Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Frequent fires eliminate fleshy fruit production

Marcus A. Lashley[a,*], M. Colter Chitwood[b], Christopher S. DePerno[b], Christopher E. Moorman[b]

[a] Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Box 9690, Mississippi State, MS 39762, USA
[b] Department of Forestry and Environmental Resources, Fisheries, Wildlife, and Conservation Biology, North Carolina State University, 110 Brooks Avenue, Raleigh, NC 27607, USA

ARTICLE INFO

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

* Corresponding author.
E-mail address: marcus.lashley@msstate.edu (M.A. Lashley).

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 m^2 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
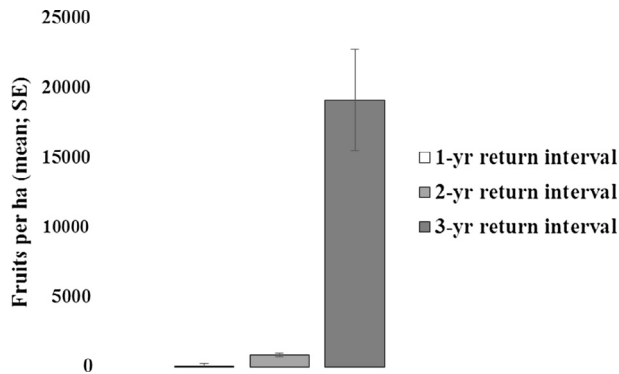
Fig. 1. The effects of fire-return interval on understory fruit production (mean; SE) in the longleaf pine ecosystem at Fort Bragg Military Installation, North Carolina, June–September 2014. Fruit counts reflect the sum of fruits detected in each month of sampling. Note that the 2-yr fire-return interval includes the sum of fruits detected in the same and year after fire (i.e., chronosequential design) whereas the 3-yr fire-return interval only includes fruits detected in the last year of the rotation.
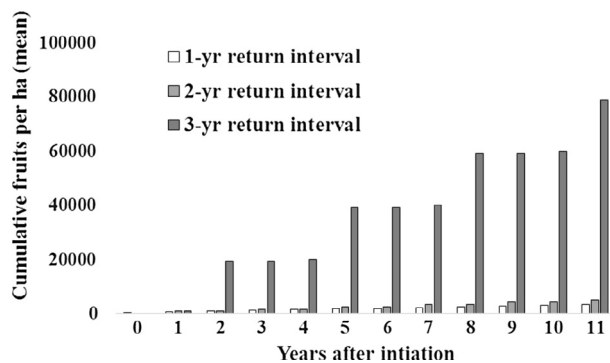

Fig. 2. Projected cumulative fruit production over a 12-year period following the initiation of each fire-return interval based on data collected at Fort Bragg Military Installation during 2014. This figure is intended for visualization of the projected differences in fruit production over a typical fire management plan timeframe. Estimates are based on results from the respective treatment and are applied recurrently to the respective time-since-fire over time for the respective fire treatment.

transects in all replicates and treatments). One genus dominated the fruit production in each fire-return interval: *Toxicodendron* was 95% of the fruit detected in the 3-yr return interval, *Vaccinium* was 96% of the fruit detected following the 2-yr return interval, and *Gaylussacia* was 77% of the fruit detected in the 1-yr return interval. As such, the phenology of fruiting in each return interval followed that of the dominant genera peaking in September in the 3-yr return, July in the 2-yr return, and June in the 1-yr return. During data collection, we noted that all fruits detected in the 1-yr and 2-yr fire-return interval treatments were located within patches of vegetation that apparently were not consumed by the previous fire despite the presence of fruit-bearing genera in areas that had burned. We projected the cumulative fruit production expected from each fire-return interval given our observations over a 12-year duration. Cumulative fruits produced in the 3-yr return interval was projected to be almost 16-fold and 23-fold that expected in the 2-yr and 1-yr fire-return intervals, respectively, over the course of 12 years (Fig. 2).

4. Discussion

The widespread application of < 3-yr fire-return intervals may result in reduced fruit production on the landscape. Although < 3-yr fire-return intervals rarely are applied at this scale in the LLPE and we did not monitor frugivore populations in this study, coupling our results with reports of frugivore population declines in other ecosystems where this practice is widespread (Woinarski and Legge, 2013; Valentine

et al., 2014) suggest that reduced fruit production following large-scale frequent fires may affect frugivore populations negatively. Thus, fire prescription recommendations may need to be revised to minimize the potential negative impacts of frequent fire regimes on fruit production and frugivores should this practice be adopted over large areas. We suggest the loss of fruit production may arise from the lack of heterogeneity in fire frequency, given that fire disturbances positively affect fruit production in longer return intervals (McCord et al., 2014). Similarly, homogenously applied fire frequencies may simplify other forest structural characteristics in the longleaf pine ecosystem (Lashley et al., 2014a). Likewise, the mosaic in plant community conditions that would be created by variability in fire return may be lacking in other frequently burned systems and may be the root of issues with declining wildlife populations there as well (Braithwaite, 1995; Price et al., 2005; Bradstock et al., 2005; Woinarski and Legge, 2013; Valentine et al., 2012). Because flora and fauna vary widely in their response to fire, there is little doubt that heterogeneity in fire prescriptions is required to maximize biodiversity (Bradstock et al., 2005). In fact, heterogeneity in fire applications has been the proposed as the basis for conservation in some fire-maintained ecosystems (Fuhlendorf and Engle, 2001) because of the positive impacts that heterogenous forest structure (and food resources) has on total biodiversity (Brockett et al., 2001; Fuhlendorf et al., 2006, Harper et al., 2016).

Similar to reports from other fire maintained ecosystems, our results suggest that lack of mosaic in fire spread at the stand level could potentially have negative effects on some wildlife species (Bradstock et al., 2005; Braithwaite, 1995; Price et al., 2005). The fire mosaic may be important to frugivores because fruit production may be restricted to the unburned patches. For taxa less dependent on fruit, other studies reported the mosaic may be important for cover or other food sources (Braithwaite, 1995; Price et al., 2005; Lashley et al., 2015b; Chitwood et al., 2017). Also, because the more frequent fires allow less time for fuel to accumulate, we anticipated that the lower fuel load may increase the patchiness of the fires which could allow understory fruits to persist in ≤ 2 year intervals. However, our data suggest that the shorter intervals did not increase patchiness. The lack of mosaic in fire-spread is a result of the distribution of fuels affecting fire behavior at fine scales in the understory (Ellair and Platt, 2013), the firing techniques used, the intentional burnout of unburned patches for fuel reduction, and the relatively narrow range of climatic conditions in which managers are allowed to burn (Cheney et al., 1993). What constitutes a mosaic is a question of scale that depends on the life histories of the taxa of interest (Brockett et al., 2001; Fuhlendorf and Engle, 2001, Bradstock et al., 2005, Fuhlendorf et al., 2006). Thus, depending on the taxa of interest, a fire mosaic may be encouraged in frequently burned ecosystems in 2 ways: (1) at the stand level through a mosaic of fire-spread resulting in unburned patches; and (2) at the landscape level by varying fire-return intervals and seasonality. We suggest efforts should be made to encourage the desirable fire mosaic at both scales. However, literature on how best to encourage a mosaic in fire-spread at the stand level is lacking. Given the potential importance of the fire mosaic to wildlife, there is need for further investigation of how firing techniques interact with fuels and climatic conditions to affect fire-spread at a fine scale across fire-dependent ecosystems.

Despite recommendations for more frequent fire, < 3-yr fire-return intervals are not yet commonly applied in the LLPE. Likewise, reports of declines in frugivorous wildlife in the LLPE are uncommon. However, the problem of precision in fire applications within the LLPE is indeed widespread (Hiers et al., 2016). Currently, much of the LLPE is managed under a 3-yr fire return interval with little variation (Hiers et al., 2014), despite dendrochronology indicating historical fire regimes ranging from biannual to 12-yr intervals (Stambaugh et al., 2011). This precision problem (i.e., failure to represent variability; Hiers et al., 2016) could result in a perpetual fire trap for some key mast producing hardwood species (Lashley et al., 2014a). Our failure to detect fruit-bearing species in the midstory and overstory strata further supports

that the lack of mosaic in fire-spread within stands, and the notion that it could prevent midstory and overstory fruit production even with a 3-yr fire-return interval. Removing the functional roles of those fruit producers from the ecosystem at large scales could have obvious direct effects on wildlife species that consume mast from midstory and overstory plant species or use it for another habitat component (i.e., red-headed woodpeckers *Melanerpes erythrocephalus* [Kilgo and Vukovich, 2012], fox squirrel *Sciurus niger* [Prince et al., 2016], white-tailed deer *Odocoileus virginianus* [Lashley et al., 2015b]). Despite records of mature oaks (*Quercus* spp.) that are endemic to the LLPE commonly occurring under historical fire regimes (Greenberg and Simons, 1999), efforts to limit these species from reaching maturity are still common because of some specific management objectives (Hiers et al., 2014).

Similar to Beckage et al. (2005), we caution managers on the development of fire management plans based on the response of few focal flora or fauna in fire-maintained ecosystems because of the potential negative consequences of homogeneous fire applications. Likewise, although our data reveal potentially majors issues with < 3-yr fire-return intervals, we do not recommend that all stands be maintained on > 2-yr fire-return intervals. Rather, we recommend managers target a distribution of fire-return intervals that represent mean and variation of historical reference fire regimes (i.e., 0.5–12 yr return intervals in LLPE; Stambaugh et al., 2011). Further, we encourage fire managers to evaluate patchiness at the stand level following prescribed burns and adjust firing techniques to encourage patchiness as needed.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.034.

References

Beckage, B., Platt, W.J., Panko, B., 2005. A climate-based approach to the restoration of fire-dependent ecosystems. Restor. Ecol. 13, 429–431.

Bradstock, R.A., Bedward, M., Gill, A.M., Cohn, J.S., 2005. Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. Wildlife Res. 32, 409–423.

Braithwaite, R.W., 1995. Fire intensity and the maintenance of habitat heterogeneity in a tropical savanna. Calmscience Suppl. 4, 189–196.

Brockett, B.H., Biggs, H.C., Van Wilgen, B.W., 2001. A patch mosaic burning system for conservation areas in southern African savannas. Int. J. Wildland Fire 10, 169–183.

Buler, J.J., Moore, F.R., Woltmann, S., 2007. A multi-scale examination of stopover habitat use by birds. Ecology 88, 1789–1802.

Cantrell, M.A., Britcher, J.J., Hoffman, E.L., 1995. Red-cockaded woodpecker management initiatives at Fort Bragg Military Installation. In: Kulhavy, D.L., Hooper, R.G., Costa, R. (Eds), Red-cockaded Woodpecker: Recovery, Ecology and Management. Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin State University, Nacodoches, TX, USA, pp. 89–97.

Cheney, N.P., Gould, J.S., Catchpole, W.R., 1993. The influence of fuel, weather and fire shape variables on fire-spread in grasslands. Int. J. Wildland Fire 3, 31–44.

Chitwood, M.C., Lashley, M.A., Sherrill, B.L., Sorenson, C., DePerno, C.S., Moorman, C.E., 2017. Macroarthropod response to time-since-fire in the longleaf pine ecosystem. For. Ecol. Manage. 391, 390–395.

Ellair, D.P., Platt, W.J., 2013. Fuel composition influences fire characteristics and understory hardwoods in pine savanna. J. Ecol. 101, 192–201.

Fuhlendorf, S.D., Engle, D.M., 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns: we propose a paradigm that enhances heterogeneity instead of homogeneity to promote biological diversity and wildlife habitat on rangelands grazed by livestock. Bioscience 51, 625–632.

Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A., Leslie, D.M., 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecol. Appl. 16, 1706–1716.

Glitzenstein, J.S., Streng, D.R., Masters, R.E., Robertson, K.M., Hermann, S.M., 2012. Fire-frequency effects on vegetation in north Florida pinelands: another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. For. Ecol. Manage. 264, 197–209.

Glitzenstein, J.S., Streng, D.R., Wade, D.D., 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and northeast Florida, USA. Nat. Areas J. 23, 22–37.

Greenberg, C.H., Simons, R.W., 1999. Age, composition, and stand structure of old-growth oak sites in the Florida high pine landscape: implications for ecosystem management and restoration. Nat. Areas J. 19, 30–40.

Griffiths, A.D., Garnett, S.T., Brook, B.W., 2015. Fire frequency matters more than fire size: testing the pyrodiversity–biodiversity paradigm for at-risk small mammals in an Australian tropical savanna. Biol. Cons. 186, 337–346.

Harper, C.A., Ford, W.M., Lashley, M.A., Moorman, C.E., Stambaugh, M.C., 2016. Fire effects on wildlife in the central hardwoods and appalachian regions, USA. Fire Ecology 12, 127–159.

Hiers, J.K., Jackson, S.T., Hobbs, R.J., Bernhardt, E.S., Valentine, L.E., 2016. The precision problem in conservation and restoration. Trends Ecol. Evol. 31, 820–830.

Hiers, J.K., Walters, J.R., Mitchell, R.J., Varner, J.M., Conner, L.M., Blanc, L.A., Stowe, J., 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. J. Wildl. Manage. 78, 383–393.

Hiers, J.K., Wyatt, R., Mitchell, R.J., 2000. The effects of the fire regime on legume reproduction in longleaf pine savannas: is a season selective? Oecologia 125, 521–530.

Howe, H.F., 1986. Seed dispersal by fruit-eating birds and mammals. In: Murray, D.R. (Ed.), Seed Dispersal. Academic Press, New York, New York, USA, pp. 123–190.

Jordano, P., 2000. Fruits and frugivory. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities, second ed. UKCABl Publ, Wallingford.

Kilgo, J.C., Vukovich, M., 2012. Factors affecting breeding season survival of red-headed woodpeckers in South Carolina. J. Wildl. Manage. 76, 328–335.

Kirkman, L.K., Goebel, P.C., Palik, B.J., West, L.T., 2004. Predicting plant species diversity in a longleaf pine landscape. Ecoscience 80–93.

Lashley, M.A., Thompson, J.R., Chitwood, M.C., DePerno, C.S., Moorman, C.E., 2014b. Evaluation of methods to estimate understory fruit biomass in temperate forests. PLoS one. http://dx.doi.org/10.1371/journal.pone.0096898.

Lashley, M.A., Chitwood, M.C., Harper, C.A., DePerno, C.S., Moorman, C.E., 2015a. Variability in fire prescriptions to promote wildlife foods in the longleaf pine ecosystem. Fire Ecol. 11, 62–79.

Lashley, M.A., Chitwood, M.C., Prince, A., Elfelt, M., Kilburg, E., DePerno, C.S., Moorman, C.E., 2014a. Subtle effects of a managed fire regime: a case study in the longleaf pine ecosystem. Ecol. Ind. 38, 212–217.

Lashley, M.A., Chitwood, M.C., Kays, R., Harper, C.A., Moorman, C.E., DePerno, C.S., 2015b. Prescribed fire affects female white-tailed deer habitat use during summer lactation. For. Ecol. Manage. 348, 220–225.

McCarty, J.P., Levey, D.J., Greenberg, C.H., Sargent, S., 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. For. Ecol. Manage. 164, 277–291.

McCord, J.M., Harper, C.A., Greenberg, C.H., 2014. Brood cover and food resources for wild turkeys following silvicultural treatments in mature upland hardwoods. Wildl. Soc. Bull. 38, 265–272.

Mitchell, R.J., Hiers, J.K., O'Brien, J.J., Jack, S.B., Engstrom, R.T., 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. Can. J. For. Res. 36, 2724–2736.

Peterson, D.W., Reich, P.B., 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecol. Appl. 11, 914–927.

Price, O., Edwards, A., Connors, G., Woinarski, J., Ryan, G., Turner, A., Russell-Smith, J., 2005. Fire heterogeneity in Kakadu national park, 1980–2000. Wildlife Res. 32, 425–433.

Prince, A., Chitwood, M.C., Lashley, M.A., DePerno, C.S., Moorman, C.E., 2016. Resource selection by southeastern fox squirrels in a fire-maintained forest system. J. Mammal. 97, 631–638.

Radford, I.J., Andersen, A.N., 2012. Effects of fire on grass-layer savanna macro-invertebrates as key food resources for insectivorous vertebrates in northern Australia. Austral Ecol. 37, 733–742.

Reynolds-Hogland, M.J., Mitchell, M.S., Powell, R.A., 2006. Spatio-temporal availability of soft mast in clearcuts in the Southern Appalachians. For. Ecol. Manage. 237, 103–114.

Sanaiotti, T.M., Magnusson, W.E., 1995. Effects of annual fires on the production of fleshy fruits eaten by birds in a Brazilian Amazonian savanna. J. Trop. Ecol. 11, 53–65.

Sorrie, B.A., Gray, J.B., Crutchfield, P.J., 2006. The vascular flora of the longleaf pine ecosystem of Fort Bragg and Weymouth Woods, North Carolina. Castanea 71, 129–161.

Stambaugh, M.C., Guyette, R.P., Marschall, J.M., 2011. Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. J. Veg. Sci. 22, 1094–1104.

Stephens, S.L., Moghaddas, J.J., Edminster, C., Fiedler, C.E., Haase, S., Harrington, M., Youngblood, A., 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. Ecol. Appl. 19, 305–320.

Syphard, A.D., Franklin, J., Keeley, J.E., 2006. Simulating the effects of frequent fire on southern California coastal shrublands. Eco. App. 16, 1744–1756.

Uys, R.G., Bond, W.J., Everson, T.M., 2004. The effect of different fire regimes on plant diversity in southern African grasslands. Biol. Cons. 118, 489–499.

Valentine, L.E., Fisher, R., Wilson, B.A., Sonneman, T., Stock, W.D., Fleming, P.A., Hobbs, R.J., 2014. Time since fire influences food resources for an endangered species, Carnaby's cockatoo, in a fire-prone landscape. Biol. Cons. 175, 1–9.

Valentine, L.E., Schwarzkopf, L.I.N., Johnson, C.N., 2012. Effects of a short fire-return interval on resources and assemblage structure of birds in a tropical savanna. Aust. Ecol. 37, 23–34.

Woinarski, J.C.Z., Legge, S., 2013. The impacts of fire on birds in Australia's tropical savannas. Emu 113, 319–352.