Quantifying Potential Fruit Production by Three Common Clonal Shrub Genera in Eastern Hardwood Forests

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Abstract - Fruit crop-size estimates are little better than indices unless tied to plant abundance. We developed a "standardized fruit crop" (SFC) using 11 years of fruit-density data in replicated transects to estimate long-term average (versus within-year) production by *Vaccinium* spp. (blueberry), *Gaylussacia* spp. (huckleberry), and *Rubus* spp. (blackberry) if applied to shrub-area inventories. We sampled blueberry and huckleberry in mature forest where canopy cover and shrub area were constant, and blackberry—a "pioneer" shrub—in shelterwood harvests where light availability decreased with stand development. Annual average (±SE) blueberry SFC (fruits/m^2 shrub area) varied from 1.3 ± 0.9 to 18.8 ± 15.8; long-term (11-yr average) SFC (95% CIs) was 6.8 ± 1.8 (3.2–10.3). Annual average huckleberry SFC varied from 1.8 ± 1.3 to 19.8 ± 10.8; long-term average SFC was 11.6 ± 1.8 (8.0–15.3). In shelterwoods, blackberry shrub area and (disproportionately) SFC increased, peaked 3–6 years post-harvest, then declined with canopy closure. When only peak years were included, average blackberry SFC was 90.3 ± 11.3 (67.7–113.0) and is a more reliable estimate for high-light environments. Our SFCs cannot reliably predict crop sizes within any given year or area but provide a forest planning tool to estimate average (over the long-term) or potential fruit production that can be tailored to specific stands and landscapes by application to shrub-area inventories.

Introduction

Fleshy fruit or "soft mast" is an important food resource for both game and nongame wildlife species; most birds and mammals consume at least some fruit (Martin et al. 1961), and it is likely critical for birds during fall migration (Willson 1986) and for over-wintering birds when availability of arthropods is negligible (Greenberg and Forrest 2003, Whitehead 2003). Fleshy fruit provides an easily attainable source of energy and nutrition that can influence the health, survival, and population sizes of many vertebrate species (e.g., Borgmann et al. 2004, McCarty et al. 2002, Rogers 1976, Willson 1986). Clonal shrubs including *Vaccinium* spp. (blueberry), *Gaylussacia* spp. (huckleberry), and *Rubus* spp. (blackberry) are widespread across the temperate zone and contribute a large proportion of total fruit in eastern hardwood forests (Greenberg et al. 2007, Perry et al. 1999, Reynolds-Hogland et al. 2006). Because of fleshy fruit's importance to wildlife, managers and researchers have devoted much effort to qualitatively ranking (e.g., "poor" to "good"; Morris et al. 2024, Olfenbuttel 2023) or quantifying (e.g., Greenberg et al. 2007, 2012; Lashley et al. 2014; Mitchell and Powell 2003; Perry et al. 1999; Powell and

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Seaman 1990; Reynolds-Hogland et al. 2006) fruit crops of these important shrub genera. Such studies are difficult to compare due to differences in sampling protocols, reporting units (e.g., fruit counts; wet or dry weight of whole fruits or pulp only), or the summing of total fruits produced across genera. More importantly, most cannot adequately account for interannual variability in fruit crops (e.g., they were short-term studies) and/or directly tie fruit production to the coverage, or area of fruit-producing shrub genera across stands or landscapes.

The distribution and abundance of different fruit-producing shrub species—hence the potential for fruit production within a particular forest stand or landscape—is highly variable and heavily influenced by disturbance history and associated changes in light availability (Greenberg et al. 2007, 2011; Reynolds-Hogland et al. 2006). Studies suggest that blueberry and huckleberry crop sizes are lower under low-light conditions (e.g., mature forests) than in heavily disturbed sites with higher light availability, where they rapidly resprout from below-ground rhizomes (e.g., Matlack et al. 1993) and produce fruit (e.g., Greenberg et al. 2007, 2012; Perry et al. 1999; Reynolds-Hogland et al. 2006). In contrast, blackberry is a disturbance-adapted "pioneer" clonal shrub that is largely absent from closed-canopy forests. Blackberry rapidly colonizes recently disturbed sites with high light availability (e.g., clearcut and shelterwood harvests) from the seedbank (e.g., Graber and Thompson 1978, Keyser et al. 2012), proliferates, and produces abundant fruit within 3–5 years before declining within 7–10 years as shade increases with forest-stand development (e.g., Donoso and Nyland 2006, Mitchell and Powell 2003, Oliver and Larson 1996, Walters and Nyland 1989). Other factors such as topography and seed dispersal by birds and other vertebrates (Jordano 2000) influence the distribution and abundance of fruit-producing species, whereas weather variables such as spring freezes, drought, and precipitation patterns can contribute to interannual variation in fruit-crop sizes by affecting pollination and flower and fruit development (e.g., Benjamin and Winfree 2014, Dietz et al. 2021, Hicklenton et al. 2003, Rodrigo 2000, Selås 2000).

Spatial variation in the abundance of different fruit-producing shrub genera along with high interannual variability in fruit-crop sizes highlight the need to account for both shrub area and fruit density if quantitative (versus qualitative) estimates of fruit availability are desired. Within-year fruit production estimates require annual, labor-intensive fruit counts and are effectively no better than qualitative indices in estimating fruit availability unless they can be applied to the abundance of fruit-producing shrubs within a forest stand or landscape (see Lashley et al. 2014). Additionally, fruit counts conducted within 1 or a few years may not be typical of longer-term average fruit production.

We developed and applied a method to estimate average fruit production at stand and landscape scales using replicated, multi-year estimates of both shrub area and fruit density (fruits/m^2 shrub area; e.g., Greenberg 2020, Rose et al. 2012). Specifically, we employed 11 years of fruit production and shrub-coverage data to propose a simple and efficient planning tool that can be used to estimate average or potential fruit production by 3 common eastern clonal shrub genera—blueberry, huckleberry, and blackberry—at multiple spatial scales and tailored to their abundance across forest stands or landscapes. To control for possible within-genera differences in fruit production between shaded, closed-canopy forests and recently disturbed forests with heavily reduced canopy cover, we sampled blueberry and huckleberry only in mature forests, and blackberry was sampled only in young 2-age stands created by recent shelterwood regeneration harvests. Our objectives were to (1) provide estimates of annual standardized fruit crop (SFC; fruits/m^2 shrub area) and quantify the extent to which fruit crop sizes differ among years, and; (2) provide long-term (11-year) average SFC estimates for application to the coverage (m^2) of these clonal shrub genera to predict potential fruit production at the stand or landscape scale.

Methods

Study area

Our study was conducted in the Pisgah and Grandfather ranger districts of the Pisgah National Forest in Buncombe, Haywood, McDowell, and Transylvania counties, NC. Study sites were located across a wide range of topographic features including aspect, slope position, and percent slope; elevations varied from 500 to 1200 m. Average annual rainfall in the region (Asheville area, 2000–2016) was 119 cm (min–max: 85–191 cm; NOAA National Weather Service 2017). Soils were predominantly Dystrochrepts and Hapludults (Pittillo et al. 1998). Mature forest age was 80–100 years at study establishment. Forests were dominated by *Liriodendron tulipifera* L. (Yellow-Poplar), *Quercus rubra* L. (Northern Red Oak), *Magnolia* spp. (magnolia), *Fraxinus americanus* L. (White Ash), *Fagus grandifolia* Ehrh. (American Beech), (*Tsuga canadensis* (L.) Carrière (Eastern Hemlock), and *Halesia carolina* L. (Carolina Silverbell) on moister (cove hardwood) sites; subxeric (upland hardwood) sites were dominated by *Q. coccinea* Muenchh. (Scarlet Oak), *Q. montana* Willd. (Chestnut Oak), *Q. velutina* Lam. (Black Oak), *Nyssa sylvatica* Marsh. (Blackgum), and *Oxydendrum arboreum* (L.) DC (Sourwood), with abundant *Kalmia latifolia* L. (Mountain Laurel) in the understory. *Acer rubrum* L. (Red Maple), *Carya* spp. (hickory), *Cornus florida* L. (Flowering Dogwood), and *Q. alba* L. (White Oak) were common throughout (Pittillo et al. 1998, McNab 2011).

Study design

The SFC method proposed here was part of a long-term "fruit study" (established in 1999) comparing stand dynamics and fleshy fruit, samara, and nut production between unmanaged mature (80–100 years at study establishment), closed-canopy forest and 2-aged stands with low basal area (BA) retention created by shelterwood-with-reserves regeneration (termed "shelterwoods") harvests in southern Appalachian upland- and cove-hardwood forests (Greenberg et al. 2007; see Greenberg et al. 2023 for more detail on stand structure in mature and shelterwood study stands). Shelterwood harvests were conducted in 1998–1999. About 15–20% of the original mature tree BA—mostly scattered oaks and hickories—was retained to create a heterogeneous stand structure and maintain hard mast (acorns and hickory nuts) production for wildlife while facilitating the initiation and development of tree regeneration. Shelterwood stand size averaged 7.0 ha (min–max: 3.2–10.5 ha) and were generally the same age as mature stands (80–100 years old) when they were harvested. All regenerated stands were site-prepared within a year of harvesting by cutting all stems 2.5–20 cm diameter at breast height (dbh) (Pisgah district) or 5–25 cm dbh (Grandfather district) and ≥ 1.4 m tall. The cut stump surfaces of Red Maple, Flowering Dogwood, Carolina Silverbell, Sourwood, Yellow-Poplar, *Sassafras albidum* (Nutt.) Nees (Sassafras), *Robinia pseudoacacia* L. (Black Locust), *M. fraseri* Walt. (Fraser Magnolia), Blackgum, *Rhododendron* spp. (rhododendron), and Mountain Laurel were treated with herbicide (Garlon 3A, 50–50 mix; Dow AgroSciences, Indianapolis, IN).

For the long-term "fruit study", we selected 31 stands of 2 silvicultural treatments: recent shelterwood (SW) harvests (n = 15) and mature (M) forest controls (n = 16) based on availability of stands that met our age and silvicultural-treatment criteria. We attempted to locate M near SW stands to minimize variability due to location and topography. We randomly positioned one 20 m × 50 m (0.1 ha) plot in each study site ≥25 m from stand edges, roads, or trails. Study sites were remote and not easily accessible to humans, thus minimizing the likelihood of berry picking that might affect fruit-density estimates. We established a 4 m × 50 m (0.02 ha) transect along both sides of the 50-m centerline through the larger plot, which we further subdivided into 20 (10 on each side of the centerline) contiguous 2 m × 5 m (10 m^2) quadrats for clonal-shrub measurements and fruit counts. We visually estimated the percent cover of blueberry, huckleberry, and blackberry, and counted all fruits (ripe, unripe, and damaged) within each quadrat along the 4 m × 50 m transects during June and July (peak fruiting months; Greenberg et al. 2007) 1999–2008 and again in 2016 (total of 11 years over a 17-year period); we used the month with the highest fruit count (June or July) for each plot for estimating fruit production. We counted blueberry and huckleberry fruits (berries) individually. Blackberry fruits (technically, each "fruit" is an aggregate of drupelets; we considered these to be 1 fruit) are produced in clusters. Thus, we counted blackberry fruits by clusters, then multiplied the number of clusters by the mean number of fruits per cluster, based on counts of fruits within several clusters each year. Individual field technicians conducting shrub-area estimations and fruit counts differed somewhat across transects and years but were overseen and trained by 1 lead technician most years.

Our goal was not to compare fruit production or shrub-recovery dynamics between closed-canopy, mature forest and recently harvested shelterwood stands, but instead to provide a method for predicting average fruit crop sizes where the shrub was present, and under relatively controlled conditions. Therefore, for blueberry and huckleberry analyses we used only the subsets (which differed between the genera) of M transects with established populations (e.g., relatively consistent cover estimates and ≥4 m^2 shrub area per transect across sampled years) (blueberry n = 4 transects; huckleberry n = 8 transects). Blackberry only occurred in SW transects (except for small, transient patches in M), so we only included SW transects in analyses. Blackberry showed a distinct pattern of post-harvest colonization, increase, then decline over time as growing young trees approached canopy closure (Greenberg et al. 2023) and was present in all 15 SW transects only during 2001–2007 (10 in 1999; 14 in 2008; 11 in 2016). We only included the subset of total transects where blackberry was present in a given year, but (unlike for blueberry and huckleberry) included transects with low coverage (>0 m^2 shrub area) in our analyses of shrub area and SFCs in order to examine dynamic changes in both shrub coverage and fruit production over time; thus, the number of transects used (sample size) varied somewhat among years.

Statistical analysis

For data analyses, we lumped blueberry species *Vaccinium staminium* L. (Deerberry) and *V. pallidum* Ait. (Lowbush Blueberry) (*V. corymbosum* L. [Highbush Blueberry] occurred within some transects but was not included because it is nonclonal); huckleberry species *Gaylussacia ursina* (M.A. Curtis) Torr. and Gray ex A. Gray (Bear Huckleberry) and *G. baccata* (Wangenh.) K. Koch (Black Huckleberry); and blackberry species *Rubus allegheniensis* Porter (Common Blackberry), *R. odoratus* L. (Flowering Raspberry), and *R. phoenicolasisus* Maxim. (Wineberry) into genera because some species (e.g., Black Huckleberry, Flowering Raspberry, Wineberry) were infrequent, and thus, sample sizes needed for precise crop-size averages or data analyses were inadequate. Additionally, field personnel tasked with fruit sampling may find it time consuming or difficult to distinguish among species within these genera.

We categorized percent-cover estimates for target shrub genera into 6 cover classes (Daubenmire 1959) within each of the 20, contiguous quadrats located along each side of the centerline transect. Cover classes and midpoints of each (used in our calculations) were: 1 = 0.1–4.9%, midpoint 2.5%; 2 = 5–24.9%, midpoint 15.5%; 3 = 25–49.9%, midpoint 37.5%; 4 = 50–74.9%, midpoint 62.5%; 5 = 75–94.9%, midpoint 85%; and 6 = 95–100%, midpoint 97.5%. We calculated the area (m^2) of each shrub species based on percent-cover midpoint estimates within each 10-m^2 quadrat and summed by genus across all quadrats within transects for total shrub area (m^2) per transect. We also summed fruit counts across all 20 quadrats within transects for each year. We recognize that error is inherent in both fruit counts and visual estimates of shrub area and likely vary somewhat among observers (bias; Daubenmire 1959). We assumed that our use of cover classes and midpoints for shrub-area estimates, inclusion of multiple subsamples (quadrats) within transects, and replicated transects across multiple years for both fruit counts and shrub-area estimates reduced those effects on our calculations. We calculated a "standardized fruit crop" (fruit density, or fruits/m^2 shrub area; SFC) by dividing the total number of fruits (ripe, unripe, and damaged) by the total estimated area (m^2, calculated as described above) of shrub within each transect. We averaged SFCs for each shrub genus across transects for each year to calculate annual SFCs. Additionally, we used SFCs for each shrub genus across all transects and years pooled, and also for blackberry (only) during the span of years when both shrub area and SFCs peaked (presumably due to changing light conditions over time in SW), to calculate long-term average SFCs with 95% confidence limits.

We calculated cumulative mean SFCs with 95% confidence limits for each shrub genus to examine how each successive sampled year improved confidence in the estimated long-term SFC mean.

We used Pearson's product-moment correlations to examine the relationship between blueberry, huckleberry, and blackberry shrub area (m^2 per transect) and the total number of fruits (fruit counts; not SFCs) produced by each within each year and again pooling all 11 years. We used repeated measures 1-way ANOVAs (PROC MIXED; SAS 9.3; SAS Institute, Inc., Gary, NC) in a completely randomized design with compound symmetry covariance to test each shrub genus (separately) for interannual differences in shrub-area estimates and SFCs. In all ANOVAs, we considered transect (the replicate unit) to be a random effect and the repeated subject factor. When differences among years were significant, we used least squares means tests to determine which years differed from one another. We natural log transformed (+ 1) SFC to reduce heteroscedasticity and set significance level at $\alpha < 0.05$.

Results

Average (± SE) estimates of annual (11 years) blueberry shrub area sampled in M varied from 11.2 ± 2.9 to 22.4 ± 4.9 m^2 per transect ($n = 4$ transects/year); huckleberry shrub area in M varied from 53.4 ± 13.1 to 66.1 ± 16.4 m^2 per transect ($n = 8$ transects/year) (Fig. 1). Despite variability in blueberry and huckleberry shrub-area estimates among years, temporal patterns of increase or decrease were not evident; interannual differences were likely due to observer error and our use of cover-class midpoints. Blackberry was present in all 15 SW transects between 2000–2007 but fewer immediately post-harvest (1999; $n = 10$ transects), and again several years post-harvest as regenerating trees approached canopy closure (2008; $n = 14$ transects; 2016; $n = 11$ transects). Average annual blackberry shrub area sampled in SW transects (omitting transects in years when blackberry was absent) varied from 1.5 ± 0.8 m^2 (in 2016; $n = 11$ transects) to 40.1 ± 7.8 m^2 (in 2004; $n = 15$ transects); a strong temporal pattern showed minimal coverage in 1999, increasing to a peak in 2003–2005, and followed by a decrease to minimal coverage by 2007 (Fig. 1).

Average annual ($n = 4$ transects) blueberry SFC varied from 1.3 ± 0.9 (in 2004) to 18.8 ± 15.8 (in 1999) fruits/m^2 shrub area (Fig. 1) and did not significantly differ among years ($P = 0.1603$). Long-term (11-yr; $n = 44$ transects × years) average SFC was 6.8 ± 1.8 fruits/m^2 shrub area (Table 1). Blueberry shrub area and total fruits per transect were not correlated within any single year except 2001 and 2002 but were significantly ($r = 0.53$, $P = 0.0002$) correlated when all 11 years were included (Table 2). Average annual ($n = 8$ transects) huckleberry SFC varied from 1.8 ± 1.3 (in 2007) to 19.8.10 ± 8.0 (in 2000) fruits/m^2 shrub area (Fig. 1). Huckleberry SFC differed among years ($P < 0.0001$) and most notably was lower in 2007 than all other years (Fig. 1). Long-term (11-yr; $n = 88$ transects × years) average huckleberry SFC was 11.6 ± 1.8 fruits/m^2 shrub area (Table 1). Cumulative means with 95% confidence intervals for both blueberry and huckleberry stabilized over time (Fig. 2), indicating that 11 sample years were sufficient for estimating robust long-term mean SFCs. Huckleberry shrub area and total fruits per transect were not correlated within any single year except 2016 but were correlated ($r = 0.44$, $P < 0.0001$) when all 11 years were included (Table 2). Average annual (n = 10–15 transects/yr) blackberry SFC varied from 0.5 ± 0.5 (in 1999 and 2016) to 141.0 ± 29.9 (in 2003) fruits/m^2 shrub area (Fig. 1). Blackberry SFC

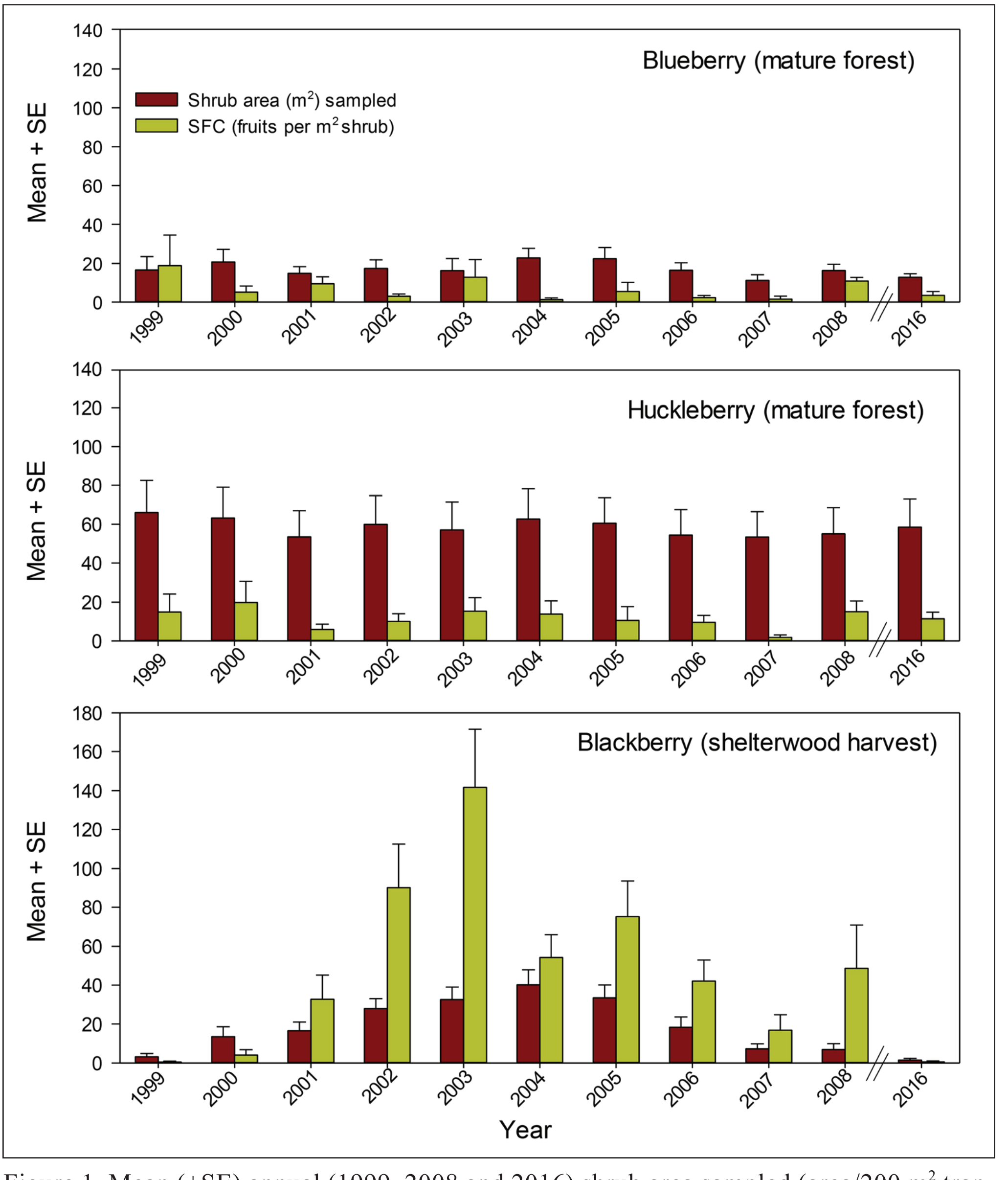

Figure 1. Mean (+SE) annual (1999–2008 and 2016) shrub area sampled (area/200 m^2 transect) and standardized fruit crop (SFC; fruits/m^2 shrub area) for blueberry (n = 4 transects) and huckleberry (n = 8) in mature forest (M), and blackberry (n = 15 transects 2000–2007; n = 10 in 1999, n = 14 in 2008, n = 11 in 2016) in young developing shelterwood regeneration harvests (harvested 1998–1999) (SW) over 11 years, Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, NC.

Table 1. Mean (± SE) long-term (11-year; 1999–2008 and 2016 pooled) standardized fruit crop (SFC; number of fruits per m^2 shrub area) and 95% confidence intervals (CI) for blueberry (n = 4 transects × 11 yrs = 44 total samples) and huckleberry (n = 8 transects × 11 yrs = 88 total samples) in mature forest (M), blackberry (n = 10 transects in 1999, n = 15 transects in 2000–2007, n = 14 transects in 2008, n = 11 in 2016 = 155 total samples) in young, developing shelterwood regeneration harvests (harvested 1998–1999)[A] (SW), and blackberry during years of peak area and SFC (2002–2005) (n = 15 × 4 yrs = 60 total samples)[B] following colonization, and prior to decline as young trees approached canopy closure in the Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, North Carolina. Long-term (average) fruit production by each species can be calculated on an area basis by multiplying its total shrub area (m^2) within a given mature forest (for blueberry and huckleberry) or recently harvested (for blackberry) stand by its long-term SFC[C].

Genus	Forest	Sample years	n	Mean ± SE SFC	95% CI
Blueberry	M	1999–2008 and 2016 (11y)	44	6.8 ± 1.8	3.2–10.3
Huckleberry	M	1999–2008 and 2016 (11y)	88	11.6 ± 1.8	8.0–15.3
Blackberry[A]	SW	1999–2008 and 2016 (11y)	155	48.7 ± 5.9	37.1–60.2
Blackberry[B]	SW	2002–2005 (peak 4y)	60	90.3 ± 1.3	67.7–113.0

[A]Blackberry SFC estimates including all 11 years likely do not reflect fruit density under full or near-full sunlight conditions and include years of shrub area establishment, peak, and decline

[B]Blackberry SFC estimates that include only peak years of both SFC and shrub area (2002–2005) most accurately reflect fruit densities under full or near-full sunlight conditions, post-establishment and prior to decline

[C]Examples: the long-term average number of fruits produced by 20m^2 of shrub area is: 20 m^2 × 11.6 SFC = 232 fruits (huckleberry), and 20 m^2 × 6.8 SFC = 136 fruits (blueberry) in mature forest, and; 20 m^2 × 90.3 SFC = 1806 fruits (blackberry, 3–6 years post-harvest).

Table 2. Results of annual (1999–2008 and 2016) and pooled (all years) Pearson's product-moment correlations of shrub area (m^2; based on midpoint of cover classes) and natural-log transformed number of fruits within 200-m^2 transects for blueberry (n = 4 transects) and huckleberry (n = 8) in mature forest (M), and blackberry (n = 10–15; transects omitted if blackberry was absent) young developing shelterwood regeneration harvests (harvested 1998–1999) (SW) in the Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, NC. * indicates staticical significance (P-values < 0.05).

	Blueberry (M)			Huckleberry (M)			Blackberry (SW)		
Year	n	r	P-value	n	r	P-value	n	r	P-value
1999	4	0.62	0.3817	8	0.60	0.1140	10	0.39	0.2677
2000	4	0.81	0.1865	8	0.53	0.1777	15	0.80	0.0003*
2001	4	0.99	0.0090*	8	0.28	0.5053	15	0.62	0.0139*
2002	4	0.96	0.0439*	8	0.60	0.1176	15	0.61	0.0150*
2003	4	0.53	0.4715	8	0.41	0.3194	15	0.54	0.0362*
2004	4	0.79	0.2071	8	0.58	0.1325	15	0.71	0.0033*
2005	4	0.03	0.9724	8	0.65	0.0811	15	0.56	0.0287*
2006	4	0.45	0.5505	8	0.69	0.0563	15	0.50	0.0553
2007	4	0.86	0.1368	8	0.14	0.7467	15	0.48	0.0730
2008	4	0.75	0.2474	8	0.62	0.1032	14	0.44	0.1125
2016	4	0.88	0.1158	8	0.71	0.0480*	11	0.99	<0.0001*
All	44*	0.53*	0.0002*	88	0.44	<0.0001*	155*	0.68*	<0.0001*

differed among years ($P < 0.0001$); most notably it was lower in 1999, 2000, and 2016 than all other years, increasing to a peak from about 2002–2005, and declining thereafter (Fig. 1). Long-term (11-yr; n = 155 transects × years) average blackberry SFC was 48.7 ± 5.9 fruits/m^2 shrub area (Table 1), and cumulative means with 95% confidence intervals stabilized over time (Fig. 2). However, our long-term blackberry SFC estimate was not reliable for application to shrub area throughout the period of post-harvest stand development due to the large initial increase, peak, then decline in both shrub area and SFC with changing light conditions (Fig. 1). Average blackberry SFC was 90.3 ± 11.3 fruits/m^2 shrub area when only peak years of both shrub area and SFC (2002–2005) were included (n = 60 transects × years), presumably the post-establishment years with high light availability, and prior to substantial canopy closure. Blackberry shrub area and total fruits per transect were correlated in 2000–2005 and 2016 as well as when all 11 years were included (r = 0.68,; $P < 0.0001$; Table 2).

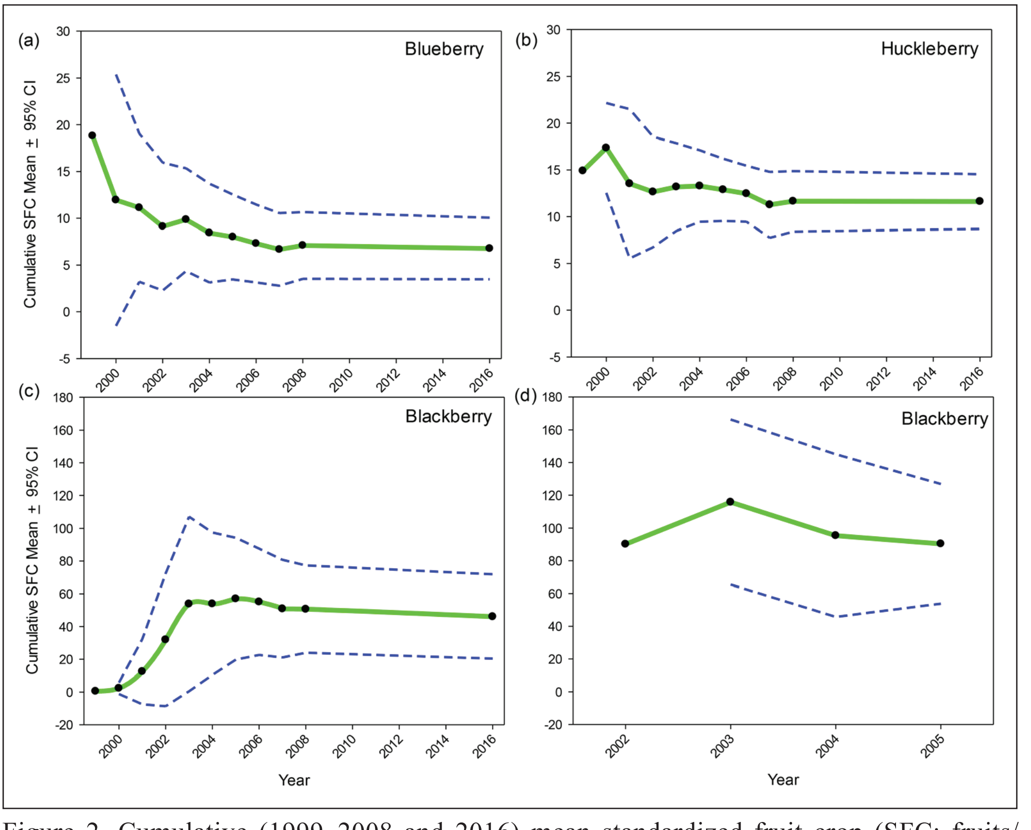

Figure 2. Cumulative (1999–2008 and 2016) mean standardized fruit crop (SFC; fruits/m^2 shrub area) with 95% upper and lower confidence intervals for (a) blueberry in mature forest, (b) huckleberry in mature forest, (c) blackberry in young developing shelterwood regeneration harvests including years of post-harvest shrub establishment, increase, and decline with increasing shade associated with stand development, and; (d) blackberry during years of peak shrub area and SFC only (2002–2005), Pisgah National Forest, Buncombe, Haywood, McDowell, and Transylvania counties, NC.

Discussion

Our SFC estimates provide a simple, efficient forest-planning tool that can be used to quantitatively estimate long-term average fruit production by 3 common, important fruit-producing shrubs, and that can be tailored to specific eastern hardwood forest stands or landscapes based on shrub abundance (area). Both fruit counts and shrub-area estimates (Daubenmire 1959) are subject to observer bias; fruit consumption by birds and mammals (e.g., McCarty et al. 2002) prior to fruit counts may introduce an additional source of error. Other studies provide qualitative ranking or quantitative estimates using different sampling protocols, reporting units (e.g., fruit counts; wet or dry weight of whole fruits or pulp only), or total "berry" estimates not specifically linked to species or genera (e.g., Greenberg et al. 2007, 2012; Lashley et al. 2014; Mitchell and Powell 2003; Perry et al. 1999; Powell and Seaman 1990; Reynolds-Hogland et al. 2006). More importantly, these studies do not link fruit density to the abundance of target shrub genera and thus cannot be tailored to specific forest stands or landscapes. In contrast, our SFCs are based on long-term, replicated estimates of fruit density (fruits/m^2 shrub area; SFCs) and are thus standardized for application to estimates of shrub coverage at multiple scales.

In our study, interannual variation in blueberry SFC was evident but not significant, whereas huckleberry SFC differed among years, most notably having a near-crop failure in 2007. Other studies suggest that blueberry and huckleberry crop sizes in mature forest vary among years (e.g., Powell and Seaman 1990) but are difficult to gauge without interannual comparisons of fruit density per unit area of shrub. The lack of significant differences in crop size among years for blueberry was likely in part due to small within-year sample sizes and/or high spatial variation in fruit production (e.g., Powell and Seaman 1990). Our results showing nonsignificant correlations between total shrub area sampled and total fruits counted within most years for both blueberry and huckleberry also likely reflected spatially variable fruit production and low sample sizes. In contrast, we found a moderately to strongly significant relationship between total blueberry and huckleberry shrub area sampled and total fruits when we increased our sample size by pooling all transects and years. Our results indicate that SFC estimates within a single year or given location cannot be reliably generalized across other years or sites. However, we suggest that our long-term blueberry and huckleberry SFC estimates (Table 1) based on replicated, multi-year sampling can be applied to shrub-area inventories as a reliable planning tool for estimating potential fruit production tailored to specific mature eastern hardwood forest stands or landscapes.

In our study, blackberry responded to shelterwood harvests with rapid increases in both shrub area and disproportionate increases in fruit density (SFC) that peaked around 2002–2005, 3–6 years post-harvest, followed by sharp declines in both. We did not concurrently measure light availability during annual sampling of blackberry coverage and fruit density but are confident that both were strongly positively associated with changes in light availability to the shrub layer that decreased over time with stand development (see Greenberg et al. 2023). Several other studies (e.g., Donoso and Nyland 2006, Lautenschlager 1999, Walters and Nyland 1989, Whitney 1982) also show this post-harvest pattern of blackberry colonization, rapid vegetative growth and spread by root suckering to a peak within 3–5 years, followed by decline, with most dying within about 10 years as young regenerating trees reach canopy closure. Abundant research also shows that blackberry fruit production follows a pattern similar to the vegetative response, with prolific fruiting starting 2–3 years post-harvest, peaking within about 3–5 years, and decreasing thereafter (e.g., Greenberg et al. 2007, 2012; Johnson and Landers 1978; Mitchell and Powell 2003; Perry et al. 1999; Reynolds-Hogland et al. 2006; Stransky and Roese 1984). Most studies, however, do not indicate whether higher fruit production is simply an artifact of greater shrub area during peak years, or if fruiting is disproportionately higher than an increase in shrub area alone. Our results show that increases in both blackberry shrub area and fruit density (SFC) contribute to prolific fruit availability during peak years. Because of this disproportionately greater increase in SFC to shrub area during peak years with high light availability, our long-term average SFCs are not applicable in recently disturbed forest stands undergoing dynamic, rapid changes in forest structure. Instead, we suggest that SFC averages based on peak years of blackberry area and SFC provide a more reliable estimate of potential fruit production that is applicable in high-light environments, 3–6 years post-disturbance and prior to canopy closure.

Several studies suggest that blueberry and huckleberry recover quickly after heavy, overstory-reducing disturbances such as clearcuts or shelterwood harvests, and may be more likely to produce fruits (Reynolds-Hogland et al. 2006) and/or produce more fruits in stands with high light availability than in heavily shaded, closed-canopy forests (e.g., Greenberg et al. 2007, 2012; Perry et al. 1999; Reynolds-Hogland et al. 2006). In our study, we did not compare blueberry and huckleberry fruit production between M and SW; instead, we deliberately limited our sampling to mature forest where a closed-canopy overstory remained relatively consistent across all sample years. Therefore, we emphasize that the long-term SFCs estimated in this study for blueberry and huckleberry are likely valid only when applied to shrub cover in mature forest conditions and should not be used to estimate potential fruit production in disturbed forests with heavy overstory removal.

Management implications

Potentially high interannual and spatial variability in fruit production (e.g., Greenberg et al. 2007, Hogland et al. 2006) limits the ability to accurately estimate within-year fruit crop sizes in the absence of annual, labor-intensive surveys. Although our SFCs cannot reliably predict crop sizes within any given year or area, they provide a tool to estimate average annual (over the long-term) or potential fruit production that can be tailored to specific eastern hardwood forest stands and landscapes with variable shrub coverage, by application to shrub-area inventories. Long-term average fruit production by each species can be calculated on an area basis by multiplying its total shrub area (m^2) within a given mature forest (for blueberry and huckleberry) or 3–6 year post-harvest stand (for blackberry) by its SFC, presented in Table 1.

For example, the long-term average number of fruits produced by 20 m^2 of shrub area for each target genus is: 20 m^2 × 11.6 SFC = 232 fruits (huckleberry), and 20 m^2 × 6.8 SFC = 136 fruits (blueberry) in mature forest, and; 20 m^2 × 90.3 SFC = 1806 fruits (blackberry) 3–6 years post-harvest in a shelterwood stand. This method provides an important forest planning tool by enabling users to tailor long-term potential fruit production estimates by 3 common, important fruit-producing shrubs in eastern hardwood forest based on replicated, multi-year estimates of both shrub area and fruit density (fruits/m^2 shrub area).

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Data Availability

Data will be made available on request.

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