



Frequent fires eliminate fleshy fruit production



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ABSTRACT

Frequent fire-return intervals (< 3-yr) have been suggested to optimize the benefits of prescribed fire in many fire-dominated ecosystems. There are several potential ecological benefits to frequent fires, such as suppression of encroaching fire-intolerant plant species, increased reproductive allocations of native herbaceous plant species, and increased plant diversity at the stand level. However, recent literature has reported a decline in frugivorous wildlife species in frequently burned landscapes, raising concern for fire-regime effects on fruit production. Thus, an assessment of the effects fire frequency on fleshy fruit abundance is needed. In a replicated field experiment following 4 or more rotations of a 1-yr, 2-yr, and 3-yr fire-return interval, we measured fruit production each month of the growing season (i.e., May–September) in the critically threatened longleaf pine (*Pinus palustris*) ecosystem – an ecosystem where frequent fire intervals commonly are recommended. Compared to the 3-yr fire-return interval, cumulative understory fruit production was 99% less following a 1-yr or 2-yr fire-return interval. In fact, all of the fruit detected in 1-yr and 2-yr treatments were detected in patches of vegetation unburned by the previous fire. Additionally, no fruits were detected on any transect in the midstory and overstory strata. These results suggest that applying fire on < 3-yr fire-return intervals across large land areas could have negative effects on soft mast-dependent wildlife species. Moreover, without a mosaic in fire-spread, even a 3-yr fire return interval may eliminate midstory and overstory fleshy fruit production over time. We recommend fire managers incorporate multiple fire-return intervals and firing techniques to capture the ecological benefits of variability in frequency and spatial extents in fire.

1. Introduction

Many plant species have evolved an energy-rich fleshy pulp that encapsulates seeds (i.e., fleshy fruit) to encourage wildlife consumption and facilitate gene dispersal of the host plant (Jordano, 2000). Concomitantly, many wildlife species evolved dietary niches to take advantage of the high-energy food source, making fleshy fruit availability a critical habitat component for those wildlife species (Howe, 1986). For example, fleshy fruits are a primary energy source for many migratory birds in the Americas during fall migration, and lack of fruit may preclude the stopover use of some areas by migrating birds despite other habitat components being intact (Buler et al., 2007). Likewise, fleshy fruit abundance may be of central importance to short-distance migrants or resident birds (McCarty et al., 2002) and has been linked to population fluctuations in some mammal species (Reynolds-Hogland et al., 2006). Thus, relatively large-scale management actions that limit the availability of fleshy fruits may negatively affect many wildlife populations.

Prescribed fire commonly is used to restore and maintain fire-dependent ecosystems. Fire-return intervals are a key component of a fire prescription and a fire-return interval often is designed to maximize some metric of ecosystem function (Hiers et al., 2000; Kirkman et al., 2004; Mitchell et al., 2006). For example, in the longleaf pine (*Pinus palustris*) ecosystem (LLPE), Glitzenstein et al. (2003, 2012) suggested burning areas as frequently as fuels would allow because that fire-return interval yielded the greatest benefit in terms of their metric (i.e., diversity of understory plants). Also, in South African grasslands, Uys et al. (2004) suggested frequent fires for ecosystem maintenance based on their metric – grass and forb diversity. Other metrics of ecosystem function, such as suppression of woody encroachment in oak savannas in North America (Peterson and Reich, 2001) and reduction of fuel loads to minimize wildfire risks (Stephens et al., 2009), are best accomplished by frequent fire-return intervals. Thus, if maximizing understory plant diversity, minimizing woody plant encroachment, or reducing wildfire risk is the management goal, a ≤ 2 year fire-return interval often is recommended (Glitzenstein et al., 2012, but see

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Syphard et al., 2006). However, because plants respond differently to fire-return interval, this approach to setting a fire-return interval may have negative consequences to other ecosystem functions (Uys et al., 2004; Syphard et al., 2006; Lashley et al., 2014a; Lashley et al., 2015a). Studies in Australia indicated marked declines in frugivorous and insectivorous birds following frequent fires (Woinarski and Legge, 2013), which may be linked to a decline in their respective food sources (Radford and Andersen, 2012; Valentine et al., 2014). Frequent fires may even eliminate fire-dependent plant species that require less frequent fire (Syphard et al., 2006). Pyrodiversity in terms of variation in fire frequency is likely needed to maximize biodiversity (Griffiths et al., 2015).

Despite the functional role of fruits and the potential effects of fire on fruit production, few studies have reported the effects of fire-return interval on these food sources. Sanaiotti and Magnusson (1995) reported that yearly fires nearly eliminated fruit production in Brazil, but noted that the historical fire regimes with which the plants evolved were less frequent than the yearly burns in their study. In the LLPE, where plants have evolved with frequent fires, Lashley et al. (2015a) suggested understory fruit production could be eliminated with the widespread application of < 3 yr fire-return intervals, based on their study of fruit in each year of a 3-yr fire return interval. However, their observational study of years-since-fire within a 3-yr fire-return interval did not explicitly test the effects of shorter fire-return intervals on fruit production. They also suggested that shorter intervals could create a sparser fuel bed to carry fire and thus burn more patchy allowing fruit production to persist. Therefore, a long term experiment is needed to confirm the relationship between fruit production and fire-return interval in systems that evolved with relatively frequent fire-return intervals.

We used a replicated field experiment to compare the effects of a 1-yr, 2-yr, and 3-yr fire-return interval on fleshy fruit production each month of the growing season (i.e., May–September) in the LLPE. We hypothesized that fruit production would be suppressed in 1-yr and 2-yr fire-return intervals in comparison to 3-yr fire-return intervals (Sanaiotti and Magnusson, 1995; Lashley et al., 2015a). In that case, applying those frequent fires could result in widespread suppression of fruit production.

2. Methods

We sampled fruit production at Fort Bragg Military Installation (FB), North Carolina (35.1 °N, –79.2 °W). The 73,469-ha property was located in the Sandhills physiographic region of the LLPE. Since 1989, the United States Department of Defense has managed most forested stands at FB on a 3-yr rotation during growing season (April–June) (Cantrell et al., 1995). The fire regime was initiated to maintain open mid-story structural requirements for the federally endangered red-cockaded woodpecker (*Picoides borealis*) and to maximize total biodiversity of the LLPE (Cantrell et al., 1995). The long-term average yearly rainfall was 120 cm, average yearly snowfall was 7.5 cm, and there were ~175 frost-free days per year (Sorrie et al., 2006). Longleaf pine needles and wiregrass (*Aristida stricta*) were the primary fuels responsible for the spread of fire through the understory. Primary fruit-producing flora in the understory of longleaf pine stands were huckleberry (*Gaylussacia* spp.), blueberry (*Vaccinium* spp.), blackberry (*Rubus* spp.), poison oak (*Toxicodendron* spp.), and sumacs (*Rhus* spp.) (Lashley et al., 2015a).

In a randomized block design, we selected 3 upland longleaf pine forest stands in each of 3 separate watersheds (blocks) averaging ~8 km apart, with similar soil types (Candor Sands complex), and similar basal area (45–60 m² ha⁻¹). Candor sands typically are excessively well-drained, relatively low productivity, and range from 8 to 15% slopes. We selected stands averaging 40 ha in size and grouped them into 1 of 3 treatments: 1-year, 2-year, and 3-year fire-return interval. The stands on 1-year fire cycles had been burned every year in December–February since 1985 (29 rotations completed). The stands on

2-year fire cycles initiated in 2008 had been burned every 2 years in May–June, and had completed 3–4 rotations at the time of the current study. The stands on 3-year fire cycles were initiated in 1989 and had at least 4 consecutive rotations where fires had been set in May–June. The 3-year cycle was intended to be the control because that return-interval was the standard recommendation for the LLPE (Lashley et al., 2014a). *A priori* upon initial design, we anticipated that the season of fire would affect the phenology of fruit production within stands but would not affect the cumulative production of fruits across a growing season (see Lashley et al., 2015a). Thus, we decided to only report cumulative fruit production to avoid biases associated with fire season among return interval treatments. Each block contained a replicate from each treatment. To follow fruit production in each year of the rotation in the 2-yr fire-return interval treatment, 2 stands were used in a chronosequential design within each block (i.e., each stand was in a different year of the rotation). Only one stand was required for the 1-yr fire-return interval treatments because the 1-yr was necessarily measured in the same year as fire. We also used only one stand for the 3-yr fire-return interval treatment because an earlier, related study indicated that 96% of fruit production occurs in the third year after burning in LLPE (Lashley et al., 2015a). The chronosequential design in 2-yr treatments allowed us to simultaneously measure fruit production in each year of the rotation under similar climatic conditions.

We randomly placed 30 50-m transects in each treatment replicate in each of 5 months (May–September). Because the 2-yr interval had a 1-yr and 2 years-since-fire, we split the treatment into two plots and established 30 transects each month within both years of the fire return interval. In the 3-yr treatment, we only measured the fruit produced in the third year of production, which was conservative because fruits that may have been produced in the first and second years of the rotation were not added to the total cumulative production as they were in the 2-yr treatment. We used the fruit count method (Lashley et al., 2014b) to count understory fruits under 1.2 m in height and within 0.5 m of each side along a 50-m transect. Also, we monitored the midstory and overstory strata with the intention of counting fruit on any plant with canopy that intercepted each transect, but no midstory or overstory fruits (or parent fruit-bearing plants) were detected. We tallied fruits by species and extrapolated each transect fruit count into fruits per hectare. To ensure treatment did not influence biomass of individual fruits (i.e., that count and biomass would produce the same result), we collected fruits from a variety of forest types and fire histories and determined that fruits of all species consistently averaged 0.05 g per fruit (dry weight), which was consistent with a previous experiment that evaluated fruit biomass on the site (Lashley et al., 2014b).

3. Results

After initial inspection of the data, it was apparent that inferential statistics were not required because of the magnitude of difference among treatments. Thus, we used descriptive statistics to present the results. No midstory or overstory fruits (or fruit-bearing plants) were detected for the entirety of the field sampling. Understory fruit production was 99% less in 1-yr and 2-yr fire-return intervals than in the 3-yr fire-return interval (Fig. 1) and the standard error overlapped zero in the 1-yr treatment. We detected fruit on 2% of transects in 1-yr and 3% of transects in the 2-yr fire-return interval as opposed to 18% of transects in the 3-yr fire-return interval treatment. No fruits were detected in the same year as fire in the 2-yr fire-return interval. Also, we detected 25 and 27 as maximum fruit counts on a single transect in the 1-yr and 2-yr treatments, respectively, as opposed to the maximum detection of 660 fruits on a single transect in the 3-yr fire-return interval treatment. Almost all fruit detected belonged to *Toxicodendron* spp. (91% of fruit detected), *Gaylussacia* spp. (4% of fruit detected) and *Vaccinium* spp. (4% of fruit detected). Plants in each of those genera were detected frequently in all replicates and were detected on the majority of transects (i.e., each genera was detected on 80–90% of

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