disproportionately higher mortality of scarlet oak suggests that oak mortality is not uniform across the southern Appalachian landscape but is greater on low-quality sites such as subxeric ridgetops and where scarlet oaks are most abundant (Oak et al. 1996). Higher mortality in lower-quality subxeric sites could be offset by oak regeneration, which is more problematic on the higher-quality mesic sites (Dey 2002).

Simulations with oak decline highlight the management concern that heavy oak mortality with regeneration failure—the failure of oak seedlings or saplings to attain canopy status—could substantially affect acorn production over the long term by reducing the proportion of mature canopy oaks and relative abundance of oak species. Our results emphasize the importance of including oak decline scenarios in forecasting of acorn production, especially for higher-risk landscapes (Starkey and Oak 1989, Oak et al. 1996) with low site quality and abundant, aging scarlet oak.

Our acorn production forecasts highlight the need for forest management to promote successful oak regeneration to mitigate potential losses in mature oaks and acorn production, especially where oak decline is or may become a substantial problem. Forest management for successful oak regeneration is a greater challenge on intermediate- or high-quality sites than on low-quality sites (Dey 2002) and must be implemented several years before (Loftis 1990) or after (Brose et al. 1999) timber harvests. Management options including most intermediate and regeneration treatments may be designed within FVS to help managers predict acorn production capability under different forest management scenarios.

Our simulations are limited by the assumptions incorporated into FVS regarding stand dynamics and by our inability to predict (and thus incorporate) stochastic, large-scale disturbances. The mortality model in FVS is designed to reflect normal mortality rates (Dixon 2002) based on a small amount of background mortality and the approach to maximum stand density. Mortality caused by disturbance must be included via FVS extensions, EM addfiles, or keywords. Our results indicate that including oak decline disturbance dramatically increases oak mortality, especially in larger trees, resulting in reduced acorn production in the long term when sufficient oak regeneration is not present or able to successfully replace mature dead oaks.

Other stochastic disturbances common to the southern Appalachians, such as high-intensity wind events or ice storms, could also affect stand development and acorn production but were not included in our simulations. For example, 6.6% of mature, tagged oak trees were windthrown during three separate, hurricane-related wind events in 1995 (Greenberg and McNab 1998, McNab et al. 2004) and 2004 on the BCEF watershed (Greenberg et al. 2011). Windthrow-related mortality was disproportionately heavier in scarlet oak and was additional to mortality attributed directly to oak decline (Greenberg et al. 2011). Future climate change effects on upland hardwood forests in the southern Appalachians are uncertain, and average precipitation may not change substantially in the next 50 years (McNab et al. 2013). However, increased erratic weather patterns and increased drought events could exacerbate oak decline. We suggest that additional EM addfiles and keywords be

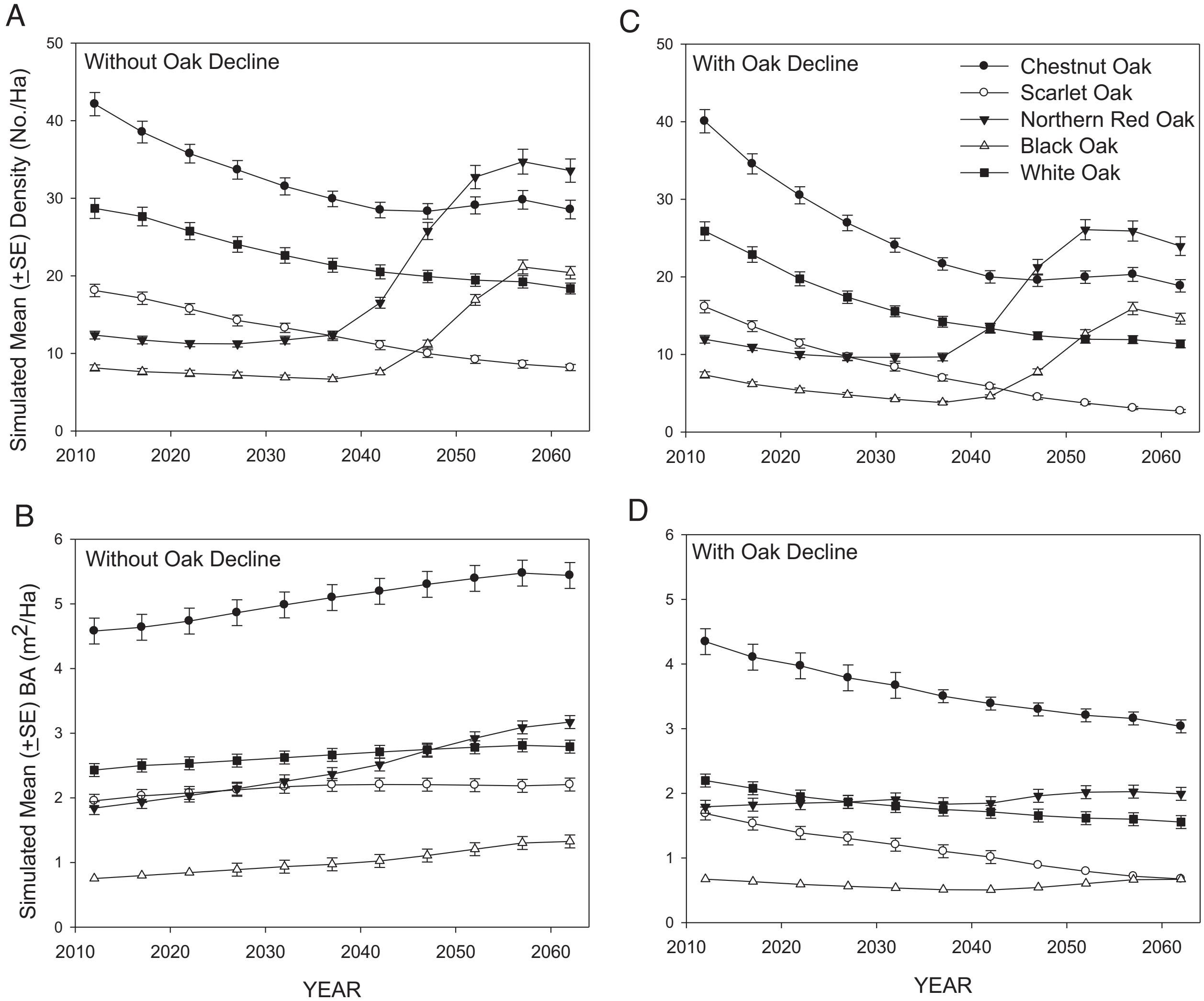

Figure 6. Forecasted (2012–2062) average (±SE) annual total (A) density (trees/ha) and (B) basal area (m²/ha) without oak decline and (C) density and (D) basal area with oak decline for acorn-producing size oak trees (defined in FVS as trees more than the 60th percentile tree for the height distribution and dbh ≥12.7 cm; see Methods), including chestnut oak, scarlet oak, northern red oak, black oak, and white oak, generated by FVS using forest inventory plots from the Bent Creek Experimental Forest, North Carolina, USA.

developed to model other common stochastic disturbances because of their potential effect on mature oak trees and acorn production in the short and longer term. Our model forecasts should be viewed as best case scenarios without inclusion of stochastic disturbances other than oak decline.

Our acorn production simulations provide estimates of long-term average acorn production potential under a no-management scenario based on the initial and projected number, species, and size of oak trees occurring within our study area. Land managers can use FVS with their own forest inventory data to tailor average acorn yield estimates to specific landscapes and forest management scenarios. However, because ACORN models in FVS are based on average acorn production (Rose et al. 2012), it is unlikely that estimates for any species or location within a given year will be accurate. Land managers wishing to gauge acorn crop size for a particular year will still need to conduct visual surveys to rank or index production. However, visual surveys are time-consuming and provide only a relative ranking of acorn crop size for a particular year, rather than quantitative estimates of the actual average number or mass of acorns that can potentially be produced on a given landscape over the long term (Greenberg and Warburton 2007).

Conclusion

The FVS ACORN function provides a powerful tool for long-term acorn production planning that can be tailored to individual landscapes and forest management scenarios to generate and forecast quantitative estimates of average acorn production capability. Oak species composition, abundance, and size are heavily influenced by topography and forest management, resulting in acorn production potentials that are unique to each landscape and changing continuously over time. The use of forest inventory data in the model allows acorn production estimates to adjust for current and projected oak abundance, distribution, size, growth, and mortality rates, combined with differences in average acorn production capacity among oak species.

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