ABSTRACT

LASHLEY, MARCUS ALAN. The Importance of Including Natural Variability in Fire Prescriptions: Fruits, Forages, and White-tailed Deer Space Use. (Under the direction of Christopher Moorman and Christopher DePerno).

Practitioners have espoused the emerging paradigm of ecosystem-based land management to restore and maintain functioning ecosystems. As a result, management prescriptions often are based on historical and empirical references of keystone ecological processes. A keystone process in the longleaf pine ecosystem is fire disturbance, which historically occurred most frequently during the growing season. Currently, the emphasis in this ecosystem is on frequent early growing-season fire disturbances. Hence, land managers have applied fire based on average historical frequencies and primarily during the growing season. However, little is known about the effects of this fire regime on native plants and wildlife sensitive to fire season and frequency, particularly when natural stochastic variability is ignored. Therefore, I measured plant distributions, growth, and reproductive allocations (fruit production) of native fire-adapted flora, hypothesizing differing fire seasons and fire-return intervals would be necessary to maximize heterogeneity on the landscape. During the 2011 and 2012 growing seasons, I assessed the distribution of important hard and soft mast producing tree species, understory vegetative biomass, and overstory and understory fruit production of native plants in relation to fire frequency and seasonality in the longleaf pine-wiregrass ecosystem at Fort Bragg Military Installation, North Carolina. Also, I used compositional analysis to measure the influence of time-since-fire and fire season on deer selection of burned areas and the impacts of burning on 95% home range and 50% core area space used and site fidelity. Understory plant biomass was greatest following dormant-season fires. Wiregrass biomass was greatest in upland pine stands, but was unaffected by season of

burning. In longleaf pine stands, 94% of the fruit was detected 2 years after growing-season fire and 6% one year after growing-season fire. Fruit production was greater in July following dormant-season fire and in September following growing-season fire but was greatest in upland hardwood stands because of the mosaic in fire spread in the vegetation type. Unnatural distributions of important hardwood mast producers near man-made firebreaks and variability in fruiting response and plant biomass to timing and frequency of fire, indicate stochastic variability in fire season and frequency is essential to the maintenance of landscape heterogeneity, high plant diversity, and abundant fruit production. Further, our compositional analysis showed that deer selected unburned drainages and areas that had been burned ≥2yr previously, while avoiding areas that had been burned more recently. Individuals with greater percentage of their home range burned increased the size of their core area during the same year of the fire, but not their overall home range area. Furthermore, site fidelity across years decreased as the percentage of the core area in the previous year was burned. Guided by our best knowledge of variability in historical fire regimes, varying fire applications should include growing- and dormant-season fires, incorporating shorter and longer fire-return intervals, incorporating a variation in firing techniques, and avoiding burning adjacent areas in the same year. These recommendations will better emulate historical fires and, therefore, cater to a larger array of native taxa, including threatened and endangered flora and fauna.

The Importance of Including Natural Variability in Fire Prescriptions: Fruits, Forages, and White-tailed Deer Space Use

by
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DEDICATION

I dedicate this accomplishment to my wife Christine, mother Lynn, and father Joey, who provided me with nothing but support and encouragement throughout my life. Christine has supported me in every way through my stressful times as a doctoral student. My mother and father fostered my love for wildlife and encouraged me to be the humble, respectful, and passionate man I am today.

BIOGRAPHY

The author was born in a small town in Alabama. He developed a passion for wildlife and wildlife management at a young age which was facilitated by a love for hunting and fishing. He completed a B.S. at Mississippi State University in Forestry and Wildlife Management. He went on to earn a M.S. at the University of Tennessee studying the effects of silvicultural treatments on forage availability for white-tailed deer which led him to complete this dissertation at North Carolina State University. He is planning to continue research evaluating fire effects on wildlife food abundance in the longleaf pine ecosystem as a postdoctoral researcher at NCSU until securing a research faculty position at a land grant institution.

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CHAPTER 1

SUBTLE EFFECTS OF A MANAGED FIRE REGIME: A CASE STUDY IN THE LONGLEAF PINE ECOSYSTEM

ABSTRACT

Land managers often use fire prescriptions to mimic intensity, season, completeness, and return interval of historical fire regimes. However, fire prescriptions based on average historical fire regimes do not consider natural stochastic variability in fire season and frequency. Applying prescribed fire based on averages could alter the relative abundance of important plant species and structure. I evaluated the density and distribution of oak (*Quercus* spp.) and persimmon (*Diospyros virginiana*) stems and mast after 22 years of a historical-based growing-season fire prescription that failed to consider the variability in historical fire regimes. I randomly established 30 25-m transects in each of 5 vegetation types and counted reproductively mature oak and persimmon stems and their fruits. In upland longleaf pine (*Pinus palustris*) stands, this fire regime killed young hardwood trees, thereby decreasing compositional and structural heterogeneity within the upland pine vegetation type and limiting occurrence of the upland hardwood vegetation type. Acorns and persimmons were disproportionately distributed near firebreaks within low intensity fire transition zones. Mast was maintained, though in an unnatural distribution, as a result of an elaborate firebreak system. Our data indicate managed fire regimes may fail to mimic spatial distribution, frequency, and intensity of historical disturbances even when the fire prescription is based on empirical reference fire regimes. To maximize structural heterogeneity and conserve key ecosystem functionality, fire prescriptions should include variations in frequency, season,

application method, and fire weather conditions rather than focusing on an average historical fire regime.

Key Words acorns, firing technique, fire seasonality, persimmons, prescribed fire, stochastic variability

INTRODUCTION

Maintaining biodiversity at the landscape scale is a complex goal for land managers. As a result, management goals and prescriptions often are focused on habitat requirements of species of special concern (e.g., endangered species) (Bean, 2009; Franklin, 1993). However, homogeneous management for specialized target species can result in unintended or unnoticed changes in ecosystem structure or abundance of non-focal species (Bean, 2009; Doremus, 1997; Franklin, 1993). In this case, it may be prudent to use multiple indicators, and not just the species of concern, to monitor ecosystem health. For example, groups of bryophytes (Pinho et al., 2012) or plant assemblages may be used as indicators for terrestrial ecosystem health or landscape heterogeneity (Baumberger et al., 2012; Druckenbrod and Dale, 2012; Vilches et al., 2013).

Heterogeneity of vegetation structure and composition has been considered a precursor to maintaining biodiversity (Baumberger et al., 2012; Simberloff, 1997), and fire regimes have a profound impact on plant community heterogeneity at the landscape scale (Whitlock et al., 2010). In fact, heterogeneous applications of fire were necessary to maintain the differing structural requirements of specialized ant species (Anderson, 1991), vertebrate diversity in the boreal forest of British Columbia (Brunnel, 1995), avian species diversity in the North American tall grass prairies (Fuhlendorf et al., 2006), lizard species diversity in the wet-dry tropics of Australia (Braithwaite, 1987), and legume diversity in the longleaf pine (*Pinus palustris*) ecosystem (Hiers et al., 2000). Similarly, the biodiversity of the longleaf pine ecosystem depends on a combination of relatively high rainfall, porous, sandy soils, and an active cycle of fires, which naturally created a mosaic of plant communities (Greenberg, 2001). Further, in this system, longleaf pine forest is the prevailing vegetation type, making other less prominent plant communities (e.g., upland hardwood) easy to overlook. Although the importance of heterogeneity in natural fire regimes to the persistence of prevailing longleaf dominated plant communities is well documented (Aschenbach et al., 2010; Beckage et al., 2005; Fill et al., 2012), less prominent vegetation types rarely are acknowledged despite their importance to the function of the ecosystem. For example, hardwood mast in longleaf pine ecosystems is readily consumed by many animal species, some of which also use the cover provided by mast-producing plants.

A growing body of literature supports the use of prescribed fire to restore and maintain fire-dependent ecosystems and managers have attempted, in many cases, to advocate fire regimes that emulate nature. However, prescribed fires may not emulate nature without including historical variability even if they are based on historical references of average frequencies and seasons. Therefore, homogenous fire regimes could differentially promote some native taxa and fail to promote others. To determine if a historically based fire regime yielded a heterogeneous distribution of hardwoods, I measured the distribution and density of reproductively mature oak (*Quercus* spp.) and common persimmon (*Diospyros virginiana*) stems and fruits after 22 years of managed prescribed fire regime at Fort Bragg Military Installation (FB), North Carolina, USA. I extrapolated mast and stem density to evaluate landscape-scale availability of acorns and persimmon fruits and reproductively mature oak and persimmon stems. Our objective was to evaluate landscape level effects of a homogeneously applied ecosystem-based fire prescription on distributions of select hardwoods and mast. I selected oaks and persimmons as indicators of ecosystem health because historically these tree species persisted only in areas burned less frequently and intensely in the longleaf pine ecosystem (Greenberg, 2001; Greenberg and Simons, 1999), and because the mast from the two species is a keystone food source for many wildlife (Kellner et al., 2013). Furthermore, ecosystem changes associated with decline of these and other hardwood tree species may go unnoticed because hardwoods were historically less prevalent than longleaf pine, were heterogeneously distributed across the landscape, and were not considered beneficial to the focal endangered species which is the major driver of the fire management regimes at FB and across the longleaf pine ecosystem (i.e., red-cockaded woodpecker –*Picoides borealis*; Cantrell et al., 1995). I hypothesized hardwood stems and associated mast would be unnaturally confined along human-induced fire shadows (e.g., firebreaks) in upland pine stands because of the lack of variability in fire applications.

METHODS

Study area

Fort Bragg Military Installation (FB) (73,469-ha; 35.1°N, -79.2°W) is located within the threatened longleaf pine-wiregrass (*Aristida stricta*) ecosystem of the Sandhills physiographic region in North Carolina, USA (Figure 1). Fort Bragg received an average yearly rainfall of 120 cm and averages ~175 frost-free days per year in the recorded past until

2006 and was characterized by rolling hills with elevation ranging from 43 m to 176 m (Sorrie et al., 2006). At FB, dominant mast producing tree species include turkey oak (*Quercus laevis*), common persimmon, sand post oak (*Q. stellata*), bluejack oak (*Q. incana*), blackjack oak (*Q. marilandica*), and blackgum (*Nyssa sylvatica*). Their fruits are eaten by squirrels (*Sciurus* spp.), gray fox (*Urocyon cinereoargenteus*), striped skunk (*Mephitis mephitis*), white-tailed deer (*Odocoileus virginianus*), coyote (*Canis latrans*), raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginianus*), eastern cottontail (*Sylvilagus floridanus*), and numerous birds, including northern bobwhite (*Colinus virginianus*) and wild turkey (*Meleagris gallopavo*) (Glasgow, 1977). Hunter-harvest records at FB indicate that populations of several mast-dependent game species, including white-tailed deer and southern fox squirrel (*S. niger niger*), have declined concomitantly with the application of the current fire prescription (J. Jones, personal communication).

In accordance with management recommendations for red-cockaded woodpecker, about 8% of the forest is targeted for annual thinning to maintain ~11.5 m^2/ha basal area and prevent hardwood encroachment (Cantrell et al., 1995). Beginning in 1989, a 3-yr growing-season fire-return interval was initiated to maintain structural requirements for red-cockaded woodpecker and maximize biodiversity (Cantrell et al., 1995). This fire prescription was derived from climatic patterns of natural ignition sources (Beckage et al., 2005; Slocum et al. 2007; Slocum et al. 2010) and historical descriptions of forest structure (Streng et al., 1993; Waldrop et al., 1992), which indicated natural fire season varied regionally but was dominated by growing season (~75% June – August; Fill et al., 2012) with a 3-yr fire-return interval on average (Figure 2; Cantrell et al., 1995). The fire prescription at FB follows the historical average frequency and season but does not consider historical variability. Due to limitations in resources, manpower, and adequate fire weather, some stands miss a scheduled fire on occasion and are burned in the following dormant season. However, these stands are moved immediately back into the 3-yr growing-season fire-return interval. To maximize efficiency of burning, stands are initially lit with a backing fire. A backing fire is the safest and least intense firing technique and is started along a baseline such as a road, plow line, stream, or other barrier and allowed to move into the wind (Wade and Lundsford, 1990). At FB, once fires have progressed an adequate distance from the firebreak, additional fires are set around other boundaries often using the ring fire and strip head fire techniques. Firebreaks at FB are generally oriented east and west to facilitate prescribed burning and military activities.

Vegetation types

I assigned 5 vegetation types using a geographic information system overlay map of land cover and firebreaks provided by the U.S Department of Defense: Upland Hardwood (UH), Bottomland Hardwood (BH), Upland Pine (UP), managed opening (Open) and Low Intensity Fire Transition Zone (LIFTZ). I characterized UH as any upland forest stand dominated by hardwood species (primarily oak), BH as hardwood-dominated forest stands (primarily blackgum) associated with drainages, UP as upland longleaf pine-dominated forest, and Open as unforested areas maintained as grasslands. I defined LIFTZ as UP $\leq$ 25m from a firebreak. Wiregrass (primary plant influencing the spread of fire in this system; Noss, 1989) is typically less intact in hardwood-dominated stands because of a decrease in sunlight to the forest floor, and flame heights tend to be shorter and less influenced by proximity to firebreaks.

Vegetation sampling

During September 2011, I randomly established 30 25-m transects in each of the 5 vegetation types (n=120). The observers used 8×42-mm binoculars to count fruits on reproductively mature oak and persimmon for 60 seconds on each stem that overlapped the transect. Trees were deemed reproductively mature if they were dominant or co-dominant in the canopy, ≥4.5 cm diameter breast height, or were producing fruit (Greenberg and Simons, 1999). Stem densities were based on the total number of stems that fit these criteria whose canopy overlapped transects. Throughout the study, the same 3 observers conducted mast surveys to reduce biases associated with viewer detection and speed.

Data analysis

I conducted a general linear model to compare fruit density and stem density among vegetation types using SPSS (IBM, Cary, NC). I used the Tukey's Honestly Significant Difference multiple comparison test to compare means when I detected vegetation type effects. I set alpha = 0.05.

I used a vegetation type overlay in a geographical information system to calculate the area of each vegetation type. I excluded lakes and danger areas, which were areas that were completely inaccessible. I extrapolated mast density and stem density to the landscape level by multiplying the area of each vegetation type and respective mean mast and stem density.

RESULTS

Mast density

Mast was unnaturally concentrated along firebreaks following 22 years of homogeneously applied fires. Mean fruit density was greater in low intensity fire transition zones (LIFTZ) than upland pines (UP) ($P < 0.001$), bottomland hardwoods (BH) ($P < 0.001$), and openings (open)($P < 0.001$) (Table 1). Mean fruit density was greater in upland hardwoods (UH) than UP ($P < 0.001$), BH ($P < 0.001$), and open ($P < 0.001$). Mean fruit density was not different between LIFTZ and UH ($P = 0.757$). However, all detected persimmon fruits were in LIFTZ (mean fruits/25m^2 4 ±3). When extrapolated to the landscape scale, a disproportionate percentage of mast available at FB falls within LIFTZ (Table 2). Also, UH provided a disproportionate amount of mast at the landscape scale with 8% of mast produced in 2% of the area (Table 2). Mast availability was disproportionately low in all other cover types (Table 2).

Stem density

Similar to mast, hardwood stems were concentrated along firebreaks. Oak stem density was greater in LIFTZ than UP ($P < 0.001$), BH ($P < 0.001$), and open ($P < 0.001$) (Table 1). Oak stem density was greater in UH than UP ($P < 0.001$), BH ($P < 0.001$), and open ($P < 0.001$). Oak stem density was not different between LIFTZ and UH ($P = 0.154$). However, all detected persimmon stems were in LIFTZ (mean stems/25m^2 3 ±2). When extrapolated to landscape scale, a disproportionate percentage of stems (oak and persimmon) were within LIFTZ (Table 2). Also, UH provided a disproportionate number of stems at the landscape scale with 6% of stems produced in 2% of the area (Table 2). Stem density was disproportionately low in all other treatments (Table 2).

DISCUSSION

The homogeneous application of firing technique, return interval (3 years), and season (summer) of prescribed fires decreased landscape heterogeneity of plant communities by differentially promoting the prevailing cover type (longleaf pine) and suppressing less-prominent hardwoods. Our study indicates that LIFTZ are of unquestionable importance to mast-dependent taxa at FB under current management regimes. Historically, the heterogeneity of disturbances allowed succession of hardwoods in some areas (Greenberg and Simons, 1999), and fire regimes likely were more variable on the landscape than a homogeneously applied, 3-yr growing-season fire prescription (Aschenbach et al., 2010; Beckage et al., 2005; Fill et al., 2012; Greenberg and Simons, 1999). Also, stand conditions were not homogeneous but rather a heterogeneous matrix of stand ages, structural conditions, and plant communities, which included patchy distributions of mature hardwoods in longleaf dominated stands (Greenberg, 2001; Greenberg and Simons, 1999). The occurrence of specialized, xeric-adapted species and wide-ranging generalist species in the longleaf pine ecosystem indicates that variable burning intensities, intervals, and spatial extent created a range of microhabitats and stand conditions within these plant communities (Greenberg and Simons, 1999; Marcoux et al., 2013). Furthermore, fire tolerance of tree species declines with decreasing bark thickness and stem diameter (Harmon, 1984). Thus, variability in fire resistance among flora is an important consideration when managing fire-maintained ecosystems. For example, intense fires in UH likely kill persimmon before they reach maturity but not thicker-barked oaks that dominate the UH overstory (Harmon, 1984; Van Lear and Harlow, 2001). However, in LIFTZ, both oaks and persimmons were protected from intense flames because of proximity to the ignition source along firebreaks (i.e., low fire intensity is consistently maintained in close proximity to firebreaks). Conversely, fire in the forest interior of UP was intense and frequent enough to prevent fire-adapted hardwood species from reaching reproductive maturity (Greenberg and Simons, 1999). This phenomenon can be exacerbated by use of the ring fire technique, which burns hotter as the flames converge in the interior of the stand and is a technique not recommended for use in forested stands because of the possibility of damage to flora and fauna (Wade and Lundsford, 1990).

Although efforts to restore habitat for the federally endangered RCW have been successful (i.e., hardwood encroachment into UP stands has been reduced), the lack of a more diverse set of ecological indicators may lead to failed conservation of some species. For example, Kilgo and Vukovich (2012) reported red-headed woodpecker (in decline; *Melanerpes erythrocephalus*; Sauer et al. 2008) survival rates were increased by patchy distributions of cover associated with upland hardwoods in the longleaf pine ecosystem. Also, numerous other biota occurring in longleaf pine ecosystems may be negatively affected by decreasing hardwood encroachment. Further, less common vegetation types may be considered only when an ESA listed species is present. For example, the Saint Francis' satyr (*Neonympha mitchellii francisci*), a federally endangered butterfly endemic to FB, requires wetlands that are maintained by infrequent burning (Kuefler et al., 2008). Before the satyr was listed, firebreaks were used to keep fires from burning into wetlands at FB. After being listed, firebreaks near wetlands were abandoned, allowing fires to burn into wetlands. Negative implications of obstructing intermittent fire in wetlands were not considered until the presence of a listed species. Thus, current policies may encourage homogeneity when focal species require a narrow suite of vegetation conditions, particularly when competing vegetation types are not linked to other ecological indicators.

Misrepresentation of natural ecosystem functions is a common flaw in restoration and management around the globe (Marcoux et al., 2013; Vandvik et al., 2005). Contemporary conservation involves management regimes that are generally less diverse, in terms of disturbances and fine-scale temporal and spatial variability, than historical land disturbance (Vandvik et al., 2005). This trend could negatively affect biodiversity on the landscape, and negative effects could be overlooked depending on the focus of management. Variables such as the range of historical frequency, the seasonal distribution of fires, and historical variability in ignition conditions (e.g., relative humidity, wind velocity, fuel moisture, etc.) should be incorporated into fire prescriptions. Each of these variables plays a key role in fire behavior and as a result influences fire effects on biota (Agee, 1996; Cheney et al., 1996). Because these variables often are overlooked, fire regimes may be predisposed to excluding variation. For example, most land managers work during the daytime and accordingly fires may then only be lit diurnally, thereby neglecting the historical prevalence of nocturnal lightning ignitions. Furthermore, many lightning ignitions were associated with rain events and therefore some fires would be lit with high fuel moisture which limited the intensity and scope of fires (Bessie and Johnson, 1995). For example, less intense fire associated with fuels high in moisture may lead to a patchy spread of fire. In managed fire regimes where fires are lit diurnally, during summer, and rarely during high moisture conditions, as is the case at FB, management practices may never achieve the mosaic present historically. The lack of mosaic created by consistent ignition conditions could be solely responsible for the unnatural distribution of hardwoods and mast I observed at FB.

Biodiversity is driven by non-vertebrate biota and only can be conserved by landscape- or ecosystem-scaled approaches (Franklin, 1993; Walker, 1995). The challenge is designing policy to improve management of heterogeneity at the landscape scale. Furthermore, management prescriptions must be representative of historical heterogeneity in disturbances that are executable at the local level. At FB, the manpower needed to support the current prescribed fire regime is reasonable if burned areas are large and linear, which allows quick application of fire along firebreaks and efficient maintenance of the 3-yr fire-return interval. Homogeneously applied fires are efficient, but efficient application comes at the expense of landscape heterogeneity.

CONCLUSIONS

I was able to demonstrate the homogenizing effects of prescribed fire when historical variability of fire regimes was not executed. The distribution and density of hardwood stems and associated mast served as an indicator of the aforementioned homogenization because their distributions were in close proximity of ignition sources where fire temperatures were lowest. I recommend fire managers vary firing techniques, ignition locations, and firing conditions using historical variance in fire season and frequency as a guide. Furthermore, policies encouraging ecosystem-based management strategies are needed on all landscapes, and not just areas with listed species or critical habitats. Moritz et al. (2013) provided bounded ranges of variation guided by historical data as a framework for future fire regime management; their strategy could be useful to guide future fire regimes in the longleaf pine ecosystem.

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Table 1. Mean oak and persimmon mast and stem density (number/25m^2) within vegetation types at Fort Bragg military installation, NC, USA.

Vegetation type	Mast density	SE	Stem density	SE	Mean separation[a]
LIFTZ	50.97	14.96	18.5	5.03	A
Upland hardwood	48.77	10.67	16.7	1.67	A
Bottomland hardwood	0.5	0.96	1.59	0.8	B
Upland pine	3.47	1.87	3.24	1.84	B
Open	0	0	0	0	B

[a] Vegetation types with different letters were significantly different at alpha=0.05

Table 2. Landscape level percentage of oak and persimmon mast and stems by vegetation type at Fort Bragg military installation, NC, USA.

Vegetation type	% Land area	% of mast	% of stems
Firebreaks	6	0	0
LIFTZ	17	80	66
Upland hardwood	2	8	6
Bottomland hardwood	11	1	4
Upland pine	35	11	24
Open	28	0	0

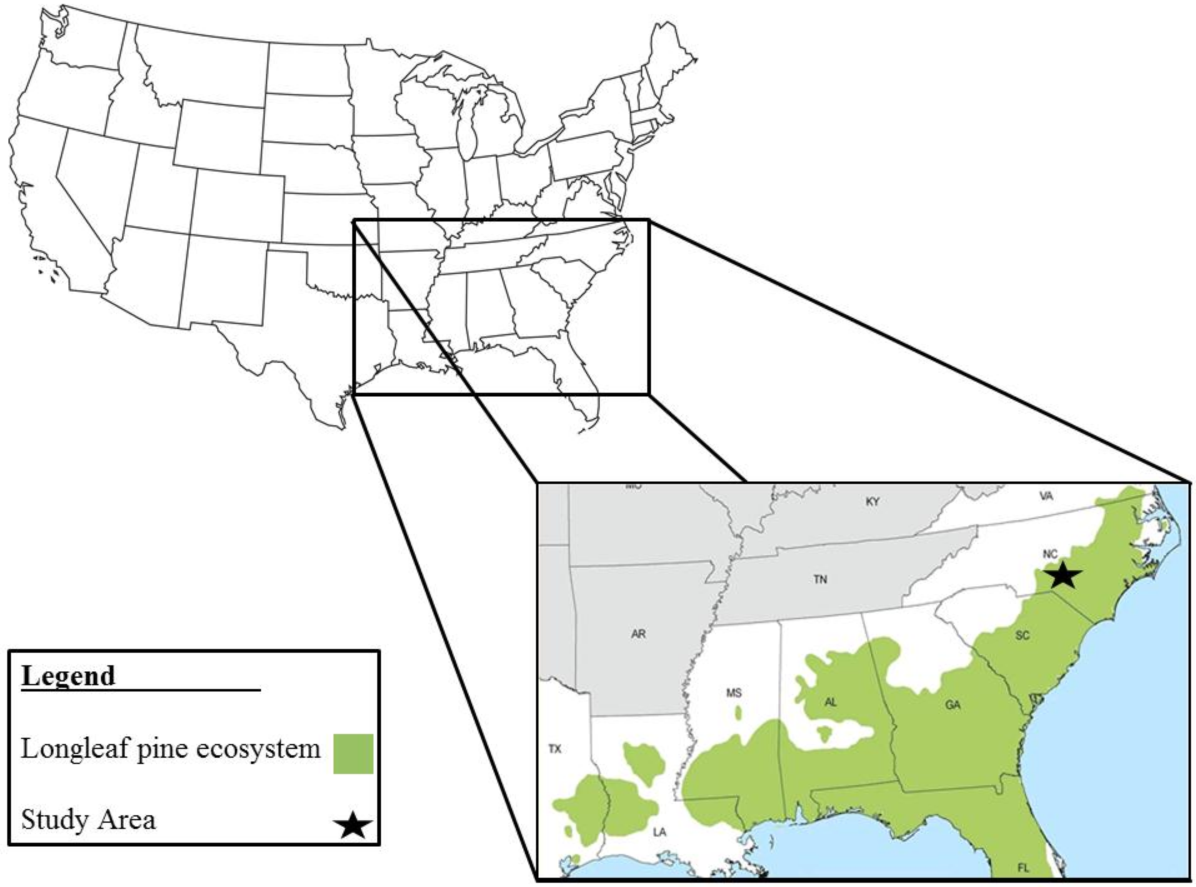

Figure 1. Location of Fort Bragg Military Installation, NC, USA.

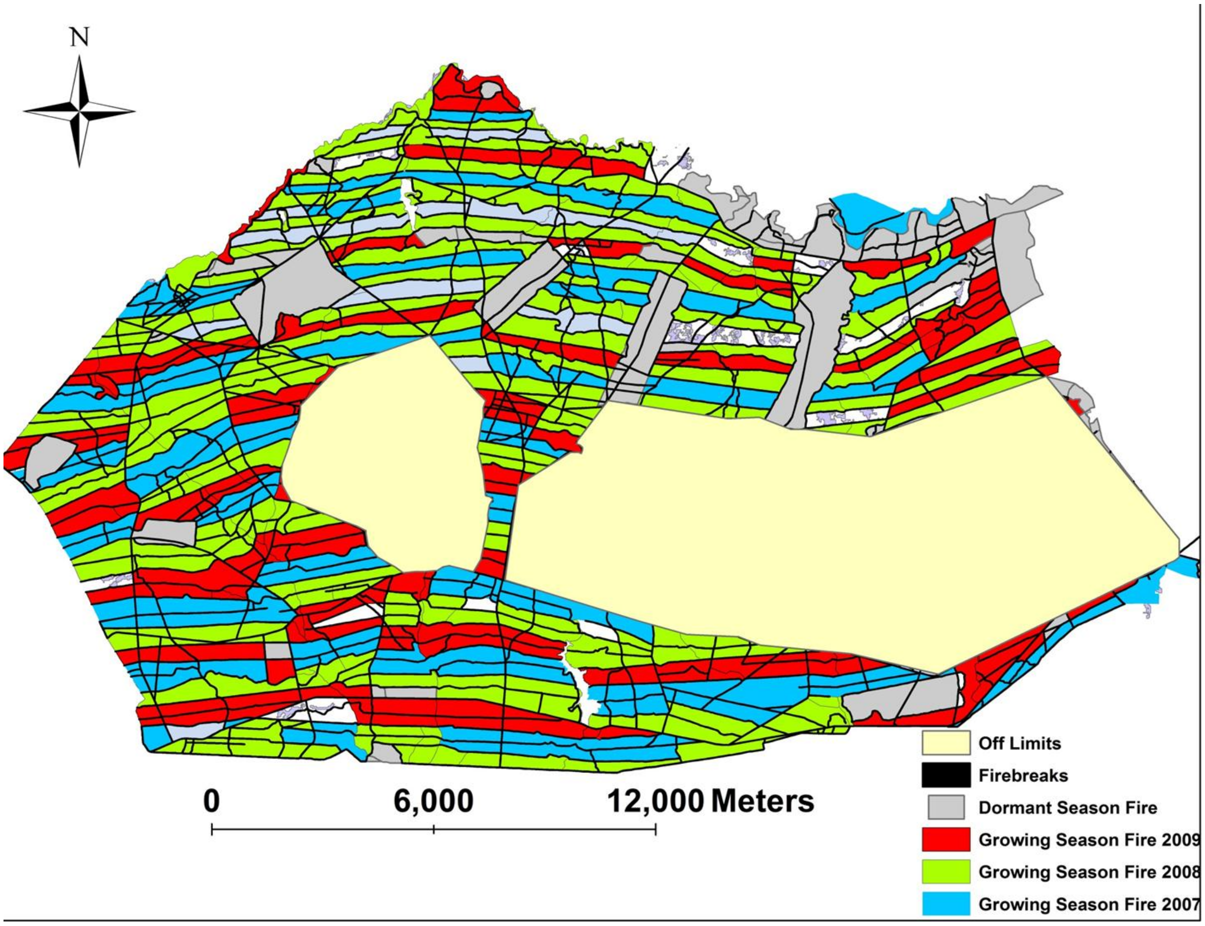

Figure 2. Three-year growing-season fire prescription and firebreak system for Fort Bragg Military Installation, NC, USA.

CHAPTER 2

DIVERGENT FLORAL RESPONSES REVEAL THE IMPORTANCE OF STOCHASTICALLY VARIABLE FIRE PRESCRIPTIONS

ABSTRACT

Practitioners have espoused the emerging paradigm of ecosystem-based land management to restore and maintain functioning ecosystems. As a result, management prescriptions often are based on historical and empirical references of keystone ecological processes. A keystone process in the longleaf pine ecosystem is fire disturbance, which historically occurred most frequently during the growing season. Currently, the emphasis in this ecosystem is on frequent early growing-season fire disturbances. Hence, land managers have applied fire based on average historical frequencies and primarily during the growing season. I hypothesized plant growth and reproductive allocations (fleshy fruit production) of native fire-adapted flora would respond differently to differing fire seasons and fire-return intervals. During the 2011 and 2012 growing seasons, I assessed vegetative biomass and fleshy fruit production of native plants in relation to fire frequency and seasonality in the longleaf pine-wiregrass ecosystem in North Carolina. Understory plant biomass was greatest following dormant-season fires. Wiregrass biomass was greatest in upland pine stands, but unaffected by season of burning. In longleaf pine stands, 94% of the fruit was detected 2 years after fire and 6% one year after growing-season fire. Fruit production was greater in July following dormant-season fire and in September following growing-season fire but was greatest in upland hardwood stands because of the mosaic in fire spread in the vegetation type. Variability in fruiting response and plant biomass among native flora indicates stochastic variability in fire season and frequency is essential to the maintenance of high plant diversity and abundant fruit production in fire-maintained ecosystems.

Key Words biodiversity, ecosystem-based management, fruit, heterogeneity, longleaf pine, plant biomass

INTRODUCTION

Historical and empirical accounts of pre-degraded reference conditions guide management prescriptions to restore and maintain ecosystems (Fill et al. 2012). Researchers use floristic responses (e.g., plant reproductive allocations, seed germination) to seasonality and frequency of fire to guide management prescriptions in fire-adapted systems, assuming natural adaptions of target flora will infer natural disturbance regimes (Platt et al. 1988; Platt 1999; Streng et al. 1993; Beckage et al. 2005; Fill et al. 2012). Therefore, accurate accounts of native species composition and related disturbance interactions are essential to successful restoration of degraded ecosystems (Society for Ecological Restoration 2004; Fill et al. 2012).

In the U.S., the highly threatened longleaf pine (*Pinus palustris*) ecosystem (LLPE) is at the forefront of ecological restoration (Landers et al. 1995; Brockway et al. 2005; Fill et al. 2012). Historically, the LLPE was one of the most extensive ecosystems in North America and occupied 38 million hectares in the southeastern United States (Frost 1993; Landers et al. 1995). Currently, ~ 800 thousand hectares remain, representing a 97% decline across the natural range (Frost 2006). Restoring the LLPE may provide ecological, economic, and social benefits including: improving habitat quality for wildlife, producing high-quality longleaf pine timber and pine straw, providing recreational opportunities, preserving natural and cultural legacies, and creating a broader range of management options for future generations (Brockway et al. 2005).

Previous studies have examined reference historical LLPE conditions based on various types of data (e.g., Beckage et al. 2005–modeling; Stambaugh et al. 2011– historical fires scars; Fill et al. 2012–plant reproductive allocations). The general consensus is that high-frequency growing-season fire regimes (≤ 3 year fire-return interval May-June; Waldrop et al. 1992; Streng et al. 1993; Stambaugh et al. 2011; Fill et al. 2012) are a keystone process and vital to restoring the LLPE (Aschenbach et al. 2010). However, the LLPE represents one of the most diverse systems in the temperate zone and simplified management strategies guided by a few focal flora and fauna may fail to accurately represent the complexity within this dynamic ecosystem (Franklin 1993; Drew et al. 1998). For example, Lashley et al. (2014) reported homogeneous fire applications could simplify forest stand structure and landscape floral composition even when prescriptions are based on historical references. Similarly, Beckage et al. (2005) raised concern for oversimplified inferences of reference conditions in fire-maintained ecosystems. Because fire frequency, intensities, and seasonality may affect flora and fauna differently (Van Lear & Harlow 2000), variable fire prescriptions are more likely to create and maintain a heterogeneous landscape (Bond & Archibald 2003).

Fire prescription recommendations from empirical data sets tend to be narrowly focused on average historical seasons and frequencies. Yet, historical fire regimes in the LLPE likely incorporated more variable fire frequencies and seasonality on the landscape than the homogeneous application of growing-season prescribed burns every 3 years (Landers et al. 1989; Greenberg & Simons 1999; Beckage et al. 2005; Aschenbach et al. 2010). For example, Fill et al. (2012) showed reproductive responses of wiregrass (*Aristida beyrichiana*) were greatest following early growing-season fires (May-June); however, many lightning-generated fires occurred in other months (Fill et al. 2012). Furthermore, Clewell (1989) reported wiregrass plants persist for extended periods without fire. Hence, wiregrass reproductive responses indicate adaptations to frequent growing-season fires, yet other characteristics of wiregrass simultaneously indicate adaptations to infrequent growing-season fire. In the LLPE, Stambaugh et al. (2011) concluded that fire seasons were variable and frequencies varied from 0.5- to 12-year fire-return intervals based on historical fire scars. It is this variability in fire-return intervals, coupled with variability in season, which likely shaped the dynamic LLPE and other fire-maintained ecosystems.

Managing fire regimes based on historical regime is important because conducting prescribed fires at a frequency or season outside the natural fire regime may have negative effects on community structure and species composition (Platt et al. 1988; Platt et al. 2002). Likewise, ignoring natural variability by burning only when fires occurred most prominently may negatively affect the distribution and relative abundance of some plant species. To investigate the importance of natural variation in fire regimes, I determined the effects of fire frequency (0, 1, and 2 years post fire) and season (i.e., longleaf stands burned in the dormant [January-March] and growing seasons; hereafter DUP and GUP, respectively) on understory vegetation biomass and composition and fleshy fruit abundance in the LLPE. I examined native plant vegetative biomass and fruit abundance in response to fire season by sampling stands burned in the dormant season (February) and early growing season (May–June). I compared vegetative biomass and fruit abundance in the prevailing longleaf pine vegetation type to other less prevalent vegetation types (upland hardwoods and bottomland hardwoods) and compared fruit abundance following 0, 1, and 2 years post growing-season fires in longleaf pine stands. I hypothesized a unique suite of native flora would respond positively to each fire season and frequency, thus illustrating the importance of stochastic variability in fire prescriptions to restore and maintain fire-adapted plant communities.

METHODS

Study area

I sampled vegetative biomass and fruit abundance at Fort Bragg Military Installation (FB) in Cumberland, Harnett, Hoke, and Moore counties, North Carolina (35.1°N, -79.2°W). The 73,469-ha property was located in the Sandhills physiographic region in the northernmost remnants of the LLPE. Since 1989, the United States Department of Defense has managed burn blocks on a stringent 3-yr growing-season (April–June) fire-return interval targeting the prevailing longleaf pine vegetation type (Cantrell et al. 1995). However, upland hardwood and bottomland hardwood stands are interspersed within some burn blocks and are subjected to the same fire regime, though fire behavior may differ based on moisture and fuels. The fire regime was initiated to maintain structural requirements for the federally endangered red-cockaded woodpecker (*Picoides borealis*) and to maximize biodiversity of the LLPE (Cantrell et al. 1995). Because of limitations in resources, manpower, and adequate fire weather, some stands not burned as scheduled are burned the following dormant season

(January–February). However, these stands are moved immediately back into the 3-yr growing-season fire-return interval. Average yearly rainfall was 120 cm, plus 7.5 cm of snow and ~175 frost-free days per year (Sorrie et al. 2006). There was a moderate drought in 2011 followed by a normal rainfall year in 2012 according to the State Climate Office of North Carolina Primary vegetation types included longleaf pine, upland hardwoods, bottomland hardwoods, and managed openings (see Sorrie et al. 2006 for detailed floristic accounts). Fort Bragg Military Installation was considered an important contributor to the floristic diversity of the LLPE with more than 1200 plant species, 61 of which are rare and 3 of which are federally endangered (Sorrie et al. 2006).

Stand selection

I assigned 3 major vegetation types using a geographic information system (GIS) overlay map of land cover and firebreaks provided by the U.S Department of Defense: Upland Hardwood (UH), Bottomland Hardwood (BH), and Upland Pine (UP). I characterized UH as any upland forest stand dominated by hardwood species (primarily oak, *Quercus* spp.), BH as hardwood-dominated forest stands (primarily blackgum, *Nyssa sylvatica*) associated with drainages, and UP as upland longleaf pine-dominated forest. I selected representative stands in each vegetation type to measure plant responses to fire frequency and season and compared the relative contribution of each vegetation type to plant diversity and fruit production. I selected stands with similar soil types in UP and UH (Candor Sands complex) to reduce any biases that could be associated with soil productivity. After controlling for soil type, I selected UP stands based on the season (DUP and GUP) and time since burned (0yr, 1yr, 2yr) in GUP (for fruit abundance). All selected UH stands were nested within GUP stands.

Vegetative biomass

I randomly placed 40 1.2-m×1.2-m×1.2-m woven-wire panel exclusion cages in UH, DUP, GUP burned 1 or 2 years prior, and BH stands (n=160) in January – March 2011. Cages were designed to exclude herbivores, thereby allowing us to measure any effect of herbivory on understory biomass. I collected all leaf biomass from woody species and entire herbaceous plants (excluding fibrous stems) within cages and paired un-caged plots placed a randomly generated distance (10-100m) and bearing from the caged plot from 1–14 August 2011 and and cages were randomly relocated and sampling was repeated in 2012 (Lashley et al. 2011). Samples were separated by species, bagged in small paper bags, and dried in an air-flow dryer at 50°C (Lashley & Harper 2012). I weighed dried samples to the nearest 0.01 gram and calculated vegetative biomass per hectare by summing plant weights from a plot and extrapolating to kg/ha. I further grouped total biomass into 1 of 5 plant types (Tree, Shrub, Vine, Forb, and Grass) to quantify the relative contribution of each forage class in each vegetation type and fire timing. I separated wiregrass biomass from other grass biomass because of the relative importance to the LLPE.

I conducted a genera survey during June and August of 2011. I randomly located 45 3-m^2 plots in each of the 4 vegetation types (UH, DUP, GUP, and BH) during each of the 2 months (n=360) and counted stems of each vascular plant genus (Lashley et al. 2011;

Lashley & Harper 2012). I used stem count data and cage data (n=320 cages × 2 years) to evaluate genus richness/m^2 in each cover type by counting the total number of genera/m^2.

Fruit abundance

I randomly placed 30 25-m transects in DUP, GUP, UH, and BH stands in each of 4 months (June–September) of 2011 and 2012 (n= 480 each year). In GUP, 10 of the transects/month were placed in 0-yr, 1-yr, and 2-yr since fire, respectively. I used counted fleshy fruits (excluding seeds) to measure understory fruit abundance under 1.2m and within 0.5m of each side along a 25-m transect. Fruits were tallied by species, month, vegetation type, and year. I extrapolated each transect fruit count into fruits/ha. I compared total fruit abundance per month over 2 growing seasons among vegetation types and time since fire categories.

Statistical analyses

I used a univariate general linear model to compare understory vegetative biomass among vegetation types with vegetation type as the independent variable and total biomass, tree biomass, shrub biomass, vine biomass, forb biomass, grass biomass, or wiregrass biomass as the dependent variables. I used a univariate general linear model to compare understory fruit abundance among vegetation types. Using a similar model, I compared fruit density among the 3 categories of time since fire in GUP. I used a square root transformation to correct for non-normality when necessary. All data sets failed Levene’s test ($P<0.001$), which indicated the data had unequal variances. Therefore, I used Tamhane’s T2 multiple comparison test (IBM 2012), a conservative mean comparison test that does not assume equal variances, to compare means when vegetation type had a significant effect on biomass estimates.

RESULTS

Vegetative biomass

Vegetative biomass was not affected by herbivory ($P=0.99$), so I combined caged and un-caged plots for analyses. Total biomass was greater in DUP ($P<0.01$) and GUP ($P=0.01$) than UH. Tree biomass was greater in DUP ($P<0.001$), GUP ($P<0.001$), and UH ($P<0.001$) than BH. Shrub biomass was greater in BH ($P<0.001$) than DUP ($P<0.001$), GUP ($P<0.001$), and UH ($P<0.001$). Vine biomass was greater in BH than GUP ($P=0.03$). Forb biomass was greater in DUP ($P<0.001$) and GUP ($P<0.001$) than BH (Table 1). Grass biomass (excluding wiregrass) was greater in GUP than DUP ($P=0.03$). Wiregrass biomass (excluding other grasses) was similar in DUP and GUP ($P=0.10$), greater in DUP than BH ($P<0.001$), greater in GUP than BH ($P<0.001$) and UH ($P<0.001$), and greater in UH than BH ($P<0.001$) (Table 1).

Fruit abundance

Total fruit abundance was 2-3 times greater in UH than the other vegetation types over the course of the growing season. In June, fruit abundance was similar among vegetation types ($P=0.37$). In July, fruit abundance was greater in DUP than BH ($P=0.02$). In August, fruit abundance was greater in UH than DUP ($P=0.02$), GUP ($P=0.01$), and BH ($P=0.02$) (Table 2). In September, fruit abundance was greater in BH than DUP ($P<0.01$) and GUP ($P=0.01$) (Table 2).

Within GUP, fruit abundance was greater in 2 years since fire (3366.96±1468 fruits/ha) than 1 year since fire (220± 85; *P*=0.01) and same year as fire (0±0; *P*=0.005). Fruit abundance was greater in 1 year since fire than same year as fire (*P*=0.03).

Genus richness

I detected 144 plant genera in the study. None of the genera detected included rare, threatened, or endangered species. I detected the most genera in BH (106 genera) followed by GUP (76 genera), DUP (71 genera), and UH (69 genera). Bottomland hardwood had 20 unique genera (not detected in any other vegetation type), DUP had 4 unique genera, GUP had 1 unique genus, and UH had 6 unique genera. BH had greater genera/m^2 than DUP (*P*<0.001), GUP (*P*<0.001), and UH (*P*<0.001).

DISCUSSION

My results suggest fire frequencies that vary are likely to promote the widest array of native plant taxa and associated food and cover resources for wildlife. For example, fruit abundance differed relative to time since burn in GUP. I detected no fruits in the same growing season as fire and very few occurred the following growing season. Therefore, in units burned on a 1- or 2-year fire-return interval, understory fruit production essentially would be eliminated when the stand burned complete, which may negatively affect many avian and mammal species that consume fruits and could negatively impact plant reproduction (Willson 1986; Jordano 2000). However, White et al. (1990) reported grass-dominated understories may only be maintained by a <3-year fire-return interval. Furthermore, Glitzenstein et al. (2003) reported <2-year fire-return intervals promote and maintain herbaceous-dominated understories by suppressing woody encroachment.

Therefore, fire frequencies should be varied to encourage herbaceous plants most common 1-2 years after fire and woody plants and associated fleshy fruits that are more prevalent 3-5 years after fire.

Similarly, homogeneous application of any single fire season will fail to promote the maximum diversity of plant classes and fleshy fruit production on the landscape. Fire timing plays a key role in flowering synchrony and duration, and differentially affects leguminous-forbs and other flowering plants with divergent flowering phenologies (Platt et al. 1988; Howe 1994; Hiers et al. 2000). In our study, fruit abundance after growing- and dormant-season fires followed different trends month to month. Furthermore, growing-season fires promoted a grass-dominated understory, whereas dormant-season fires promoted forbs, vines, shrubs, and trees. Although the biomass of wiregrass was greater following growing-season fires, the trend was statistically weak. The similarity in wiregrass biomass between growing- and dormant-season fires could have resulted because of the species' adaptations to infrequent growing-season fire (Clewell 1989) and because wiregrass allocates reproductive energy similarly following growing-season fires and following dormant-season fires conducted on warm days (Brockway & Lewis 1997).

In upland hardwood communities, the sparse distribution of pyrophytic fuels (i.e., wiregrass and longleaf pine needles) may result in a more heterogeneous fire mosaic than typically occurs following prescribed fires in upland pine types (Ellair & Platt 2013). Upland hardwoods present in the LLPE capture more light than pines and shade-out understory herbaceous plants, including wiregrass (Greenberg & Simons 1999). Because wiregrass is the primary plant facilitating the spread of fire in LLPE (Clewell 1989; Hardin & White 1989;

Noss 1989; Jones et al. 1994), fires historically would have burned less intensely and in patchier distributions in stands with less wiregrass biomass (Ellair & Platt 2013). Because wiregrass biomass was lower in UH than in GUP, fires were more likely to meander through UH; conversely, the open canopies of the pine stands allowed contiguous coverage by wiregrass and pine needles, and fostered more complete fires in GUP and DUP. The meandering fires in UH likely protected some stems of fruiting understory plants from top-kill, sustaining fruit production even in the same year of fire. As a result, UH harbored a large portion of fruit available during August and September, even in the same growing season and in the growing season after fire.

Management practices often conflict with research recommendations (i.e., the "knowing–doing" gap; Costanza et al. 2013), especially in fire-dependent ecosystems where management strategies can be complex (Higgs 2005). Researchers have suggested that current prescribed burning programs that do not encompass natural variability are not accomplishing ecosystem-wide restoration of LLPE (Van Lear et al. 2005). In fact, empirical data support the application of variable fire prescriptions, which allow the conservation plant diversity (Bond & Archibald 2003; Fuhlendorf et al. 2006; Stambaugh et al. 2011). Perhaps the emphasis on frequent growing-season fires and suppression of hardwood encroachment has invoked a form of tunnel-vision among LLPE managers that can occur when incomplete management recommendations reach the land manager (Currie 1999). Instead, I recommend land managers mimic the historical variability in fire, which will allow more heterogeneity in vegetation types, and thus, accomplish the original mandated goal of maximizing biodiversity.

I suggest a variety of strategies that can be used to promote fire-influenced heterogeneity in fire-maintained systems. Heterogeneity can be maintained at the landscape level by varying fire season, frequency, and intensity among burn units. Within a burn unit, temporal heterogeneity can be encouraged by varying the time between fires, the season of subsequent fires, and the firing techniques and firing conditions used for each prescribed burn (Cheney et al. 1993). Additionally, in the LLPE, some upland hardwood stands should be allowed to persist, because of the inherent heterogeneity of post-fire understory conditions and continuous availability of fleshy fruit in the vegetation type. Furthermore, fires allowed to burn into drainages generally will be suppressed by high moisture levels there; on our study site, these less frequently burned drainages contained unique plant assemblages and abundant fruits late in the growing season. I recommend managers randomly assign a fire prescription (i.e., stochastic variability in firing techniques, season, return frequency, fire intensity, and weather conditions) to each burn block to maximize structural and floral diversity. In fact, Robbins & Meyers (1992) developed a matrix which managers in the LLPE could use to select random fire seasons and frequencies for each burn unit. The range of variation they prescribed was supported by historical accounts of fire conditions in the LLPE ecosystem (Frost 1993). For example, it is thought that ~70% of fires occurred during the growing season based on the historic distribution of lightning-ignited fires (Fill et al. 2012) and that fire return intervals in upland pine stands ranged from biannual to 12-year fire-return intervals (Stambaugh et al. 2011). Randomly assigning treatments with parameters guided by literature and ongoing research will more likely restore and maintain the heterogeneous forest structure, floral, and faunal composition of the LLPE and other fire-maintained forest ecosystems (Greenberg 2001, Bond & Archibald 2003).

IMPLICATIONS FOR PRACTICE

- Practitioners should incorporate dormant- and growing-season fires to maximize the window of fleshy fruit availability through the growing season
- Practitioners should incorporate dormant- and growing-season fires to maximize understory plant species and structural diversity
- Variability in fire-return intervals are necessary to maximize fleshy fruit production and plant reproductive responses
- Allowing a mosaic of fires within stands is important for restoring the longleaf pine ecosystem

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Table 1. Mean vegetative biomass (kg/ha) and standard error (SE) in dominant vegetation types at Fort Bragg Military Installation, North Carolina, August 2011 and 2012.

Vegetation Type[a]	Total	SE	Wiregrass	SE	Grass	SE	Forb	SE	Vine	SE	Shrubs	SE	Trees	SE
BH	374	20	0.5	0.5	25	8	2	0.4	17	3	214	32	29	6
DUP	484	16	105	15	10	2	19	3	11	3	63	15	156	30
GUP	455	12	145	18	26	5	14	2	5	3	52	10	126	21
UH	327	11	75	12	11	3	8	4	15	4	28	4	113	18

[a] Bottomland Hardwood (BH), Upland Pine following Dormant-season fire (DUP), Upland Pine following Growing-season fire (GUP), Upland Hardwood (UH).

Table 2. Mean fruit produced (fruits/ha) and standard error (SE) in dominant vegetation types at Fort Bragg Military Installation, North Carolina, 2011 and 2012.

Vegetation Type	Total Fruit	June	SE	July	SE	August	SE	September	SE
BH	9287	947	330	1240	617	620	245	6480	3165
DUP	8093	373	239	6600	2260	1080	563	40	28
GUP	7334	487	352	2787	1383	567	290	3493	1595
UH	19427	307	150	4813	1703	8027	4220	6280	4192

[a] Bottomland Hardwood (BH), Upland Pine following Dormant-season fire (DUP), Upland Pine following Growing-season fire (GUP), Upland Hardwood (UH).

CHAPTER 3

WHITE-TAILED DEER BURNED AREA SELECTION AND SITE FIDELITY FOLLOWING PRESCRIBED FIRE

ABSTRACT

The effects of prescribed fire on white-tailed deer (*Odocoileus virginianus*) forage availability and quality have been well studied; however, reports on deer selection of burned areas and space use in response to fire are scant, particularly in the context of fire season and time-since-fire. Prescribed fire initially decreases available cover and potentially increases forage quality, which may affect deer adversely or positively during the sensitive summer lactation period. Furthermore, in the longleaf pine (*Pinus palustris*) ecosystem, fire rotations are frequent (≤3yr) often resulting in burned areas comparable to the average size of the summer home range of deer. Therefore, information is needed evaluating whether burning a large portion of a home range is beneficial through stimulating succulent vegetation or harmful through the reduction of cover. In June-August 2011 and 2012, we used GPS data from 16 adult female deer to assess the effects of fire season and time-since-fire on burned area selection, space use (i.e., 95% home range and 50% core area sizes), and core area site fidelity (i.e., area of overlap in core area between years). Using compositional analysis, we determined deer selected unburned drainages and burned areas >1yr-since-fire, essentially avoiding burn units burned in the same growing or dormant season. Core area size increased as the percentage of the home range burned increased, but the size of the home range remained unaffected. Site fidelity decreased and core area size increased as the percentage of the 2011 core area burned in 2012 increased. Deer avoided recently burned areas and

progressively showed greater selection for burned areas as time-since-fire increased, likely seeking less recently burned areas to mitigate the loss of cover, which is consistent with space use trends observed when a necessary resource is in limited supply. Burning large contiguous areas may temporarily force deer to increase space used in response to a reduction in cover, which could be particularly stressful to females during lactation. Thus, we recommend varying fire regimes to include dormant- and growing-season and longer time-since-fire, which may reduce the burning of large contiguous areas that result in large-scale loss of cover.

INTRODUCTION

Prescribed fire commonly is used to manage habitat for wildlife across fire-influenced ecosystems (Bowman et al. 2009). For example, frequent (1-3yr interval) growing-season prescribed fire is used to restore and maintain the longleaf pine (*Pinus palustris*) ecosystem (LLPE) (Aschenbach et al. 2010, Beckage et al. 2005, Fill et al. 2012, Van Lear et al. 2005). However, fire-related research has focused primarily on the appropriate season, application, and frequency of fire in relation to plant community responses, and our knowledge of the effects of fire season and frequency on some fauna is lacking (Aschenbach et al. 2010, Beckage et al. 2005, Fill et al. 2012, Stambaugh et al. 2011, Van Lear et al. 2005). Hence, most studies fail to include adaptations of local fauna when providing management recommendations which could result in negative impacts to fauna sensitive to fire season, frequency, and scale.

Growing-season fires conducted in May and June in the LLPE overlap the lactation period of white-tailed deer (*Odocoileus virginianus*; hereafter deer). Because the lactation period (June – August) is the most nutritionally stressful physiological condition for female deer (Hewitt 2011), they may be especially sensitive to growing-season fire regimes on frequent return intervals, especially when relatively large areas are burned each year. Deer may be affected positively by fire because younger plant growth stimulated by fire is more palatable and higher in nutritive quality (Jones and Case 1990, Leigh et al. 1991, Lewis et al. 1982, Wood 1988), though the nutritional quality of plants is not necessarily increased following fire (Shaw et al. 2010). Furthermore, forage availability for deer can be improved for 3-5 growing seasons after the fire disturbance (Edwards et al. 2004, Lashley et al. 2011, Masters et al. 1993, Masters et al. 1996), though plant density during the same year of fire may be decreased (McCord et al. 2014).

Alternatively, deer may be affected negatively by prescribed fire during lactation if available cover declines (McCord et al. 2014), because lactating females are tightly linked to cover (Kie and Bowyer 1999, Naugle et al. 1997). Following disturbances other than fires, deer and other ungulates seek dense cover despite the potential increase in available nutrition. For example, Cimino and Lovari (2003) reported female roe deer (*Capreolus capreolus*) shifted home ranges to avoid areas where cover (i.e., agricultural crops) was removed. Similarly, VerCauteren and Hygnstrom (1998) demonstrated deer shifted home ranges away from harvested crop fields to permanent cover. However, Beauchesne et al. (2013) reported woodland caribou (*Rangifer tarandus*) exploited recently disturbed, high-quality foraging areas during nutritionally strenuous periods (late winter and lactation in their study) despite the decrease in available cover. Therefore, deer generally may avoid recently burned areas where cover is reduced, but lactating females may seek out these areas if plant nutritional quality is improved.

Few studies have evaluated the effects of prescribed fire on deer space use. Ivey and Causey (1984) determined that deer avoided recently burned areas in the same year as the fire in favor of unburned drainages unless prescribed fires spread through the area in a mosaic configuration where some cover was retained. However, they had a small sample size (2 individuals) and few relocations per individual (<400 each). Meek et al. (2008) reported neither male nor female deer selected burned areas even when only the crepuscular times of primary feeding activity were considered. However, they concluded drought conditions in their semi-arid study site hindered the regeneration of high-quality forbs expected to regenerate following fire and may have explained the lack of attractiveness of burned areas. Because of small sample sizes and confounding weather conditions, little is known about how deer respond to fire disturbances. Moreover, the influence of season of fire and time-since-fire on deer selection of burned areas and space use are scant in the literature. Given the importance of fire in many ecosystems (Bowman et al. 2009) and the sensitivity of lactating deer to changes in understory structure (Kie and Bowyer 1999, Naugle et al. 1997), we measured the effects of fire season and time-since-fire on burned area selection, space use (i.e., 95% home range and 50% core area sizes), and core area site fidelity (i.e., area of overlap in core area between years) by adult female white-tailed deer during the summer lactation period. Furthermore, we evaluated the effects of increased percentages of summer home range and core area burned on the amount of space used by deer and site fidelity of core areas across years.

METHODS

Study Area

We conducted our study at Fort Bragg Military Installation (hereafter Fort Bragg), a 73,469-ha property owned by the U.S. Department of Defense and located in the Sandhills physiographic region in the LLPE of central North Carolina. Uplands were dominated by longleaf pine forests and were managed with growing-season prescribed fire on a 3-yr fire-return interval (Cantrell et al. 1995). Fort Bragg has an extensive manmade firebreak network, which parcels burned areas into individual units averaging 43ha (Lashley et al. 2014[a]). Some areas are missed during the targeted burn year and are burned in the following dormant season (December-March). Treating missed areas in this manner results in a small area of the study site with longer than 3 years-since-fire intervals and dormant-season fires even under the 3-yr fire-return interval. Densely vegetated (primarily *Lyonia* spp. and *Ilex* spp.) drainages were interspersed throughout the landscape and infrequently burned because of moisture. Deer population density was low (2-4 deer/km^2), and harvest records corrected for hunter effort indicated the deer population declined from 1989 to present (J. Jones, Fort Bragg Wildlife Branch, personal communication), commensurate with the initiation of the current growing-season dominated fire regime at Fort Bragg (Cantrell et al. 1995).

Deer Capture

During January-May, 2011, we captured 16 female deer ≥ 1.5-year-old using tranquilizer guns. We used Telazol (5 mg/kg; Midwest Veterinary Supply, Burnsville, MN), xylazine hydrochloride (2.5 mg/kg; Congaree Veterinary Pharmacy, Cayce, SC), and ketamine hydrochloride (5 mg/kg; Midwest Veterinary Supply, Burnsville, MN) in 2-cc transmitter darts. We fit 200g tracking collars (Wildcell, Lotek Wireless Inc., Newmarket, Ontario, Canada) and ear tags on each individual. At 80-minutes post-injection, we reversed the xylazine hydrochloride with tolazoline hydrochloride (10 mg/kg; Midwest Veterinary Supply, Burnsville, MN) and visually monitored the deer from a distance until full recovery. The tracking collars transmitted GPS relocations to a remote site via the SMS network. All data were uploaded to Movebank (www.movebank.org) (Kranstauber et al. 2011, Wikelski and Kays 2014). In Movebank, we censored data that were obvious collar error (e.g., positions outside the continental United States) and data from first 2 weeks of deployment (~3% of locations) because of potential capture bias to movements (Quinn et al. 2012). Deer capture and handling protocols were approved by the North Carolina Wildlife Resources Commission and the North Carolina State University Institutional Animal Care and Use Committee (10-143-O).

Fire Data

We categorized all portions of the study area based on fire history using a geographic information system and data provided by Fort Bragg. We designated 10 categories based on the last fire occurrence 1) same year as a growing-season fire (April-June; 0yrG), 2) same year as a dormant-season fire (December-March; 0yrD), 3) 1 year post growing-season fire (hereafter 1yrG), 4) 1 year post dormant-season fire (1yrD), 5) 2 years post growing-season fire (2yrG), 6) 2 years post dormant-season fire (2yrD), 7) 3 years post growing-season fire (3yrG), 8) 3 years post dormant-season fire (3yrD), 9) 4 or more years post growing-season fire (4yrG), and 10) the drainages that were rarely or never burned and generally contained high-quality cover.

Summer Home Range and Core Area Calculation

We used the adehabitat package (Calenge 2006) of R statistical software version 3.0.1 (R Foundation for Statistical Computing, Vienna, Austria) to calculate a summer 95% home range (hereafter home range) and summer 50% core area (hereafter core area) using the classical kernel method for each individual for each 3-month summer season (Worton 1989). We imported each home range and core area into ArcMAP 10.0 (ESRI, Redlands, California) and overlaid each with the 10 delineated burn categories. We used GIS to calculate the area of the 2011 and 2012 home ranges and core areas, the percentage of core areas overlapping between years (i.e., site fidelity), the change in size of home ranges and core areas from 2011 to 2012, the percentage of the 2011 home ranges and core areas that were burned in 2012, the percentage of 2011 and 2012 home range and core area burned in the same year, and the percentage of each burn classification (i.e., 0yrG-4yrG and 0yrD-3yrD) in the home range by individual each year. Also, we calculated the percentage of relocations occurring in each burn classification each year.

Data Analysis

To determine selection of burn category by deer, we calculated use (percentage of relocations in each burn category) versus availability (percentage of the 95% home range in each burn category) and performed a compositional analysis in the R statistical software (Aebischer and Robertson 1992, Aebischer et al. 1993). We assumed the diel period did not influence deer selection of burned areas (Meek et al. 2008) or general use of some areas for cover or foraging (Coulombe et al. 2011). Additionally, we fit standard least squares regression models to determine if newly burned areas affected the size of the home range and core area, site fidelity of core area, and change in size of the home range and core area from 2011 to 2012. We used the percentage of the 2011 home range and core area burned in 2012, the percentage of the 2011 home range and core area burned in 2011, and the percentage of the 2012 home range and core area burned in 2012 as predictor variables.

RESULTS

Burned area selection

Deer showed strong selectivity for burned areas that had at least 1-year-since-fire (Lambda=0.41, $P<0.01$, DF=9; Table 1). Also, Drainage was selected more than all of the growing-season fire categories, but was selected similarly to the dormant-season categories ≥1-year-since-fire (Table 1). When holding the year-since-fire constant, deer tended to select dormant-season categories over growing-season categories (Table 1). Though not significant at the 0.05 alpha level, the trend of deer selecting dormant-season over growing-season had no exceptions.

Fire effects on space use

The summer core area and home range sizes across years were 43.5±10 and 204±54 ha, respectively. Deer showed 64±6% site fidelity. The percent of the 2012 core area burned was not related to the change in size of summer core area from 2011 to 2012 ($P=0.1$), but was positively correlated with the change in size of the home range ($P=0.03$) and core area site fidelity ($P<0.01$; Table 2). That is, deer with more core area burned in 2012 were more likely to use more overall space but maintained greater site fidelity of their core area. Moreover, site fidelity decreased as the percentage of the previous year's core area burned in 2012 increased ($P=0.04$; Table 2). Thus, deer with new burns in the core of their home range were more likely to shift their range. Also, the size of the core area increased as the percentage of home range burned increased (*P*=0.03; Table 2), whereas the percentage of the 95% home range burned was not correlated with the size of the home range (*P*=0.1; Table 2).

DISCUSSION

Deer avoided newly burned areas likely because of the lack of cover. Several other studies have reported deer avoided areas they had previously used after available cover was removed either by fire or harvesting of agricultural fields (Ivey and Causey 1984, VerCauteren and Hygnstrom 1998, Cimino and Lovari 2003, Meek et al. 2008, Walter et al. 2009). Deer often avoid open areas with little cover to avoid predation risk (Root et al. 1988, Thaker et al. 2011), which is likely the case at Fort Bragg which has high predation rates of coyotes (*Canis latrans*) on adult females and neonates during the lactation period (Chitwood et al. 2014[a], Chitwood unpublished data, Lashley et al. 2014[b]). Ungulates avoid open areas in particular when predation risk is driven by canids or humans (Root et al. 1988, Thaker et al. 2011). Therefore, the application of fire in large contiguous land areas and short fire-return intervals may negatively affect deer through the reduction of cover in large portions of their home range during the lactation period, when cover is extremely important (Kie and Bowyer 1999, Naugle et al. 1997).

Deer may have avoided newly burned areas because of a temporary reduction in forage availability. Coulombe et al. (2011) demonstrated deer movements were better explained by forage density than lateral cover; however, they cautioned this relationship would probably reverse when a deer population is below nutritional carrying capacity and under high predation risk. Deer density is likely well below nutritional carrying capacity at

Fort Bragg because deer are not affecting the understory plant biomass (Lashley et al. *In Review*) and predation risk is clearly high given the high neonate and adult mortalities due to coyotes (Chitwood et al. 2014[a], Chitwood unpublished data, Lashley et al. 2014[b]). Also, female roe deer are particularly sensitive to reductions in available cover and avoid areas when cover is removed and forage availability remains similar (Cimino and Lovari 2003). Further, VerCauteren and Hygnstrom (1998) determined deer selected agricultural fields when cover was available but before forage availability was high, and then deer shifted home ranges away from harvested fields to permanent cover even though waste grains were still available for consumption. Therefore, a reduction in available cover is the more likely mechanism explaining the avoidance of recently burned areas in our study.

Deer increased core area size in response to increased percentage of their core area burned, likely to accommodate the decrease in available cover. Similarly, previous studies reported ungulates use larger home ranges when resource availability (in our case cover) is low (Relyea et al. 2000, Tufto et al. 1996, VerCauteren and Hygnstrom 1998). Moreover, other studies have documented ungulates increase movement rates, space use, and use larger core areas to avoid increased predation risk (Kilpatrick and Lima 1999, Naugle et al. 1997, Root et al. 1988, VerCauteren and Hyngstrom 1998, Williams et al. 2008). Whatever the mechanism, females normally restrict their home range and core area size during fawning (Bertrand et al.1996), but we observed the opposite response to increased percentage of the core area burned. Therefore, prescribed fires that consume large portions of the summer home range of a lactating deer may subject the individual to additional stresses associated with ranging into alternative, less familiar areas outside the normal core area. Unfamiliarity with new areas may reduce milk production if feeding efficiency or nutritional intake is reduced (Ditchkoff 2011) or increase depredation of adults and neonates (Bonte et al. 2012). In fact, this potential effect could partially explain the large proportion of neonate starvations (25%) and overall poor neonate survival (14%) recently reported at Fort Bragg (Chitwood et al. 2014[b], Chitwood unpublished data).

Several studies have reported home range sizes of deer vary with the availability of resources (Stewart et al. 2011), but home range size is likely similar from year to year despite changing resources, such as cover (Nelson and Mech 1999). Similarly, the amount of the home range burned did not influence home range size in our study. Individuals may be unlikely to alter home range sizes from year to year because social structure and intraspecific competition fluctuate little between years (Stewart et al. 2011). Furthermore, lactating females are solitary during the lactation period, decreasing their likelihood of expanding their home range to overlap with other conspecifics (Bertrand et al. 1996). Therefore, home range size remains constant in response to fire, even when core area sizes are altered, which suggests deer form core areas based on resource availability while home ranges are more related to interactions with conspecifics (Coulombe et al. 2011).

Deer probably increased core areas as more of their core area was burned to incorporate larger areas when cover availability was decreased. In this case, site fidelity increases because a larger core area associated with more burned area is more likely to overlap with the previous year, even though deer avoided the newly burned areas. Our results contradict Campbell et al. (2004) who noted that site fidelity was not influenced by disturbance (though they studied timber harvest). However, they reported deer were relocated outside their pre-harvest ranges more routinely than control deer (Campbell et al. 2004), which is similar to the increases in core area sizes we observed.

Traditionally, it was thought that fire benefitted deer immediately because of increased forage quality in the same year as fire (Wood 1988). However, our study indicates deer avoid areas burned in the same year similar to other studies (Ivey and Causey 1984, Meek et al. 2008). Increasing selection with time-since-fire is likely reflective of the increase in available cover each year for 5-10 years following fire as plants regenerate in the understory. We did not include deer selection of fire-suppressed uplands because none were available at Fort Bragg, but we expect deer would avoid these areas because of the eventual succession of plants out of the understory stratum several years after fire. Therefore, deer benefit from periodic prescribed fire, despite the temporary loss of cover, because cover is increased in the understory for several years post-fire (Lashley et al. 2011). Without fire, plants providing cover succeed into the midstory resulting in the loss of cover in long-term fire-suppressed areas (Brockway et al. 1998, Moser and Yu 2003).

The scale of burning is an important consideration in fire regimes. For example, at Fort Bragg the average burn block size (43 ha; Lashley et al. 2014[a]) is similar to the average core area of the deer we monitored. Also, adjacent areas often are burned in the same year (Lashley et al. 2014[a]), which could result in burned areas larger than the home ranges of deer we observed. Burning large portions of their home range in the same year may pose a problem to lactating females, particularly if mosaics of cover are lost with consistent firing techniques and burning conditions (Ivey and Causey 1984, Lashley et al. 2014[a]). Historically, lightning generated fires were sometimes expansive; however, lightning in the Southeast generally occurred most frequently late in the afternoon and was associated with rainfall (Watson and Holle 1996), which inevitably created a mosaic of burned area and cover (Greenberg 2001). When this mosaic is maintained at the landscape scale, deer may readily use recently burned areas (Ivey and Causey 1984). However, current fire regimes are unlikely to create mosaics at the stand level with intact wiregrass (*Aristida stricta*) in the understory. This is because prescribed fires are commonly lit during the late morning in a set range of conditions that exclude rainfall and lower intensity fire behavior that occurs at night (Sacket and Wade 1970). Aside from altering firing conditions and techniques, the landscape level mosaics of burned area and cover must be maintained by the selection of areas burned rather than relying on heterogeneity in fire expansion within a stand.

CONCLUSIONS

In our study, deer selected against newly burned areas with a clear partiality to less recently burned areas and densely vegetated drainages. Because deer avoid newly burned areas and fire reverses the decrease of space use normally observed during lactation, efforts should be taken to minimize burning large contiguous land areas during a single year. Managers should avoid burning adjacent areas during the same year to minimize the depletion of cover during the lactation period and allow variability in the season of burn and fire-return interval to create adequate availability of dormant-season burned areas and areas with longer time-since-fire.

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Table 1. Pair-wise comparison of summer burned area selection of GPS-tagged white-tailed deer in longleaf pine ecosystem in relation to the time since the most recent fire and season of fire on Fort Bragg Military Installation, North Carolina, 2011 and 2012. A + indicates that the burned area in the row was relatively selected over the burned area in the column, while a - indicates that the burned area in the row was relatively selected less than the burned area in the column (a single sign indicates the relationship is non-significant and triple sign indicates the relationship is significant at alpha=0.05).

Burn Category [a]	0yr D[b]	0yr G[b]	1yr D	1yr G	2yr D	2yr G	3yr G	3yr D	4yr G	Drainage
0yr Dormant	0	+	-	---	-	---	-	---	---	---
0yr Growing	-	0	---	---	-	---	---	---	---	---
1yr Dormant	+	+++	0	+	+	+	+	-	+	-
1yr Growing	+++	+++	-	0	-	-	-	---	-	---
2yr Dormant	+	+	-	+	0	-	+	-	-	-
2yr Growing	+++	+++	-	+	+	0	+	-	+	---
3yr Growing	+	+++	-	+	-	-	0	-	-	---
3yr Dormant	+++	+++	+	+++	+	+	+	0	+	-
4yr+Growing	+++	+++	-	+	+	-	+	-	0	---
Drainage	+++	+++	+	+++	+	+++	+++	+	+++	0

[a] Lambda=0.41, P<0.001, DF=9.

[b] D=dormant-season fire and G=growing-season fire.

Table 2. The effects of percent of summer home range (HR) and core areas (CA) burned on the change in size, site fidelity, and total area used by white-tailed deer at Fort Bragg Military Installation, North Carolina, USA, 2011 and 2012.

Response	**Term**	**Estimate**	**SE**	**T-Ratio**	**P-Value**
Change in size of 50% CA	Intercept	-4	21.5	-0.2	0.86
	%2011CAburned2012	0.1	0.9	0.1	0.91
	%2011CAburned2011	0.4	0.6	0.6	0.58
	%2012CAburned2012	1.8	1.1	1.6	0.14
	%overlapburned2012	-0.7	1.2	-0.6	0.58
	%11HRBurned2012	-0.4	1.1	-0.4	0.7
Site Fidelity of CA	Intercept	68.8	8.7	8	<0.01*
	%2011CAburned2012	-0.9	0.4	-2.4	0.04*
	%2011CAburned2011	0.3	0.2	1.4	0.2
	%2012CAburned2012	1.4	0.5	3	<0.01*
	%overlapburned2012	0.5	0.5	1	0.36
	%11HRBurned2012	-0.6	0.4	-1.3	0.22
Change in size of 95% HR	Intercept	-11.6	16.2	-0.7	0.49
	%2011CAburned2012	0.7	0.7	1	0.32
	%2011CAburned2011	0	0.5	0.1	0.93
	%2012CAburned2012	2.1	0.9	2.5	0.03*
	%overlapburned2012	-1.7	0.9	-1.9	0.08
	%11HRBurned2012	0	0.8	-0.1	0.96
50% CA Size	Intercept	95.4	12.3	7.8	<0.01*
	%CABurn	0.1	0.6	0.2	0.83
	%HRBurn	1.8	0.8	2.3	0.03*
95% HR Size	Intercept	424.7	67.8	6.3	<0.01*
	%CABurn	3.7	3.3	1.1	0.27
	%HRBurn	6.9	4.4	1.6	0.13

*Denotes significance at alpha=0.05.