The Journal of Wildlife Management 76(5):1036–1046; 2012; DOI: 10.1002/jwmg.343

Habitat Relations

Long-Term Patterns of Fruit Production in Five Forest Types of the South Carolina Upper Coastal Plain

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ABSTRACT Fleshy fruit is a key food resource for many vertebrates and may be particularly important energy source to birds during fall migration and winter. Hence, land managers should know how fruit availability varies among forest types, seasons, and years. We quantified fleshy fruit abundance monthly for 9 years (1995–2003) in 56 0.1-ha plots in 5 forest types of South Carolina's upper Coastal Plain, USA. Forest types were mature upland hardwood and bottomland hardwood forest, mature closed-canopy loblolly (*Pinus taeda*) and longleaf pine (*P. palustris*) plantation, and recent clearcut regeneration harvests planted with longleaf pine seedlings. Mean annual number of fruits and dry fruit pulp mass were highest in regeneration harvests (264,592 ± 37,444 fruits; 12,009 ± 2,392 g/ha), upland hardwoods (60,769 ± 7,667 fruits; 5,079 ± 529 g/ha), and bottomland hardwoods (65,614 ± 8,351 fruits; 4,621 ± 677 g/ha), and lowest in longleaf pine (44,104 ± 8,301 fruits; 4,102 ± 877 g/ha) and loblolly (39,532 ± 5,034 fruits; 3,261 ± 492 g/ha) plantations. Fruit production was initially high in regeneration harvests and declined with stand development and canopy closure (1995–2003). Fruit availability was highest June–September and lowest in April. More species of fruit-producing plants occurred in upland hardwoods, bottomland hardwoods, and regeneration harvests than in loblolly and longleaf pine plantations. Several species produced fruit only in 1 or 2 forest types. In sum, fruit availability varied temporally and spatially because of differences in species composition among forest types and age classes, patchy distributions of fruiting plants both within and among forest types, fruiting phenology, high inter-annual variation in fruit crop size by some dominant fruit-producing species, and the dynamic process of disturbance-adapted species colonization and decline, or recovery in recently harvested stands. Land managers could enhance fruit availability for wildlife by creating and maintaining diverse forest types and age classes. © 2012 The Wildlife Society.

KEY WORDS bottomland hardwoods, clearcut regeneration, Coastal Plain forest, fruit, pine plantation, Savannah River Site, soft mast, timber harvest, upland hardwoods, wildlife food.

Fleshy fruits are an important energy source for many vertebrate species, including both game and nongame wildlife (Martin et al. 1951). In North America, most birds and mammals consume fruit at least occasionally (Martin et al. 1951, Willson 1986), and many species rely heavily on fruit during some seasons. For example, fruit can be a critical resource for migratory birds in the fall (Willson 1986, Parrish 1997, Buler et al. 2007, Smith et al. 2007) and for overwintering short-distance migrants or resident birds in winter (McCarty et al. 2002; Borgmann et al. 2004; Kwit et al. 2004*a*, *b*), when arthropods and other forest food sources are scarce (Skeate 1987, Greenberg and Forrest 2003, Whitehead 2003). Several studies indicate that post-fledging birds move into early successional vegetation in the fall (Rivera et al. 1998, Marshall et al. 2003, Whitehead 2003, White et al. 2005, Vitz and Rodewald 2006), where fruits are abundant and accessible. Fruit consumption and availability have also been linked to mammalian survival and reproductive success (Rogers 1976, Eiler et al. 1989, Reynolds-Hogland et al. 2007).

Received: 23 December 2010; Accepted: 21 November 2011; Published: 6 February 2012

Additional Supporting Information may be found in the online version of this article.

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Surprisingly little is known about how fruit production and fruiting species composition varies among forest types, age classes, and seasons in the southeastern United States. Several studies show that fruit production is greater in young, recently harvested stands of several forest types, including upland hardwood (Reynolds-Hogland et al. 2006; Greenberg et al. 2007, 2011) and pine (*Pinus*)-hardwood forests (Halls 1973, Perry et al. 1999), and slash pine (*P. elliottii*; Johnson and Landers 1978) or loblolly pine (*P. taeda*; Campo and Hurst 1980) plantations, compared to mature, closed-canopy forests. More fruit is also produced in forest openings created by natural disturbances (Blake and Hoppes 1986). High light conditions and reduced competition after canopy-reducing disturbances likely promote fruiting by many plant species, which can persist for several years after disturbance. Because fruit is an important dietary component for many wildlife species, land managers will benefit from information on how much fruit is produced by different species in different forest types or stages of stand development, in different seasons and years.

We quantified fleshy fruit abundance monthly in 5 managed and unmanaged forest types (we use the term "forest type" to denote vegetation association and stage of stand development) that are common in the Piedmont and Coastal Plain physiographic region of the southeastern United States. These included mature upland hardwood and bottomland hardwood forests, mature loblolly pine and longleaf pine (*P. palustris*) plantations, and recent clearcut regeneration harvests planted with longleaf pine seedlings. Here, we describe spatial and temporal variation in fruit production and composition among the 5 forest types during a 9-year study from January 1995 to December 2003.

STUDY AREA

We conducted our study on the United States Department of Energy's Savannah River Site (SRS), a National Environmental Research Park located in Aiken and Barnwell Counties, South Carolina, USA (33°18′N, 81°37′W). The site was within the Sandhill and upper Coastal Plain physiographic regions. Forested areas covered >80% of the site (Workman and McLeod 1990). The majority of this area consisted of a patchy mosaic of managed, even-aged longleaf pine and loblolly pine stands of varying age-classes, and to a lesser extent, upland and bottomland hardwood forests (Odum 1991, White and Gaines 2000). Prior to 1951, when reforestation efforts began with planting of pines, most of the uplands at the SRS were in agricultural fields or bare ground (White 2005). Upland and bottomland hardwood stands in our study were approximately 60–75 years old.

Pine plantations and upland hardwood stands in our study were generally on dry, sandy soils of uplands and ridges; bottomland hardwoods occurred along stream terraces and floodplains with loamy-clayey soils (Kilgo and Blake 2005). In 1999, we measured the diameter at breast height (dbh) of all trees ≥10 cm dbh in each of our study plots to derive an estimate of average tree density and basal area per forest type.

Mature bottomland hardwoods had a nearly continuous canopy layer of trees including swamp black gum (*Nyssa biflora*), sweet bay (*Magnolia virginiana*), and oak (*Quercus* spp.); vines such as poison ivy (*Rhus radicans*) and greenbriar (*Smilax* spp.); a well-developed understory stratum including holly (*Ilex* spp.), red bay (*Persea borbonia*), and blueberry (*Vaccinium* spp.); and a pronounced ground layer of sphagnum moss (*Sphagnum*), woody stems, and herbs including sedges, partridge berry (*Mitchella repens*), and Jack-in-the-pulpit (*Arisaema triphyllum*). Average (±SE) tree density was 622.0 ± 45.2 trees/ha, and average basal area was 26.8 ± 1.8 m^2/ha in bottomland hardwoods.

Mature upland hardwood forests were characterized by a well-developed canopy of *Quercus* spp., hickory (*Carya* spp.), and *P. taeda*; an understory that included flowering dogwood (*Cornus florida*), American holly (*I. opaca*), and sparkleberry (*V. arboreum*); and a relatively sparse ground layer. Average tree density was 575.0 ± 40.3 trees/ha, and average basal area was 18.1 ± 1.2 m^2/ha in upland hardwoods.

Regeneration harvest plots initially consisted of *Pinus* seedlings and disturbance-adapted plant species such as pokeweed (*Phytolacca americana*), but had developed a canopy of planted longleaf pine (maximum height = 6 m) and a well-developed understory including wax myrtle (*Morella cerifera*), *R. copallina*, black cherry (*Prunus serotina*), and wild plum (*P. umbellata* and *P. angustifolia*) by the end of our study. A ground layer of grasses, sedges, *V. stamineum*, poison oak (*R. toxicodendron*), and prickly pear cactus (*Opuntia compressa*) also occurred in regeneration harvests. In 1999, average tree (≥10 cm dbh) density was 4.0 ± 2.7 trees/ha, and average basal area was 0.1 ± 0.1 m^2/ha in regeneration harvests.

Mature longleaf and loblolly pine plantations had a homogeneous canopy layer of *Pinus*, few understory shrubs and trees (e.g., *M. cerifera*, *Quercus* spp.), and a sparse ground layer that often included low-lying vegetation (e.g., *V. stamineum*, *R. toxicodendron*) and vines such as muscadine grape (*Vitus rotundifolia*) and *Smilax* spp. Average tree density was 367.7 ± 34.8 trees/ha, and average basal area was 20.8 ± 1.9 m^2/ha in longleaf plantations. Average tree density and basal areas were 473.1 ± 38.5 trees/ha and 23.6 ± 1.3 m^2/ha, respectively in loblolly plantations.

Forest structure and light conditions in both hardwood forest types remained relatively unchanged during the study period. In regeneration harvests, however, growth and development of vegetation, and consequent changes in stand structure and light availability were highly dynamic. In many of our pine plantation stands, prescribed burns (most in Jan–Mar, 1 in Jul) were conducted 1–3 times (6 of 10 stands in regeneration harvests, 10 of 13 in loblolly plantations, and 8 of 13 in longleaf plantations) during the 9-year study period. Different stands were burned in different years. Midstory removal (removal of all midstory shrubs and trees to reduce competition with pines) also occurred in 3 of 13 longleaf plantations stands (1 in 1996; 2 in 1999). Prescribed burning and midstory removal are both common management practices in pine plantations throughout the southeastern United States. Therefore we considered these common management

applications to be typical disturbances in regeneration harvests, loblolly plantations, and longleaf plantations, and did not attempt to specifically address their effects on fruit production.

METHODS

We established 1 0.1-ha rectangular plot (50 m × 20 m) in each of 56 stands representing bottomland hardwoods, upland hardwoods, regeneration harvests, longleaf plantations, and loblolly plantations. We randomly established the point of origin and orientation (azimuth) of each plot, all ≥50 m from stand edge. All plots were separated from one another by at least 600 m and were assumed to be independent in terms of fruit production. Ten plots were located in each mature bottomland hardwoods, upland hardwoods, and regeneration harvests. The regeneration harvest stands were created using the clearcutting method (1992–1993), site-prepared using herbicide (8 stands) and (or) prescribed fire (9 stands) or shear and raking (1 stand), and machine planted with longleaf pine (8 stands) or loblolly (2 stands) seedlings in 1993 or 1994. Thirteen plots each were located in stands of closed-canopy longleaf plantations and loblolly plantations that were ≥40 years old.

We censused all fleshy fruits monthly in each study plot from January 1995 to December 2003. We categorized all fruits as ripe, unripe, or damaged by insects, microbes, or desiccation. We defined fruit functionally, as a seed-containing structure with a nutritious outer coating (i.e., pulp) consumed by vertebrates. Methods for estimating the number of fruit on a given plant depended on the species' life-form and the number of fruiting individuals of that species in a plot. For non-clonal species, we tagged all fruiting individuals (regardless of potential underground connections) and estimated number of fruits on each, except when we encountered >10 individuals in a given plot. In those cases, we sampled 10 randomly chosen individuals and multiplied the mean number of fruits by the total number of fruiting conspecifics. When possible, we counted all fruits on a given plant. Otherwise, we counted fruits from portions (e.g., branches) of the plant, and these counts were extrapolated to the entire plant. For clonal species (e.g., *V. stamineum*, huckleberry (*Gaylussacia* spp.), blackberry (*R. cuneifolius*), *R. toxicodendron*, and *M. repens*) we counted the number of fruits in a 4 m × 50 m strip down the center transect of the plot and multiplied the total by 5 to estimate the number of fruits of that species in the entire 0.1-ha plot.

We determined dry mass of ripe fruit pulp from off-plot samples of ripe fruits. For every species, we based these calculations on samples of 10 fruits from each of 10 fruiting individuals ($n = 100$ fruits/species). Half of the samples remained intact (i.e., whole fruit samples), and the other half had all pulp removed (i.e., seeds only). We then placed samples in a drying oven (55°C) for 7 days, and determined dry mass (g) of ripe pulp per fruit from the difference. We calculated fruit production for each species by multiplying the average dry pulp weight of 1 fruit by the number of fruits counted within a plot, and extrapolating to g/ha. We based all data on fruit production on dry mass of fruit pulp (i.e., excluding seeds, which are generally not digested by frugivores).

We used a 2-way repeated measures mixed-effects analysis of variance (ANOVA), assuming plot within forest type to be a random factor, and forest type and year to be fixed effects, to compare annual fleshy fruit production (dry mass of pulp and number of fruits) by species and total (all species combined) among treatments (forest types) and years (1995–2003), and to test for treatment × year interactions. For each species, we used the month of greatest average fruit production (including ripe, unripe, and damaged fruit) for inter-annual comparisons (summing fruit counts across months would have resulted in an inflated fruit count, since the same fruits were often counted from month to month). We calculated total annual fruit mass in each forest type by summing the month of maximum production for each species. We also used a 2-way repeated measures mixed-effects ANOVA to compare fruit species richness (the total number of plant species that produced fruit in a given year) among forest types and years, and to compare total fruit production among forest types and months. We assessed each year separately using 1-way ANOVA to determine whether total dry pulp mass or number of fruits differed among forest types or among years within forest types. We log-transformed (ln + 1) fruit production data to reduce heteroscedasticity. We performed all post hoc tests for data with unequal sample size (number of plots per forest type) using least squares means tests. To additionally explore spatial variation in fruit production by fleshy fruit-producing species, we used 1-way ANOVA with Tukey's multiple comparison procedure as the post hoc test, on arcsine square-root transformed annual ($n = 9$) proportion of plots with fruiting plants. We considered $P < 0.05$ as significant for all tests.

RESULTS

Species Composition and Richness

During our 9-year study, 60 species produced fruit, including 57 native species, 1 cultivar (crab apple; *Malus angustifolia*), and 2 non-native invasive species (Chinese privet; *Ligustrum sinense*, and Japanese honeysuckle; *Lonicera japonicum*; Online Supplemental Appendix 1, available at www.onlinelibrary.wiley.com). Across all years and plots, species richness of fruiting plants by forest type (in descending order) was upland hardwoods (31 species), bottomland hardwoods and regeneration harvests (29 species each), loblolly plantations (27 species), and longleaf plantations (20 species) (Online Supplemental Appendix 1). Species richness of fruiting plants was highest in upland hardwoods, bottomland hardwoods, and regeneration harvests, and lowest in loblolly plantations and longleaf plantations (Table 1). Richness also differed among years and we found a significant year × forest type interaction (Table 1).

Production of Total Dry Pulp Mass and Number of Fruits Among Forest Types

Mean (±SE) annual production of total dry fruit pulp mass was highest in regeneration harvests (12,008 ± 2,392 g/ha),

Table 1. Mean percent total number (% no.) and percent total mass (% mass) across all years (1995–2003) and forest types, and mean (±SE) annual dry pulp mass (g/ha) of species that produced ≥10% of dry pulp mass, number of fruits, or both within a forest type at the Savannah River Site, South Carolina. Species richness of fruiting plants, annual mean total mass, and annual mean total number of fruits produced (no./ha) in each forest type are listed at bottom of table. Different letters within rows denote significant differences among the forest types. Values with a dagger (†) indicate species that comprise ≥10% of mean total dry pulp mass (g) within a forest type (column). Values with a double dagger (‡) indicate species that comprise ≥10% of mean total number of fruits within a forest type.

Species[a,b]	% no./% mass (g)	Forest type[c]					RM ANOVA[d]		
		UHF ($n = 10$)	BHF ($n = 10$)	LOBP ($n = 13$)	LLP ($n = 13$)	RH ($n = 10$)	P_{for}	P_{yr}	$P_{for \times yr}$
COFL	6.1/9.0	2,149.3 ± 432.1A†‡	113.4 ± 37.1B	328.6 ± 114.4B†	92.1 ± 44.0B	0.0 ± 0.0B	**	***	***
ILOP	5.7/7.3	564.6 ± 179.7A†‡	1,719.9 ± 414.1B†‡	0.1 ± 0.1C	0.3 ± 0.3C	0.0 ± 0.0C	***	***	***
MOCE	18.2/0.9	0.0 ± 0.0A	0.0 ± 0.0A	27.9 ± 8.1A‡	20.1 ± 12.2A‡	229.7 ± 44.0B‡	***	**	**
NYBI	4.2/6.0	0.0 ± 0.0A	1,883.0 ± 405.1B†‡	0.0 ± 0.0A	0.0 ± 0.0A	0.0 ± 0.0A	***	***	***
RHCO	24.3/2.1	33.0 ± 22.9A‡	0.0 ± 0.0A	7.0 ± 3.0A	11.8 ± 5.8A	595.6 ± 147.8B‡	***	***	***
RHTO	7.2/1.8	7.4 ± 3.4AB	0.0 ± 0.0A	158.5 ± 41.0C‡	183.5 ± 74.0BC‡	98.8 ± 29.8BC	NS	NS	***
RUCU	2.4/4.1	0.0 ± 0.0A	0.0 ± 0.0A	<0.05 ± 0.0A	0.4 ± 0.3A	1,282.3 ± 561.7B†	***	***	***
VAAR	1.4/1.4	390.2 ± 125.5A‡	4.4 ± 2.2B	1.8 ± 0.8B	13.1 ± 6.7B	14.8 ± 6.3B	***	***	*
VAST	17.1/43.4	553.2 ± 135.6A†	8.0 ± 4.6B	1,546.9 ± 354.8A†‡	3,141.9 ± 850.0AC†‡	6,923.5 ± 2,278.8C†‡	***	***	***
VIRO	1.5/10.4	927.7 ± 135.2A†	127.0 ± 31.0B	744.2 ± 166.0AC†	294.2 ± 81.1BCD	860.7 ± 213.5ACD	**	***	*
Total mass		5,078.9 ± 528.8A	4,620.7 ± 676.7A	3,261.3 ± 492.1B	4,101.7 ± 877.0B	12,008.6 ± 2,392.1A	**	***	**
Total number		60,769 ± 7,667AB	65,614 ± 8,351AB	39,532 ± 5,034BC	44,104 ± 8,301C	264,593 ± 37,444A	***	***	**
Species richness		6.8 ± 0.2A	8.1 ± 0.3A	4.6 ± 0.2B	3.5 ± 0.2B	7.3 ± 0.3A	***	***	***

[a] See Online Supplemental Appendix 1 for a table that includes all plant species producing fruit, including mean individual fruit mass and common names.

[b] COFL, *Cornus florida*; ILOP, *Ilex opaca*; MOCE, *Morella cerifera*; NYBI, *Nyssa biflora*; RHCO, *Rhus copallina*; RHTO, *Rhus toxicodendron*; RUCU, *Rubus cuneifolius*; VAAR, *Vaccinium arboreum*; VAST, *V. stamineum*; VIRO, *Vitis rotundifolia*.

[c] Forest types are upland hardwood forest (UHF), bottomland hardwood forest (BHF), mature loblolly pine plantation (LOBP), mature longleaf pine plantation (LLP), and young (harvested in 1993) clearcut regeneration harvests planted in longleaf pine (RH).

[d] Repeated measures analysis of variance. P values are for comparisons among forest types (P_{for}), year (P_{yr}), and forest × year interaction effects. ($P_{for \times yr}$). Asterisks in columns denote P values <0.001 (***), <0.01 (**), and <0.05 (*). NS = not significant ($P > 0.05$).

upland hardwoods (5,079 ± 529 g/ha), and bottomland hardwoods (4,621 ± 677 g/ha), and lowest in longleaf plantations (4,102 ± 877 g/ha) and loblolly plantations (3,261 ± 492 g/ha; Table 1). Total mass differed among years ($F_{8,408} = 10.1$, $P_{yr} < 0.001$) and forest types ($F_{4,51} = 5.1$, $P_{for} = 0.002$; Table 1). Average total mass production also exhibited a forest type × year interaction ($F_{32,408} = 1.9$, $P_{for \times yr} = 0.003$; Table 1). Among years, total fruit mass ranged from 1,927 ± 346 to 10,934 ± 2,147 g/ha in upland hardwoods; 1,337 ± 182–11,402 ± 4,341 g/ha in bottomland hardwoods; 921 ± 304–8,603 ± 2,906 g/ha in loblolly plantations; 927 ± 486–13,474 ± 6,338 g/ha in longleaf plantations, and 1,641 ± 675–38,226 ± 16,636 g/ha in regeneration harvests (Fig. 1a). Within years, pulp production differed among forest types except in 1995 ($F_{4,51} = 2.5$; $P = 0.053$) and 1998 ($F_{4,51} = 2.2$; $P = 0.082$). Within years, pulp production was generally highest in regeneration harvests, upland hardwoods, and bottomland hardwoods, and lowest in loblolly plantations and longleaf plantations (Fig. 1a). In upland hardwoods, bottomland hardwoods, loblolly plantations, and longleaf plantations inter-annual variation in dry pulp biomass production was high but production consistently averaged <13,500 g/ha, and showed no consistent trends over time (Fig. 1a). In contrast, inter-annual dry pulp mass production in regeneration harvests was highly variable and showed a trend of substantial decline from the study's origin through 2002 (9 years post-harvest; Fig. 1a).

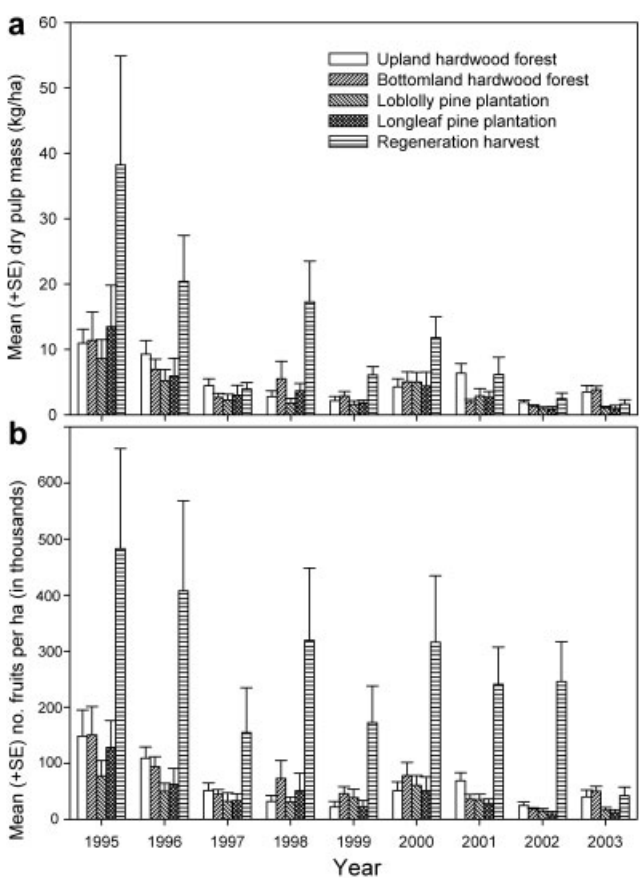

Figure 1. Mean (±SE) (a) annual total dry pulp mass (kg/ha) and (b) number of fleshy fruits produced in 5 forest types at the Savannah River Site, South Carolina, 1995–2003.

Mean annual number of fruits produced per ha was greatest in regeneration harvests (264,592 ± 37,444), bottomland hardwoods (65,614 ± 8,351), and upland hardwoods (60,769 ± 7,667), and fewest in longleaf plantations (44,104 ± 8,301) and loblolly plantations (39,532 ± 5,03; Fig. 1b). Fruit abundance differed among years ($F_{8,408} = 10.1$; $P_{yr} \leq 0.001$), by forest type ($F_{4,51} = 7.04$; $P_{for} \leq 0.001$), and demonstrated a forest type × year interaction ($F_{32,408} = 1.84$; $P_{for \times yr} = 0.004$; Table 1). The average number of fruits produced annually per ha ranged from 21,843 ± 10,072 to 148,213 ± 46,771 in upland hardwoods; 18,645 ± 1,959–150,362 ± 50,736 in bottomland hardwoods; 14,806 ± 4,253–77,582 ± 27,238 in loblolly plantations; 9,349 ± 4,665–128,027 ± 48,081 in longleaf plantations; and 42,207 ± 15,230–482,784 ± 178,346 in regeneration harvests (Fig. 1b). Within any given year, the number of fruits produced differed among forest types ($F_{4,51} \geq 2.73$; $P \leq 0.039$ in all years), and was generally greatest in upland hardwoods, bottomland hardwoods, and regeneration harvests, (Fig. 1b). In upland hardwoods, bottomland hardwoods, loblolly plantations, and longleaf plantations inter-annual variation in average total number of fruits produced was high, but production consistently averaged <151,000 fruits/ha in any given year, and showed no temporal pattern of increase or decrease among years (Fig. 1b). In contrast, in 1995 the average number of fruits produced in regeneration harvests (482,785 ± 50,735) was 3–6 times greater than the average number of fruits produced in any other forest type that year, and the total number of fruits produced in regeneration harvests remained greater than in the other forest types through 2002 (9 years post-harvest; Fig. 1b).

Fruit numbers and pulp mass differed among months ($F_{11,5937} = 225.5$; $P_{mo} \leq 0.001$ and $F_{11,5937} = 354.1$; $P \leq 0.001$, respectively) and forest types ($F_{4,51} = 12.1$; $P_{mo} \leq 0.001$ and $F_{4,51} = 11.8$; $P \leq 0.001$, respectively), with a significant month × forest type interaction ($F_{44,5937} = 7.6$; $P_{mo} \leq 0.001$ and $F_{44,5937} = 55.6$; $P \leq 0.001$, respectively; Fig. 2). Dry fruit pulp was plentiful June–September, peaking in July and August (Fig. 2a). Beginning in October, availability of fruit pulp declined monthly, with lowest mass availability in April (Fig. 2a). The number of individual fruits per ha was greatest June–October, and began to decline in November, decreasing each month thereafter to a low in April (Fig. 2b).

Dominant Fruit-Producing Species and Forest Types

Only 10 species produced on average ≥10% of dry pulp mass, number of fruits, or both (henceforth referred to as dominant species) within any given forest type (Table 1; Online Appendix 1). However, relative importance of species producing the greatest biomass and numbers of fruit differed among forest types (Table 1). In upland hardwoods, *C. florida* and *I. opaca* produced the most mass and individual fruits; *R. copallina* and *V. arboreum* were also numerically dominant, whereas *V. stamineum* and *V. rotundifolia* were

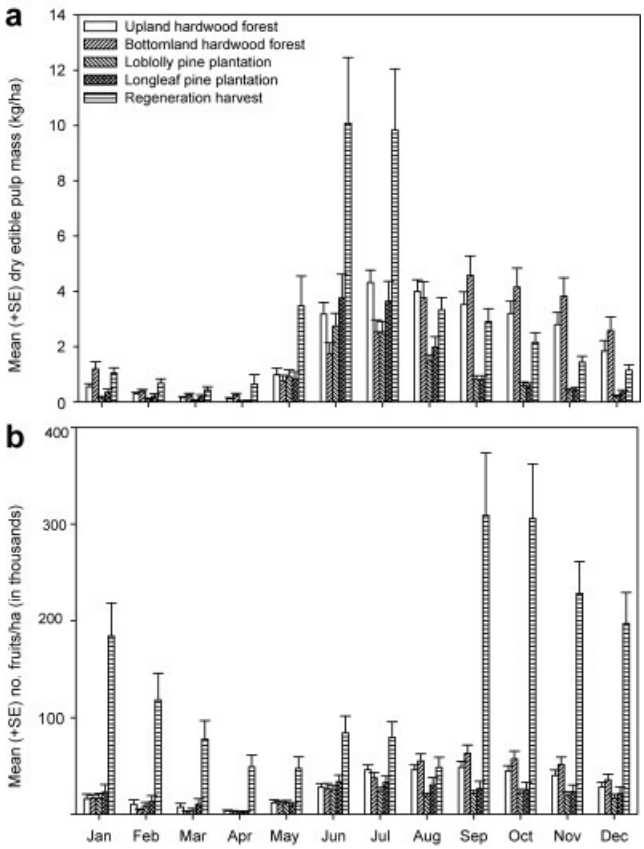

Figure 2. Mean (±SE) (a) total dry pulp mass (kg/ha) and (b) number of fruits/ha available each month (Jan–Dec) in each of 5 forest types at the Savannah River Site, South Carolina, 1995–2003.

dominant producers of dry pulp mass (Table 1). In bottomland hardwoods, *I. opaca* and *N. biflora* produced the most dry pulp mass and individual fruits. In loblolly plantations, *V. stamineum*, *C. florida*, and *V. rotundifolia* were dominant producers of fruit mass and number of fruits produced, whereas *M. cerifera* and *R. toxicodendron* produced large numbers of fruit. In longleaf plantations, *V. stamineum* dominated production of dry pulp mass and total fruits; *M. cerifera* and *R. toxicodendron* also produced >10% of total individual fruits. In regeneration harvests, *V. stamineum* was a dominant producer of fruit mass and number; *R. cuneifolius* was also a dominant fruit mass producer, whereas *M. cerifera* and *R. copallina* produced a large proportion of individual fruits in regeneration harvests (Table 2).

Spatial Variation in Fruit Production by Species

Fruit production by all species was spatially variable. Several species produced fruit only within a single forest type and (or) a subset of plots within a forest type (Online Supplemental Appendix 2), and fruit production by most species varied among years (e.g., Fig. 3). For example, 17 species—primarily those associated with mesic conditions—only produced fruit in bottomland hardwoods (Online Supplemental Appendix 1); most of those produced fruit in <30% of bottomland hardwoods plots in any given year (Online Supplemental Appendix 2). *Mitchella repens*, *P. borbonia*, *R. radicans*, and some *Smilax* species, produced

Table 2. Mean (±SE) annual dry pulp mass (g/ha) of plant species that produced ≥10% of total mean dry pulp mass or number of fruits in any given year in young (harvested in 1993) clearcut regeneration harvests planted to longleaf pine (RH) at the Savannah River Site, South Carolina, 1995–2003. Asterisks next to species codes denote *P* values <0.001 (***), <0.01 (**), and <0.05 (*) for analysis of variance testing for differences among years. Different letters within rows denote differences among years.

	Year								
Species[a]	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**
CRFL***	125 ± 125A	129 ± 129A	238 ± 238A	159 ± 101AB	673 ± 27B	354 ± 211AB	577 ± 448AB	58 ± 39AB	108 ± 64AB
MOCE*	22 ± 22A	136 ± 84AB	67 ± 32AB	335 ± 192AB	359 ± 178AB	442 ± 197B	345 ± 147B	265 ± 110AB	96 ± 39AB
OPCO***	962 ± 539ABC	2,447 ± 954A	500 ± 241BCD	534 ± 236ABC	538 ± 306AB	466 ± 194ABC	99 ± 44BCD	37 ± 18CD	20 ± 16D
PRAN	4 ± 4	18 ± 18	479 ± 479	152 ± 152	0 ± 0	2,260 ± 2,260	166 ± 146	26 ± 26	47 ± 39
PRSE	1,123 ± 822	12 ± 9	825 ± 633	1,134 ± 1,072	117 ± 96	563 ± 409	30 ± 23	353 ± 323	17 ± 12
RHCO***	1,065 ± 796ABC	1,261 ± 783A	613 ± 396AB	432 ± 311AB	123 ± 109BC	554 ± 422ABC	506 ± 196AB	801 ± 264A	3.8 ± 3.8C
RUCU**	775 ± 512 AB	1,489 ± 877AB	473 ± 366AB	6,829 ± 4,729A	525 ± 402AB	1,159 ± 555AB	159 ± 90AB	74 ± 53AB	58 ± 47B
VAST***	31,468 ± 17,106A	12,459 ± 7,541AB	2 ± 2C	6,936 ± 3,968AB	1,891 ± 505AB	5,039 ± 1,984AB	3,212 ± 1,856AB	611 ± 330 B	693 ± 459B
VIRO	1,630 ± 644	1,759 ± 1,439	699 ± 347	470 ± 219	1,682 ± 963	539 ± 247	517 ± 178	77 ± 29	73 ± 111

[a] CRFL, *Crataegus flava*; MOCE, *Morella cerifera*; OPCO, *Opuntia compressa*; PRAN, *Prunus angustifolia*; PRSE, *P. serotina*; RHCO, *Rhus copallina*; RUCU, *Rubus cuneifolius*; VAST, *Vaccinium stamineum*; VIRO, *Vitis rotundifolia*.

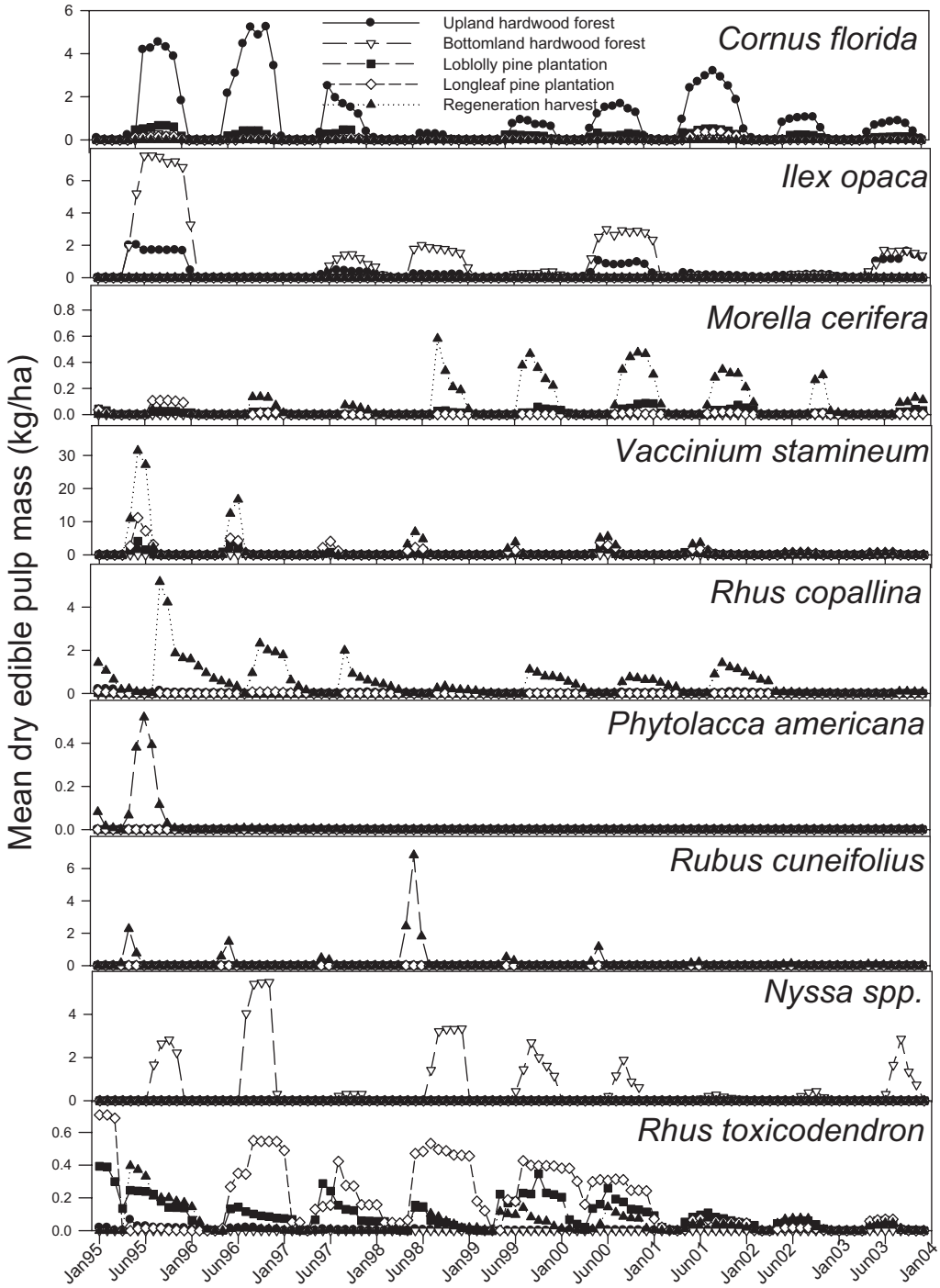

Figure 3. Mean monthly dry pulp mass (kg/ha) of some dominant fruit-producing species in 5 forest types at the Savannah River Site, South Carolina, 1995–2003.

fruit only in hardwood (upland hardwoods and bottomland hardwoods) forest types whereas others, such as *M. cerifera*, *R. toxicodendron*, *R. copallina*, and *O. compressa*, produced fruit only or primarily in young or mature pine plantations (regeneration harvests, loblolly plantations, and longleaf plantations; Online Supplemental Appendices 1, 2). Disturbance-adapted species such as *P. americana*, *R. copallina*, and *Rubus* spp. and some other ruderal species produced fruit only or predominantly in regeneration harvests, and quantities produced declined over the 9-year study period (Fig. 3).

Temporal Variation in Fruit Production by Species

Only a few species produced fruit in most years within 1 or more forest types (Online Supplemental Appendix 2). Prominent examples are: *C. florida* and *V. arboreum* in upland hardwoods; *I. opaca* in upland hardwoods and bottomland hardwoods; *M. repens*, *N. biflora*, *P. borbonia*, and *S. laurifolia* in bottomland hardwoods; *V. stamineum* in loblolly plantations, longleaf plantations, and regeneration harvests; *O. compressa*, *R. copallina*, and *R. cuneifolius* in regeneration harvests (Table 2); and *V. rotundifolia* in all 5 forest types.

Fruit crop sizes of several species differed among years (Fig. 3). For example, in upland hardwoods about 19 times more *C. florida* fruits were produced in 1996 than in 1998. In bottomland hardwoods more than 298 times more *I. opaca* fruits were produced in 1995 than in 1996, and 30 times more *N. biflora* fruits were produced in 1996 than in 2001. In longleaf plantations, about 33 times more *R. toxicodendron* fruits were produced in 1998 than in 1995.

Temporal changes in fruit production and the relative importance of some species in regeneration harvests were associated with stand development. A post-harvest (1995 and 1996) increase in fruit production in regeneration harvests compared to other forest types was primarily due to large quantities of fruit produced by *V. stamineum*, *R. copallina*, *R. cuneifolius*, and *O. compressa* (Table 2); *P. americana* also produced fruit during 1995 but composed <2% of total mass and total number of fruits in regeneration harvests that year. However, different species produced abundant fruit during different years of stand development. *Rhus copallina* was a dominant fruit producer for several years but production levels declined within 5 years post-harvest (Table 2). In contrast, *M. cerifera* fruit production increased through time and was a dominant fruit producer in regeneration harvests within 5-years post-harvest (Fig. 3). *Vaccinium stamineum* remained a dominant fruit producer in regeneration harvests during most years, with the notable exception of crop failure in 1997. Within 8 or 9 years post-harvest, fruit production by dominant species in regeneration harvests was similar to fruit production in the 4 mature forest types (Fig. 3). Fruit production (mass and number of fruits) in regeneration harvests did not differ from upland hardwoods or bottomland hardwoods because of high spatial and temporal variability in regeneration harvests (Fig. 1).

Differences in fruiting phenology (Fig. 3) and species distribution among the 5 forest types (Table 1) contributed to sustained fruit availability during most months (Fig. 2). Early spring (May) fruit species included blueberry (*V. corymbosum* and *V. elliottii*), most abundant in bottomland hardwoods, and *P. angustifolia*, *P. umbellata*, and several other species that were not associated with a particular forest type. *Vaccinium stamineum* was a summer (Jun and Jul) fruit that was most abundant in regeneration harvests, but also relatively abundant in loblolly plantations and longleaf plantations. *Rubus cuneifolius* was also available during summer, predominantly in regeneration harvests in 1998 (Fig. 3). Late summer and fall fruits included *N. biflora* (Aug–Nov) in bottomland hardwoods; *C. florida* (Jul–Nov), most abundant in upland hardwoods; and *R. toxicodendron* (Jun–Dec), most abundant in loblolly plantations and longleaf plantations, followed by regeneration harvests (Fig. 3). Winter fruits included *I. opaca* (Jun–Feb), most abundant in bottomland hardwoods and (less so) in upland hardwoods; *R. copallina* (Oct–Jul), predominantly in regeneration harvests; and *M. cerifera* (Sep–Jan), most abundant in regeneration harvests beginning about 5 years post-harvest, but also available in loblolly plantations and longleaf plantations (Fig. 3). *Smilax* spp. produced a small proportion of dry fruit pulp mass but retained fruits during winter months, with greatest amounts produced in bottomland hardwoods and upland hardwoods (Online Supplemental Appendix 1).

DISCUSSION

Fruit availability in the South Carolina upper Coastal Plain was highly variable because of differences in species composition among forest types and age classes, patchy distribution of fruiting plants both within and among forest types, fruiting phenology, high inter-annual variation in fruit crop size by some common species, and the dynamic process of disturbance-adapted species colonization and subsequent decline in recently harvested stands. Fruit number, pulp production, and species richness were consistently lower in 2 types of mature pine plantation, compared to mature upland and bottomland hardwood forest sites. This difference was likely because of drier, low-fertility sandy soils in the pine stands and lack of overstory hardwood species that produced fruit. Additionally, management that typically occurs in pine plantations such as midstory removal and prescribed burns are specifically intended to reduce densities of plants that compete with pines, contributing to reduced fruit-production. For example, fruit production by *M. cerifera* is temporarily eliminated by prescribed burning, and gradually increases for 5 years or more afterward (Borgmann et al. 2004). Ewel and Atmosoedirdjo (1987) also reported less fruit production in a southeastern pine plantation relative to a bottomland hardwood forest.

Fruit production patterns in regeneration harvests likely resulted from high light levels and recent soil disturbance that promoted colonization and fruiting by disturbance-adapted species initially, with shifts to different fruit producing species as the planted pines grew to canopy closure. Declining total fruit production in regeneration harvest sites over the 9-year study period was largely the result of decreasing production by common fruit-producing disturbance-associated species such as *Rubus* spp., *R. copallina*, *O. compressa*, and *P. americana* which produced abundant fruit in 1994 (C. H. Greenberg, U.S. Forest Service, unpublished data) but was not a major component of total fruit production by 3 years post-harvest. *Vaccinium stamineum* fruit production also declined in regeneration harvests after an initial spike, likely because of decreased light availability with increasing canopy closure. Decreased production by those species was offset somewhat by fruiting of *M. cerifera* as it recovered by sprouting and produced large quantities of fruit in regeneration harvests. In our study, pulp mass and fruit producing species richness did not differ between regeneration harvests and both hardwood forest types, upland hardwoods and bottomland hardwoods; this was likely because of the high spatial and temporal variability in fruit production and species producing fruit in regeneration harvests compared to upland hardwoods and bottomland hardwoods over the 9-year study period. Other studies also showed increased fruit production in recently harvested pine plantation (e.g., Halls and Alcaniz 1968, Johnson and Landers 1978, Campo and Hurst 1980, Stransky and Roese 1984) and other recently disturbed forest types (see Greenberg et al. 2011), and that the suite of species produc-

ing the most fruit changed with stand maturation and canopy closure (Johnson and Landers 1978, Greenberg et al. 2011).

Among the 60 species producing fleshy fruit during our study, only a few produced the majority of total dry pulp mass and (or) individual fruits. With respect to production of dry fruit pulp, *V. stamineum* dominated (43% of total), followed by *V. rotundifolia* (10%), *C. florida* (9%), *I. opaca* (7%), *Rubus* spp. (4%), and *N. biflora* (6%). Other species produced large numbers of small fruits (i.e., dominated numerically): *R. copallina* (24%), *M. cerifera* (18%), and *R. toxicodendron* (7%). Although these species did not contribute greatly to total mass, they are nonetheless important food resources for wildlife. For example, the fruit of *M. cerifera* is a critical food for yellow-rumped warblers (*Dendroica coronata*) and influenced their local distribution in winter at our study site (Borgmann et al. 2004, Kwit et al. 2004*a*). Likewise, *R. toxicodendron* fruits are removed by wildlife more quickly and more completely than fruits of practically all other species at our site (McCarty et al. 2002), suggesting they are a highly preferred and nutritious food source. Thus, managers cannot assume that species producing the most fruit are necessarily the most commonly consumed or preferred by wildlife.

More generally, temporal variation in fleshy fruit production was punctuated by the erratic nature of fruit production in some species in all forest types. Substantial variation in crop size among years by several dominant species in the 4 mature forest types (where light conditions were relatively static during the study period) suggests masting. Masting implies synchronous fruit production by individuals within a population that results in boom or bust crop years (Silvertown 1980). Large crops in some years (booms) and complete failures in other years (busts) are well documented for oaks (see Greenberg and Warburton 2007) and some studies have likewise suggested masting in some species that produce fleshy fruits (Herrera et al. 1998). However, synchronized fruiting by oak populations does not occur in all years, and moderate crop sizes are also common (see Greenberg and Warburton 2007). In our study, *I. opaca* produced no fruit in 4 years, *N. biflora* and *R. toxicodendron* produced none in 3 years, and *C. florida* produced none in 1 year. However, crop sizes also fluctuated dramatically among years for those species, even during non-failure years. For example, dry pulp mass production by *I. opaca* was nearly 5 times greater in 1995 than in 1997. Variation in crop size may be affected by weather during flowering or fruit development, inter-annual differences in energy allocation to growth versus fruit production, or other factors. Although we did not analyze fruiting synchrony among conspecifics and our study period was too brief to document consistent cycles of fruit production for any species, the potential for masting patterns by some fleshy fruit producing species warrants further exploration.

Several abundant fruiting species were strongly associated with specific forest types and (or) years, likely because of differences in topography, soil moisture, and history of disturbance and management (Odum 1991, White and Gaines 2000). For example, *C. florida* was a dominant fruit producer in upland hardwoods, whereas *I. opaca* and *N. biflora* were dominant fruit producers in bottomland hardwoods but produced relatively little or no fruit in the other 4 forest types. In contrast, *R. toxicodendron* and *M. cerifera* were dominant fruit producers in loblolly plantations and regeneration harvests, but did not produce substantial amounts of fruit in the upland hardwood or bottomland hardwood forest types. Some species, such as *R. copallina* and *R. cuneifolius* were closely associated with recently disturbed sites (regeneration harvests). *Vaccinium stamineum* produced a large proportion of dry fruit pulp mass in upland hardwoods (11%), loblolly plantations (47%), longleaf plantations (76%), and regeneration harvests (58%), but not in bottomland hardwoods.

Several other less abundant fruit-producing species also were exclusively or nearly exclusively associated with specific forest types. For example, *A. triphyllum*, *I. glabra*, *M. virginiana*, *M. repens*, *P. borbonia*, *R. radicans*, *S. laurifolia*, *S. rotundifolia*, *V. corymbosum*, and *V. elliottii* occurred and produced fruit exclusively or nearly exclusively in bottomland hardwoods and contributed to the overall greatest species richness of fruit species in bottomland hardwoods. Species that produced relatively minor amounts of fruit mass nonetheless contributed cumulatively to differences in total fruit production among forest types or seasons. Further, the importance of each fruit species is difficult to evaluate because any given species may be uncommon in the diets of most animal species, yet could be critical to a few.

Fruit availability also varied seasonally, with different species—many associated with only 1 or a few forest types—producing or retaining fruit during different months and for differing lengths of time. Generally, fruit production was greatest from late spring through fall. Common summer fruits included *V. stamineum* (occurring in all 5 forest types but most abundant in regeneration harvests). *Rubus* spp. was also a common summer fruit, but only in regeneration harvests 4–5-years post-harvest (1997–1998). Late summer and fall fruits included *C. florida* (dominant in upland hardwoods) and *N. biflora* (dominant in bottomland hardwoods). *Rhus toxicodendron* produced fruit during summer and fall (dominant in both mature pine plantation types). Common winter fruits were *I. opaca* (dominant in bottomland hardwoods), *M. cerifera*, and *R. copallina* (both dominant in regeneration harvests). Winter fruit availability was generally greater in bottomland hardwoods, regeneration harvests, and upland hardwoods than in both mature pine plantation types.

The timing and quantity of fruit production may affect consumption rates by vertebrates (Willson and Whelan 1993). Availability of winter fruits may be critical to some over-wintering birds, and had a demonstrable influence on the abundance and distribution of hermit thrush (*Cathartus guttatus*; Kwit et al. 2004*a*) and yellow-rumped warblers (Borgmann et al. 2004) at our study site. Maintaining a diversity of fruit-producing species at a landscape level provides food for a variety of wildlife species, as some fruit species are consumed preferentially whereas others may be consumed most heavily by some vertebrates and (or) at different times of the year (McCarty et al. 2002). High

spatio-temporal variability in fruit availability among the 5 forest types we studied highlights the importance of maintaining a diversity of forest types at a landscape level.

Our estimates of total fruit mass production in mature upland hardwood forests in the upper Coastal Plain were on average 3.5 greater than estimates in similar forests of the southern Appalachians (average 1,439 g dry pulp/ha and 5,079 g/ha, respectively; Greenberg et al. 2007). Similarly, peak dry fruit pulp biomass was 2.4 times greater in young clearcuts in our study area (regeneration harvests) than in recent harvests of upland hardwood forests in the southern Appalachians (average 38,226 g/ha 2 years post-harvest, and 15,963 g/ha 5 years post-harvest, respectively). In pine-hardwood forests of the Interior Highlands of Arkansas and Oklahoma, average estimates of dry pulp mass production (including only fruit $\leq$2 m above the ground) were 28.8 times greater for 5-year old clearcut regeneration harvests than for mature forests (18,596 g/ha and 645 g/ha, respectively; see Greenberg et al. 2011).

Geographic and site differences may contribute to some differences in total fruit production estimates among physiographic regions, as these factors influence the presence and relative abundance of some common fruit-producing species. For example, *V. stamineum* was the dominant fruit-producing shrub in our study area, whereas *Gaylussacia ursina* (another ericaceous shrub) was the dominant fruit-producing shrub in the southern Appalachians (Greenberg et al. 2007). Other plant species, such as *M. cerifera* and *S. laurifolia*, were common winter fruit producers in our study area but do not occur in the southern Appalachians or forests further north. Different estimates of dry pulp mass for dominant fruit-producing species may also contribute to differences in estimates of relative importance or total fruit biomass production among studies or regions. For example, our dry pulp biomass estimates for *V. stamineum*, *C. florida*, *Rubus* (a different species), and *R. copallina* fruits for the upper Coastal Plain were >2 times greater than estimates for those species in the southern Appalachians in Greenberg et al. (2007). Finally, random plot placement and finite replication may lead to error in estimates of fruit production because of spatial variation in the occurrence and density of fruit-producing plants among landscapes.

Comparison of fruit mass production among studies is confounded because most studies report mass of whole dry fruits, including seeds. However, we believe that reporting dry pulp provides a more practical estimate of fruit production for land managers because seeds of fleshy fruit are not generally digested by fruit-eating wildlife and hence provide no nutritional value (Herrera 1982). Nutrient content of pulp differs among fruit species and is an important factor in fruit selection by different wildlife species (Levey and Martinez del Rio 2001); thus estimates of nutrient content must be considered along with pulp mass when determining fruit value to wildlife.

MANAGEMENT IMPLICATIONS

Young regeneration stands are especially important because they typically produce large quantities of fruit in relatively small areas and can be key foraging areas for many wildlife species (Greenberg et al. 2011). Forest management disturbances such as timber harvest, burning, and other management techniques that substantially alter forest structure and light availability to the forest floor can greatly affect fruit availability and thereby affect the use of habitats by wildlife. Nonetheless, our results show that fruit availability in regenerating forests can change quickly. Also, many common fruit producing species may produce fruits primarily in forest types or age classes other than young pine plantations. Thus, a prudent strategy for land managers to maintain availability of at least some fruit is to provide a diverse landscape of different forest types and age-classes that include young, regenerating forests (see Shifley and Thompson 2011). Although we found that most fruits in a given forest type are produced by just a few species, we suggest 2 reasons why management should not focus on those species exclusively. First, many of the most prolific producers are either associated with ephemeral forest types (i.e., regenerating clearcuts) or are highly variable in annual production of fruits. Second, fruit pulp varies substantially among species in protein, carbohydrate, and lipid content, and in the amount and chemical profile of secondary compounds (Levey and Martinez del Rio 2001). Consequently, most temperate birds and other wildlife species that consume fruit likely depend on a wide variety of fruits; a single species is unlikely to suffice, regardless of abundance.

ACKNOWLEDGMENTS

We thank J. I. Blake and the U.S. Forest Service for long-term logistical and financial support of this study (No. SU96-43-F; D.J.L. and C.H.G., PIs). Support was also provided by the Department of Energy-Savannah River Operations Office through the U.S. Forest Service Savannah River under Interagency Agreement DE-IA09-76SR00056. K. Borgmann, A. Brinton, R. Busser, C. Deppe, T. Hargrave-Roof, N. Khalil, M. Reiskind, C. Renk, and E. Uramkin assisted with fruit surveys. A. Poole provided soils information for plots. B. Parresol provided statistical guidance and review. T. L. Keyser, T. Fearer, G. Roloff, and 3 anonymous reviewers helped improve earlier versions of this manuscript.

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Associate Editor: Gary Roloff.