## RESEARCH ARTICLE

Relationships between Fire Frequency and Vegetation Type in Pine Flatwoods of East-Central Florida, USA

> David R. Breininger <sup>1</sup> Brean W. Duncan

Dynamac Corporation Kennedy Space Center, FL 32899 USA

## Nathaniel J. Dominy

Department of Ecology and Evolution University of Chicago 1101 East 57th Street Chicago, IL 60637 USA

<sup>1</sup> Corresponding author e-mail: Breindr@kscems.ksc.nasa.gov

Natural Areas Journal 22:186–193

**ABSTRACT**: Fire frequencies are usually identified for plant communities with little regard to fine-scale (small geographical area) variation. Better knowledge is needed to manage fire in landscapes having fuels that vary in their propensity to burn, especially where the details of fire patterns are critical for sustaining specialized species. We quantified variations in fire frequency among patches of different vegetation within a 300-ha fire management unit dominated by pine flatwoods. We mapped each of the four fires that occurred between 1979 and 1998, and we mapped four vegetation patch types: oak scrub, mesic flatwoods, swale marsh, and forest. Significant differences in fire frequency occurred among patch types for each of four fires. Generally, oak scrub and forests burned less frequently than mesic flatwoods and marsh. Only 2% of the area did not burn during the study period; these unburned areas were located along human-created edges or within forests. The patterns produced by these fires were suitable for promoting the demographic success of a specialized species that is declining almost everywhere else. We conclude that understanding spatial variations in fire frequencies among patch types is important for sustaining suitable habitat structure for specialized plants and animals.

# Relaciones entre Frecuencia del Fuego y Tipo de Vegetación en Bosques de Pinos de Florida Central, USA

RESUMEN: La frecuencia del fuego está usualmente identificada en comunidades vegetales con una variación desde poca consideración hasta escala fina (pequeñas áreas geográficas). Un mejor conocimiento es necesario para manejar el fuego en áreas amplias, existiendo combustibles que varían en su propensión a quemarse, especialmente donde los detalles de los patrones del fuego son críticos para mantener especies especializadas. Cuantificamos las variaciones en la frecuencia del fuego entre parches de diferente vegetación dentro de unidades de manejo de fuego de 300-ha dominadas por pinos. Mapeamos cada uno de los cuatro fuegos que ocurrieron entre 1979 y 1998, y mapeamos cuatro parches de tipos de vegetación: roble, bosques húmedos de pinos; humedales, y bosque. Diferencias significativas en la frecuencia del fuego ocurrieron entre los tipos de parche en cada uno de los cuatro fuegos. Generalmente, el roble y el bosque se quemaron menos frecuentemente que en el bosque húmedo de pinos y los humedales. Sólo el 2% del área no se quemó durante el período de estudio, estas áreas no quemadas estuvieron localizadas a lo largo de límites creados por el hombre o dentro del bosque. Los patrones producidos por esos fuegos fueron aptos para promover el suceso demográfico de una especie especializada que está disminuyendo en casi todos los demás lugares. Concluimos que el entendimiento de variaciones espaciales en la frecuencia del fuego entre los tipos de parches es importante para mantener estructura de hábitat para animales y plantas especializados.

Index terms: fire frequency, fire management, pine flatwoods, Florida scrub-jay, scrub

#### INTRODUCTION

Fire, a major process shaping natural communities, often maintains habitat conditions needed for specialized species (Abrahamson and Hartnett 1990, Myers 1990, Frost 1998). Natural fire regimes are no longer possible in many landscapes so that prescribed fire management is essential (e.g., Main and Menges 1997). Fire management planning focuses on fire return intervals, which are usually different for each vegetation type (Main and Menges 1997). Fire management units, however, often comprise different vegetation types distributed at scales that are finer than most fires and the home ranges of specialized animals (Myers 1990, Platt and Schwartz 1990, Breininger et al. 1995, Smith et al. 1997). Variations in fire patterns can produce microhabitats needed by specialized species (Mushinsky and Gibson 1991, Lyon and Smith 2000).

We investigated whether fire frequencies varied within a 300-ha landscape because of differences in the fine-scale heterogeneity of dominant vegetation. We review the significance of fine-scale variations in fire frequencies to habitat specialists, which are important indicators of natural fire regimes (Frost 1998). We argue that general observations of fire patterns for plant communities are inadequate to describe specific fire patterns within landscapes and that we need a quantitative understanding about how fires vary with vegetation type and environmental conditions.

We focused our studies on pine flatwoods---the once dominant land cover type that linked many southeastern U.S. plant communities (Abrahamson and Hartnett 1990, Platt 1999). Although it is general knowledge that certain flatwoods vegetation types burn more readily than others, no published studies have quantified how fires actually vary among types within landscapes. Humans have been reducing fire frequencies by actively suppressing fires and fragmenting pine flatwoods for 60 years (Platt et al. 1991, Main and Menges 1997, Menges and Hawkes 1998, Duncan et al. 1999). Reductions in fire frequency have caused changes that negatively impact specialized species unique to southeastern plant communities (Auffenberg and Franz 1982, Hawkes and Menges 1996). But simply reintroducing fire to these systems does not always restore the conditions needed by specialized species (Schmalzer and Boyle 1998, Breininger et al. 1999). We use the Florida scrub-jay (Aphelocoma coerulescens Bosc) as an example of a specialized species because it is an indicator of habitat conditions and a flagship species for conservation (Hawkes and Menges 1996). It is common practice to sustain the general structure and composition of Florida habitats without maintaining the key features needed for the persistence of Florida scrub-jay populations (Breininger et al. 1998, 1999).

#### BACKGROUND: LANDSCAPE HETEROGENEITY OF PINE FLATWOODS

Pine flatwoods are often a mix of hydric, mesic, and xeric vegetation types that are sometimes considered separate community types (Abrahamson and Hartnett 1990, Myers 1990). Mesic flatwoods are dominated by shrubs (saw palmetto [Serenoa repens], fetterbush [Lyonia lucida], gallberry [Ilex glabra]) and grasses (e.g., wiregrass [Aristida beyrichiana]) (nomenclature follows Wunderlin 1998). Scrubby flatwoods are ecotonal between oak scrub and mesic flatwoods communities and consist of plants from both communities (Schmalzer and Hinkle 1992, Menges and Hawkes 1998, Schmalzer et al. 1999). Xeric oak scrubs are dominated by scrub oaks (e.g., Quercus myrtifolia, Q. geminata, Q. inopina, Q. chapmanii) (Myers 1990). Oak scrub and scrubby flatwoods are not consistently mapped as separate communities, especially where the patches of scrub oaks are smaller than the minimum mapping unit or are difficult to distinguish on aerial photographs (Breininger et al. 1995).

Mesic and scrubby flatwoods have an open canopy of pines, which can include longleaf pine (*Pinus palustris*), slash pine (*P. elliottii*), and pond pine (*P. serotina*), or sand pine (*P. clasua*). Except for sand pine, these pines are resilient to most fires. Sand pines are killed by fires but produce serotinous cones bearing seeds that germinate profusely after fires. It is difficult to apply fire frequency analysis techniques (i.e., Agee 1993) to pine flatwoods because the bark of these pines is resilient to fire and most areas have been timbered within the last 70 years. Oak scrub is usually referred to as "sand pine scrub" when it contains a



Figure 1. Distribution of patch types within the Tel 4 study site at Kennedy Space Center, Florida.

dense canopy of sand pine; this generally occurs in areas subject to less frequent fires. Many types of marshes (e.g., dominated by *Spartina bakerii*, *Panicum abscissum*, *Andropogon* spp., *Calamovilfa curtissii*) are embedded within pine flatwoods (Abrahamson and Hartnett 1990). Hardwood forests often replace marshes or flatwoods following reductions in the fire regime or changes in hydrology (Duncan et al. 1999, Yahr et al. 2000).

### STUDY AREA

The study was conducted at Tel-4 on Kennedy Space Center/Merritt Island National Wildlife Refuge, which is located along Florida's Atlantic coast, USA. The U.S. Fish and Wildlife Service (USFWS) manages areas not needed by the space program. The 300-ha study area is in a fire management unit mapped as pine flatwoods, or a mixture of oak scrub, scrubby flatwoods, mesic flatwoods, marshes, and forest, depending on the minimum mapping unit and classification system. Objectives for burning this unit are to suppress all wildfires, if possible, and use prescribed fires to burn 40%-60% of the area every three to five years without specific objectives for any patch type (Adrian and Farinettii 1995). Prescribed fires are implemented using head fires produced by aerial ignitions distributed as a grid after downwind fire lines are secured by backing fires.

Topography ranges from 1 to 3 m in elevation because of coastal processes that formed ridges and troughs. Oak scrub occurs on ridges, marshes occur in troughs, and mesic flatwoods occupy intermediate areas (Schmalzer and Hinkle 1992, Breininger et al. 1995, Duncan et al. 1999). One large oak scrub ridge forms an almost continuous line from north to south in the western half of Tel 4 (Figure 1). Many smaller oak scrub ridges occur throughout the study site. The shrubs include those listed above, as well as Quercus inopina and Sabal etonia, which occur along the Lake Wales Ridge in central Florida but not along the Atlantic coast (Schmalzer et al. 1999). Mesic flatwoods dominate the site and usually have < 30% scrub oak cover (Duncan et al. 1995). Slash pine tree

canopy cover averages < 15%, except in forests. Forests are dominated by slash pine, live oak (*Quercus virginiana*), cabbage palm (*Sabal palmetto*), red maple (*Acer rubrum*), Carolina willow (*Salix caroliniana*), and red bay (*Persea borbonia*).

Analyses of aerial photographs showed that fires were common prior to 1958 and forests were rare (Duncan et al. 1999). Humans actively suppressed fires between 1958 and 1978, causing many marshes and mesic flatwoods to be replaced by forests (Duncan et al. 1999). A 1978 wildfire burned Tel 4 during this fire suppression period. Although a program of prescribed fire began after 1978, the combined sequences of three prescribed fires failed to return all forested habitats to the original vegetation types comprising the site before active fire suppression (Duncan et al. 1999).

# METHODS

We had previously mapped patches of homogenous vegetation > 20 m<sup>2</sup> on 1:2,200-scale, color infrared, aerial photographs (Duncan et al. 1999). Mapping included oak scrub (> 51% scrub oak cover), mesic flatwoods (0%–50% scrub oak cover), swale marsh, forest (> 65% tree canopy cover), ruderal grass, and other. Ruderal grass referred to grassy areas maintained by frequent mowing. Other habitats included ditches, fire breaks, roads, and concrete.

We searched USFWS fire records and aerial photography records to identify all fires that occurred from 1979 until 2000. One wildfire burned most of Tel 4 prior to available photography in 1979. However, the available 1979 photography was too late after the wildfire to clearly distinguish all fire boundaries. Three prescribed fires were conducted by the USFWS. We previously mapped a 1985 prescribed fire using aerial photographs and mapped a 1987 prescribed fire using Landsat Thematic Mapper imagery (Duncan et al. 1995). In this study, we mapped a 1991 prescribed fire by screen digitizing from a 1992 scanned and registered false color infrared aerial photograph using ARC/INFO (Environmental Systems

Research Institute 1997). We eliminated the southeast corner of the study tract where we could not distinguish fire boundaries under the forest canopy. A severe wildfire burned Tel 4 and most adjacent areas in June of 1998. For the 1998 fire, we mapped unburned patches  $> 20 \text{ m}^2$  in the field using a Trimble Navigation Pathfinder Professional XL Global Positioning System Unit (GPS) (Trimble Navigation Limited 1994). The GPS data were differentially corrected and exported into an ARC/INFO coverage.

We overlaid 200 random points within the study area to test whether fire frequency and the extent of each fire varied significantly among patch types. We eliminated points that intersected human cultural features (i.e., houses, ruderal grass, roads) and points that were within 1 m of a boundary between vegetation types. We intersected the points with the vegetation coverage and the four fire maps to generate six variables and a point identification number. For each point, we recorded the patch type, whether the point was burned or unburned in each of four fires, and the number of times each point burned. The four null hypotheses we tested were that the frequencies that points burned were independent of patch type separately for each of the four fires; a fifth null hypothesis was that the number of times points burned was independent of patch type. We tested these hypotheses using exact loglikelihood statistics (SPSS 1999). To describe results, we divided the number of points burned by the total number of points for the category of interest. For example, we divided the number of points that oak patches burned during a particular fire by the total number of points within oak. We also divided the total number of points of all patches that did not burn by the total number of points to describe how much habitat did not burn in the four fires we studied.

## RESULTS

All three prescribed fires occurred in winter during dry conditions. The 1998 wildfire occurred in June during a drought. Less habitat area burned from three prescribed fires (53%-67%) compared to the

Table 1. Vegetation type and the number of points that burned in four fires, Kennedy Space Center, Florida.

Fire	Oak Scrub (n = 30)	Mesic Flatwoods (n= 87)	Marsh (n =24)	Forest (n = 16)	Likelihood Ratio	Р	Percent of All Points That Burned
1985	12	60	23	10	21.764	< 0.001	67
1987	13	66	23	7	25.851	< 0.001	69
1992	7	54	19	3	29.041	< 0.001	53
1998	30	84	23	9	23.351	<0.001	93





wildfire in 1998 (93%; Table 1; Figure 2). The null hypothesis that the frequencies of points that burned were independent of patch type was rejected for every fire (P < 0.001). Oak scrub and forests burned less frequently than mesic flatwoods and marsh in the prescribed fires. Less than half of the oak scrub burned in any one prescribed fire, but almost all burned during the 1998 wildfire. At least 62% of the mesic flatwoods burned in every fire, and at least 79% of the marshes burned in every fire. Most areas that did not burn during the wildfire included forest and ruderal edge habitats.

The null hypothesis that fire frequency was unrelated to patch type was rejected (Table 2). Seventy one percent of the study site burned in at least three of the four fires (Table 2). Only 2% of the area did not burn during the study period and these areas were located along ruderal edges or within forests (Figure 3). Areas of mesic flatwoods or marsh that burned infrequently were adjacent or between oak scrub, ruderal edges, or forests. Most marsh that did not burn during the 1998 fire included the deepest marshes that had standing water during the fire. Forests that burned frequently were along edges of swale marshes or mesic flatwoods, and many of these were small forest patches surrounded by mesic flatwoods or marshes.

# DISCUSSION

We obtained direct quantitative data showing that vegetation patch type influenced fire patterns within our study landscapes, and that these patterns were consistent with general observations concerning the propensity of each plant community to burn. Patches of marsh and mesic flatwoods had greater propensities to burn than patches of oak scrub and forest. Wiregrass, gallberry, saw palmetto, and pine needles have long-been recognized for having the fuel structure and chemistry that gives mesic flatwoods a high propensity to burn (Shafizadeh et al., 1977, Myers 1990, Platt et al. 1991, Platt 1999). Flatwoods marshes are also composed of species that burn readily, accumulate fuels faster than oak scrub, and are probably important for increasing fire frequency in oak scrub and



Figure 3. Fire frequencies at the Tel 4 study site at Kennedy Space Center, Florida. Fire frequency patterns were produced by overlaying four maps that represented four separate fires.

Number of Times a Point Burned	Oak Scrub (n = 30)	Mesic Flatwoods (n = 87)	Marsh (n = 24)	Forest (n = 16)
0 (never burned)		1	· · · · · · · · · · · · · · · · · · ·	2
1	9	3		5
2	11	22	1	5
3	9	27	6	2
4 (burned in every fire)	1	34	17	2

scrubby flatwoods (Myers 1990, Yahr et al. 2000).

We found that most mesic flatwoods burned during every fire, which was consistent with the fire return interval of every 1-8 years suggested for mesic flatwoods (Florida Natural Areas Inventory 1990, Stout and Marion 1993, Main and Menges 1997). Fire suppression longer than 10 years might have been unusual in the evolutionary history of many flatwoods species and can produce pronounced changes in community structure (Maliakal et al. 2000). Periods of reduced fire frequency favor hardwood forests (Platt and Schwartz 1990) that can replace the open canopy structure of pine flatwoods and their associated marshes within 20 years (Duncan et al. 1999). Although many species require frequent fire, we know of no species that require unburned flatwoods ( Speake et al 1978, Means and Campbell 1981, Auffenberg and Franz 1982, Layne 1990, Breininger and Smith 1992, Menges and Kohfeldt 1995, Hawkes and Menges 1996 Menges and Hawkes 1998).

We found that forests had the lowest propensity to burn, as previously observed (Platt and Schwartz 1990). Almost no oak scrub remained unburned during the 20year study period. This is beneficial to Florida scrub-jays, which experience poor demographic success in areas that are unburned for 20 years or longer (Woolfenden and Fitzpatrick 1984, Breininger et al 1998). Fire return intervals for scrubby flatwoods are approximately every 5-20 years (Menges and Hawkes 1998). Periods of greater than 20 years without fire often result in a vegetation structure that is difficult or impossible to reverse by only prescribed fire (Schmalzer and Boyle 1998 Duncan et al. 1999). Florida scrub-jay populations declined after the extensive 1998 wildfire but gradually recovered as oaks recovered (Breininger and Oddy 2001). Although we could not map all fire boundaries of the 1979 fire, we could establish that the fire burned most of the study site. Extensive fires occurring once every 20 years might be useful because they tend to burn nearly all areas, including those resilient to fire.

We found that almost half the oak scrub burned during each prescribed fire and that 30% of the oak scrub burned three to four times during the 20-year study. These frequent fires explain why open sandy areas were common among scrub oaks at Tel 4 (Duncan et al. 1999). Open sandy areas are important microhabitats for Florida scrub-jays (Woolfenden and Fitzpatrick 1984, Breininger et al. 1995) and many specialized plants (Menges and Hawkes 1998). Most open sandy areas do not persist in scrubby flatwoods for more than a few years after fire (Schmalzer and Hinkle 1992, Hawkes and Menges 1996). Frequent fires that originate in mesic flatwoods or marshes and burn into oak scrub represent one mechanism to retain open sandy areas. Although we know of no published empirical data, conventional wisdom holds that natural fires frequently occur within Florida landscapes but that fires often burn out upon entering oak scrub, where flammability is lower (Webber 1935, Myers 1990).

Combined with meteorological factors, differences in the propensity to burn among patch types help explain why fires often burned as mosaics. The Tel 4 site is one of the few study sites where we have observed that Florida scrub-jay demographic success is usually good enough for longterm population persistence (Breininger and Oddy 2001). Each prescribed fire burned much of the matrix surrounding the oak scrub and burned far enough into the scrub to generate openings, but not so much that patches of oak scrub at optimal height were eliminated. Mosaic fires are needed to sustain Florida scrub-jay populations, but arbitrary mosaics from repeated prescribed fires often result in marginal habitat conditions that do not sustain populations (Breininger et al. 1998, 1999). Once Florida scrub-jays become breeders, they normally spend their entire lives in bne territory, averaging 10 ha in size (Woolfenden and Fitzpatrick 1984, Breininger et al. 1995). Demographic success at Tel 4 is best where each territory has a hectare of bak scrub 120–170 cm tall scattered among short scrub that has many open sandy areas from recent fires (Breininger and Oddy 2001). Oaks that are 120–170 cm tall usually have been unburned for 10 years but

not as long as 20 years (Duncan et al. 1995). Long-term scrub-jay population persistence requires that there are enough optimal territories that produce enough recruits to offset population losses in suboptimal territories (Breininger and Oddy 2001).

Many declining plant and animal populations are small and fragmented and will not persist without the development of specific management practices (Auffenberg and Franz 1982, Quintana-Ascencio and Menges 1996, Breininger et al. 1999). Our study showed that fire patterns are influenced by vegetation composition and that these variations are relevant for specialized species. Our study had many limitations regarding temporal duration and spatial scale because fires are variable processes influenced by many factors related to environmental conditions and prescribed fire techniques (Rothermal 1983, Dye 1991). Despite these limitations, cherished beliefs and general observations about the influence of vegetation composition on fire patterns need to be quantified within landscapes (Lyon et al. 2000). For example, wildfires occur under a wide range of meteorological conditions, including conditions that do not favor the spreading of flames across large areas and conditions that are too dry and dangerous for prescribed fire (Robbins and Myers 1992). More studies are needed that quantify differences in fire patterns associated with a wider range of seasons, meteorology, and landscapes that have different arrangements of fire frequencies, seasonal fire patterns, and vegetation. Although there were no objectives for burning a particular patch type more extensively than another during our study, fire managers might have more specific objectives. These types of studies are still relevant for determining whether it is possible to burn certain patch types at greater or lesser frequencies than expected. -----

#### ACKNOWLEDGMENTS

This study was funded as part of the NASA Life Sciences Support Contract facilitated by B. Summerfield, W. M. Knott III, and K. Gorman. Additional support to N.J.D. was received from the NASA Planetary Biology Internship Program facilitated by R. Wheeler. We thank F. Adrian, M. Epstein, and R. Hight of Merritt Island National Wildlife Refuge for facilitating our studies on refuge lands. We thank R. Hinkle, E. Menges, Z. Prusak, R. Schaub, P. Schmalzer, and two anonymous reviewers for helping us improve the manuscript.

Dave Breininger is Senior Ecologist, NASA Life Sciences Support Contract, Kennedy Space Center. His interests are focused on relationships between habitat suitability and population dynamics, by combining field data with remote sensing, GIS, population, and landscape models.

Brean Duncan is a Physical Geographer with the Dynamac Corporation at Kennedy Space Center, Florida. His research interests include using remote sensing, GIS, and GPS for habitat/wildlife modeling, landscape ecology, and spatial analysis.

Nathaniel Dominy recently completed his doctorate in the Department of Anatomy at the University of Hong Kong. He is interested in the evolution of the primate perceptual system and the use of GPS and GIS technologies to model the ecological factors influencing the dispersion and distribution of tropical plants.

#### LITERATURE CITED

- Abrahamson, W.G., and D.C. Hartnett. 1990. Pine flatwoods and dry prairies. Pp. 103-149 *in* R.L. Myers and J.J. Ewell, eds., Ecosystems of Florida. University of Central Florida Press, Orlando.
- Adrian, F., and R. Farinetti. 1995. Fire management plan. Merritt Island National Wildlife Refuge, Titusville, Fla. 81 pp.
- Agee, J.K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, D.C. 493 pp.
- Auffenberg, W., and R. Franz. 1982. The status and distribution of the gopher tortoise (Gopherus polyphemus). Pp. 95-126 in R.B. Bury, ed., North American Tortoises: Conservation and Ecology. Research Report 12, U.S. Fish and Wildlife Service, Jacksonville, Fla.
- Breininger, D.R., and D.M. Oddy. 2001. Fire and Florida scrub-jay source-sink dynamics in mesic flatwoods. Pp. 3-7 in D.P. Zattau, ed., Proceedings of the Florida Scrub

Symposium 2001. U.S. Fish and Wildlife Service, Jacksonville, Fla.

- Breininger, D.R., and R.B. Smith. 1992. Relationships between fire and bird density in coastal scrub and slash pine flatwoods in Florida. American Midland Naturalist 127:223-240.
- Breininger, D.R., V.L. Larson, B.A. Duncan, R.B. Smith, D.M. Oddy, and M. Goodchild. 1995. Landscape patterns in Florida scrub jay habitat preference and demography. Conservation Biology 9:1442-1453.
- Breininger D.R., V.L. Larson, B.W. Duncan, and R.B. Smith. 1998. Linking habitat suitability to demographic success in Florida scrub-jays. Wildlife Society Bulletin 26:118-128.
- Breininger, D.R., M.A. Burgman, and B.M. Stith. 1999. Influence of habitat, catastrophes, and population size on extinction risk on Florida scrub-jay populations. Wildlife Society Bulletin 27:810-822.
- Duncan, B.W., D.R. Breininger, P.A. Schmalzer, and V.L. Larson. 1995. Validating a Florida scrub jay habitat suitability model, using demography data on Kennedy Space Center. Photogrammetric Engineering and Remote Sensing 56:1361-1370.
- Duncan, B.W., S. Boyle, D.R. Breininger, and P.A. Schmalzer. 1999. Coupling past management practice and historical landscape change on John F. Kennedy Space Center. Landscape Ecology 14:291-309.
- Dye, R. 1991. Use of firing techniques to achieve naturalness in Florida Parks. Proceedings of the Tall Timbers Fire Ecology Conference 17:353-360.
- Environmental Systems Research Institute. 1997. ARC/INFO Command Reference and Users Guide. Version 7.0, The Geographic Information Systems Software. Environmental Systems Research Institute, Inc., Redlands, Calif.
- Florida Natural Areas Inventory. 1990. Tracking lists of special plants, lichens, invertebrates, vertebrates, and natural communities. Tallahassee, Fla. 111 pp.
- Frost, C.C. 1998. Presettlement fire frequency regimes of the United States: a first approximation. Tall Timbers Fire Ecology Conference Proceedings 20:70-81.
- Hawkes, C.V., and E.S. Menges. 1996. The relationship between open space and fire for species in a xeric Florida shrubland. Bulletin of the Torrey Botanical Club 123:81-92.
- Layne, J.N. 1990. The Florida mouse. Pp. 1-21 in C.K. Dodd, Jr., R.E. Ashton, Jr., R. Franz, and E. Wester, eds., Burrow Associates of the Gopher Tortoise: Proceedings of the 8th

Annual Meeting of the Gopher Tortoise Council. Florida Museum of Natural History, Gainesville.

- Lyon, L.J., and J.K. Smith. 2000. Management and research implications. Pp. 59-62 in J.K. Smith, ed., Wildland Fire in Ecosystems: Effects of Fire on Fauna. General Technical Report RMRS-GTR-42-Vol 1, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah.
- Lyon, L.J., M. H. Huff, and J. K. Smith. 2000.
  Fire effects on fauna at landscape scales.
  Pp. 43-49 *in* J.K. Smith, ed., Wildland Fire in Ecosystems: Effects of Fire on Fauna.
  General Technical Report RMRS-GTR-42-Vol 1, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah.
- Main, K.N., and E.S. Menges. 1997. Archbold Biological Station—Station Fire Management Plan. Land Management Publication 97-1, Archbold Biological Station, Lake Placid, Fla. 95 pp.
- Maliakal, S.K., E.S. Menges, and J.S. Denslow. 2000. Community composition and regeneration of Lake Wales Ridge wiregrass flatwoods in relation to time-sincefire. Journal of the Torrey Botanical Society 127:125-138.
- Means, D.B., and H.W. Campbell. 1981. Effects of prescribed burning on amphibians and reptiles. Pp. 89-90 *in* G.W. Wood, ed., Prescribed Fire and Wildlife in Southern Forests. Belle W. Baruch Forest Science Institute, Georgetown, S.C.
- Menges E.S., and C.V. Hawkes. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. Ecological Applications 8:935-946.
- Menges, E.S., and N. Kohfeldt. 1995. Life history strategies of Florida scrub plants in relation to fire. Bulletin of the Torrey Botanical Club 122:282-297.
- Mushinsky, H.R., and D.J. Gibson. 1991. The influence of fire periodicity on habitat structure. Pp. 237-259 in S. Bell, E.D. McCoy, and H.R. Mushinsky, eds., Habitat Structure: the Physical Arrangement of Objects in Space. Chapman and Hall, New York.
- Myers, R.L. 1990. Scrub and high pine. Pp. 150-193 in R.L. Myers and J.J. Ewell, eds., Ecosystems of Florida. University of Central Florida Press, Orlando.
- Platt, W.J. 1999. Southeastern pine savannas. Pp. 23-51 in R.C. Anderson, J.S. Fralish, and J.M. Baskin, eds., Savannas, Barrens, and Rock Outcrop Communities of North America. Cambridge University Press, Cambridge, U.K.
- Platt, W.J., and M.W. Schwartz. 1990. Tem-

perate hardwood forests. Pp.194-228 in R.L. Myers and J.J. Ewell, eds., Ecosystems of Florida. University of Central Florida Press, Orlando.

- Platt, W.J., J.S. Glitzenstein, and D.R. Streng. 1991. Evaluating pyrogenicity and its effects on pine savannahs. Proceedings of the Tall Timbers Fire Ecology Conference 17:143-162.
- Quintana-Ascencio, P.F., and E.S. Menges. 1996. Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. Conservation Biology 10:1210-1219.
- Robbins, L.E., and R.L. Myers. 1992. Seasonal effects of prescribed burning in Florida: a review. Miscellaneous Publication No. 8, Tall Timbers Research Station, Tallahassee, Fla.
- Rothermal, R.C. 1983. How to predict the spread and intensity of forest and range fires. Research Report INT-115, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah. 40 pp.
- Schmalzer, P.A., and S.R. Boyle. 1998. Restoring long-unburned oak-mesic flatwoods requires mechanical cutting and prescribed burning. Restoration and Management Notes 16:96-97.
- Schmalzer, P.A., and C.R. Hinkle. 1992. Recovery of oak-mesic flatwoods after fire. Castanea 57:158–173.
- Schmalzer, P.A., S.R. Boyle, and H.M. Swain. 1999. Scrub ecosystems of Brevard County, Florida: a regional characterization. Florida Scientist 62:13-47.
- Shafizadeh, F., P.S. Chin, and W.F. Degroot. 1977. Effective heat content of green forest fuels. Forest Science 23:81-89.
- Smith, R.B., D.R. Breininger, and V.L. Larson. 1997. Home range characteristics of radiotagged gopher tortoises on Kennedy Space Center, Florida. Chelonian Conservation and Biology 23:358-362.
- Speake, D.W., J.A. McGlincy, and T.A. Colvin 1978. Ecology and management of the eastern indigo snake in Georgia: a progress report. Pp. 64-73 *in* R.R. Odum and L. Landers, eds., Proceedings of Rare and Endangered Wildlife Symposium. Technical Bulletin WL4, Georgia Department of Natural Resources, Game and Fish Division, Athens.
- SPSS. 1999. SPSS/PC+Statistics 9.0. SPSS. Inc., Chicago.
- Stout, I.J., and W.R. Marion. 1993. Pine flatwoods and xeric pine forests of the southern (lower) coastal plain. Pp. 373-446 ir. W.H. Martin, S.G. Boyce, and A.C. Echternacht, eds., Biodiversity of the Southeast-