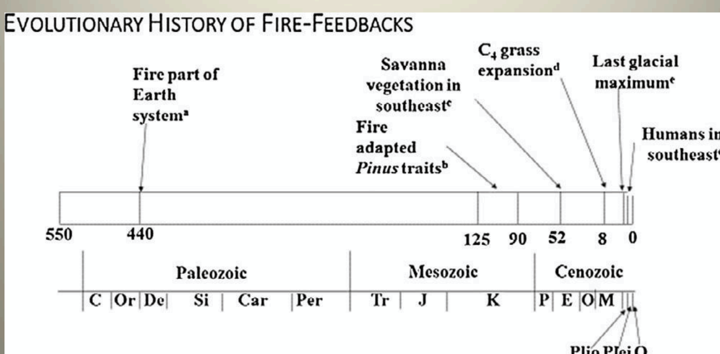
Evidence for fire as a significant part of the evolutionary environment of Florida and the Coastal Plain for millions of years

- Paleoecology
- Phylogeny (e.g., ancient taxa associated with fire-prone ecosystems)
- Fire-adaptive traits of plants and animals (especially ancient taxa)
- Fire-dependent ecosystems

The fire-vegetation relationship on Earth is really old

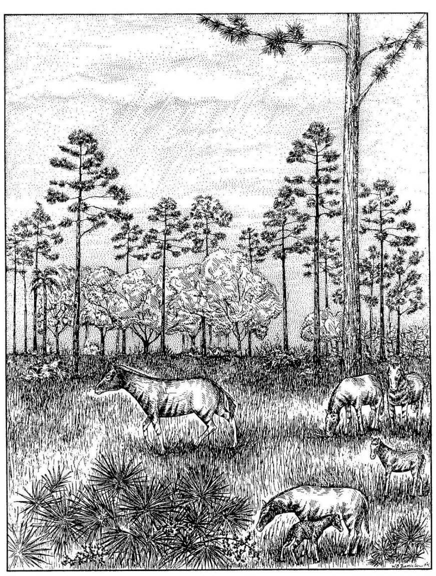


From Fill et al. (2015, *Forest Ecol Mgmt*)

Vegetation in the Coastal Plain has not changed all that much for millions of years

Graham (1999) describes vegetation in the Coastal Plain from the Middle Eocene (ca. **45 Ma**; Claiborne Formation, western KY and TN) much like that in Florida today: "On sandy flats, but removed from the tidal influence, *Pinus* and an understory of *Sabal-Serenoa*-type palms and *Ephedra* were present..."

Serenoa repens present range

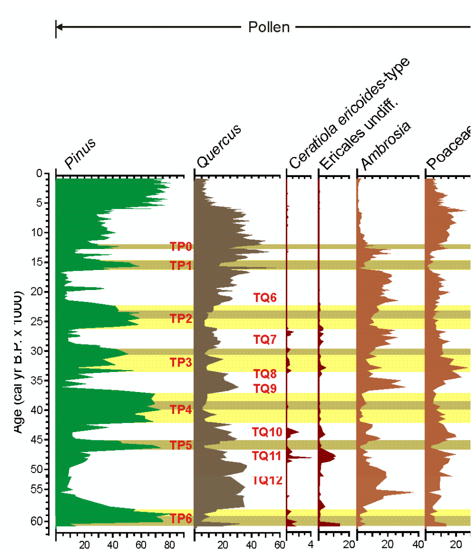


Savanna in the Southeastern Coastal Plain goes way back!

Reconstruction of pine savanna with *Parahippus leonensis*, a three-toed horse, from the Early Miocene (ca. 18 Ma) Thomas Farm site in northern peninsular Florida.

<u>Question</u>: What was the relative role of fire vs. herbivores in the maintenance of savanna vegetation at various times in history?

From MacFadden (1992)



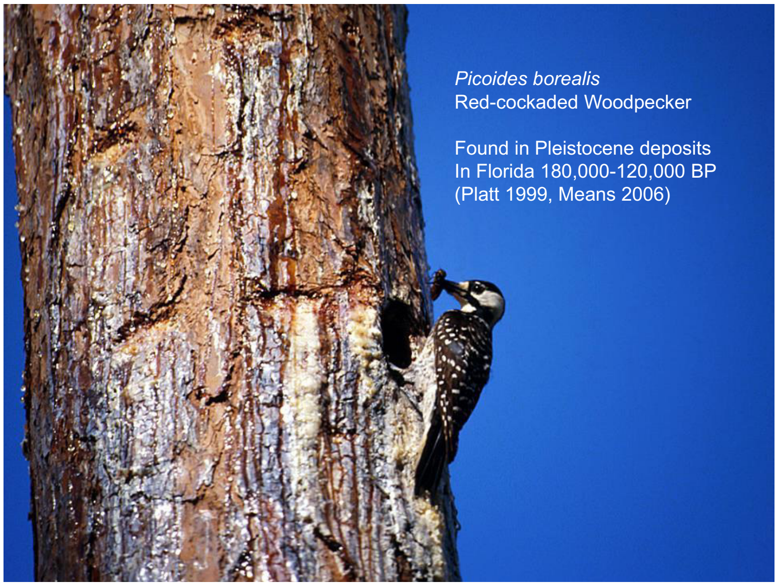
Paleoecology:

Pine-oak cycles over 62,000 years in Central Florida (Lake Tulane)

Pine in wet, warm periods
Oak in dry, cool periods

Grasses (and hickory) covary with oak (scrub vs. dry prairie)

Source: E. Grimm Adapted from Grimm et al. (2006, *Quat Sci Rev*)



Monotypic endemic genera suggest antiquity = a long evolutionary relationship with fire

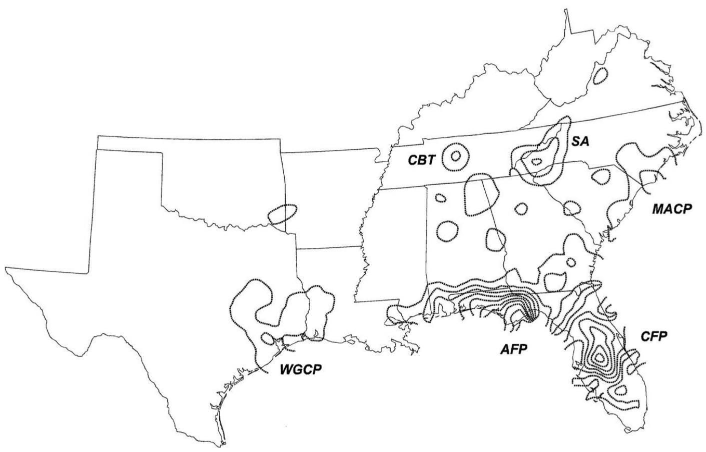
Sorrie and Weakley (2001) documented that approximately 80% of the 51* vascular plant genera endemic to the Coastal Plain are monotypic and presumably archaic; "perhaps the great majority" evolved in situ within the Coastal Plain.

Many of these ancient monotypic genera (e.g., *Serenoa, Chapmannia, Chrysoma, Dionaea, Hartwrightia, Stokesia*) are associated with grasslands/savannas and other frequently burned habitats.

*number expands regularly; now 56

Evidence of antiquity: Centers of plant endemism

Plants associated with **fire-dependent ecosystems** make up the majority of the endemic taxa, and many of these taxa are ancient. From Estill and Cruzan (2001)



Fire-adaptive traits

"Fire is a major force driving the evolution of plants and the structure and function of ecosystems globally. It thus likely operates as an important environmental filter that selects for species that have evolved to tolerate and depend on fire."

Cavendar-Bares and Reich (2012, *Ecology*)

"No species is 'fire-adapted' but rather is adapted to a particular fire regime, which among other things, includes fire frequency, fire intensity and patterns of fuel consumption."

(Keeley et al. 2011, *Trends in Plant Science*)

Fire-adaptive Traits

- Avoiding or escaping fire: Persistence in seed bank protected from heat, persistence in unburned patches (refugia), burrowing or fire-fleeing behavior
- Tolerating fire: Thick bark, underground storage organs, prolonged seedling development (e.g., grass stage), rapid growth during sensitive life history stages, re-nesting (double clutching) after nest destruction
- Exploiting or taking advantage of fire: Germination stimulated by fire cues (heat, smoke, etc.), germination of seeds in exposed mineral soil, prodigious flowering or reseeding after fire, protection of buds, resprouting after fire, epicormic branching, serotiny, shifting territories into recently burned patches
- Facilitating or promoting fire: Flammable tissues such as fallen needles (pines), live or dead leaves (grasses, some other species)

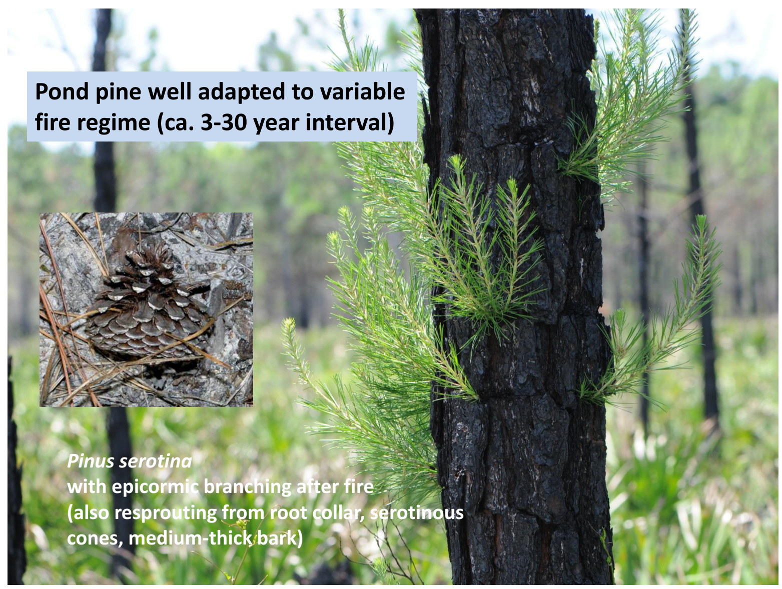
Thick bark offers protection from fire damage

Bark of blackjack oak (*Quercus marilandica*), comprising over half of the basal diameter (bark:wood = 0.55). Significant bark taper results in much thicker bark at base (within the flame zone), with less as height increases.
Hammond et al. (2015, *Ecosphere*)

Fire-protective thick bark in *Pinus* arose in the Cretaceous, ca. 126 Ma, based on molecular phylogeny and mapping of functional traits onto chronograms.

More intense fires beginning ca. 89 Ma are coincident with thicker bark and branch shedding, or serotiny with branch retention as an alternative strategy.

He et al. (2012, *New Phytologist*)



Heat and smoke stimulate germination of some plants from seed bank

- Fire cues such as smoke, heat, ash, charcoal, and increased nutrients are known to stimulate seed germination in some plants.
- Heat stimulates germination by breaking physical dormancy in seeds, usually in species with hard seed coats that are impermeable to water and require scarification for germination.
- Smoke stimulates germination through chemicals called karrikins that are thought to act as a growth hormone.
- However, overdosing either heat or smoke can result in decreased germination.

Previous studies found that *Dicerandra christmanii* had increased germination when treated with smoke water as opposed to de-ionized water (Haller et al. 2012). Lindon and Menges (2008) found that smoke stimulated germination in *Polygala lewtonii* and *Liatris chapmanii* but not in 18 other scrub species.

In a new study, smoke treatments stimulated germination for two endemic Florida scrub species, *Chrysopsis highlandsensis* and *Eryngium cuneifolium*.

King and Menges (in preparation)

Underground Storage Organs (USOs) Form Underground Forests

Euphorbia rosescens xylopodium (tuberous root)

Bejaria racemosa geoxylic suffrutex (underground tree growth form)

Smilax auriculata geoxylic suffrutex with *Quercus minima*

Steve Orzell with *Licania michauxii* (a geoxyle or "underground tree").

Underground Storage Organs (USOs)

Agents of selection are not mutually exclusive. The overall selective environment for any species may include several factors (fire, drought, herbivores, etc.) that simultaneously favor certain adaptive traits, such as USOs.

Although environmental factors other than fire can select for plant traits that subsequently serve a species well in a fire-prone environment, the **presence of many such traits spread across diverse phylogenetic lineages suggests fire as the dominant selective agent** driving the evolution of these traits.

Resprouting after fire

"Resprouting…enables many woody plant species to survive natural disturbances that kill the above-ground portion of the plant…such **"topkill" is followed by mobilization of carbohydrates…stored in roots and below-ground storage structures for growth of new stems and leaves…**

…after leaf development, the plant uses newly synthesized photosynthates for above-ground growth, replenishment of stored carbohydrates in the roots, and new root growth… **If an additional topkilling disturbance occurs before root reserves are completely recovered, then the growth rate of resprouting stems is expected to be reduced…**"

Robertson and Hmielowski (2014, *Oecologia*)

Saw palmetto *(Serenoa repens)*

Ground-nesting birds in fiery habitats typically re-nest when nests are destroyed by fire (analogous to resprouting in plants) – and require fire to maintain habitat

Bachman's Sparrow (*Peucaea aestivalis*)

Many amphibians are also adapted to frequent fire – and require it

Journal of Herpetology, Vol. 49, No. 3, 364–370, 2015

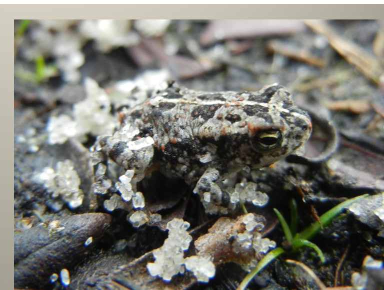
Juvenile Recruitment of Oak Toads (*Anaxyrus quercicus*) Varies with Time-Since-Fire in Seasonal Ponds

Clay F. Noss[1,2] and Betsie B. Rothermel[1]

[1]*Archbold Biological Station, Venus, Florida, USA*

In an experimental study of larval and metamorph survival in seasonal ponds burned 4 mo, 3-4 yrs, and 11 yrs in the past, <u>mean survival was significantly higher In the most recently burned ponds</u>.

Survival was significantly positively associated with pH, which was highest in the most recently burned ponds.



Solidago chapmanii – mixed adaptive strategy

"In <u>combining resprouting, clonal spread, and seedling recruitment</u>, Chapman's goldenrod differs from most other Florida upland herbs that simply resprout or depend on seedling recruitment to recover after fires. Between fires, this species persists as suppressed ramets (a persistent bud bank)."

Menges and Root (2004, *American Midland Naturalist*)

Promoting and Facilitating Fire: Pyrogenicity and Niche Construction

Natural selection by fire for plant traits that increase flammability favor plants with such traits over other species more sensitive to fire (Mutch 1970, *Ecology*)

Flammable C_4 plants (e.g., wiregrass, *Aristida beyrichiana*) and fallen pine needles. Pine needles increase fire temperatures and durations of heating relative to herbaceous fuels (Ellair and Platt 2013, *J Ecology*)

Promoting and Facilitating Fire

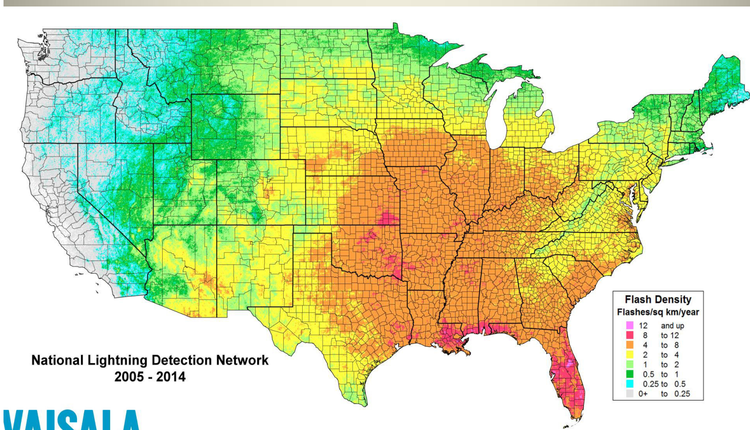
Photo by Jean Huffman

Cabbage palm (*Sabal palmetto*) - Carry fire into the canopy, torch out nearby trees, create open space, and spread fire through flaming firebrands

Fire-dependent Ecosystems

"Biomes of large parts of the world are far from their climate potential supporting flammable formations such as grasslands and savannas. We label these fire-dependent ecosystems."
Bond et al. (2005, *New Phytologist*)

Lightning frequency over much of the South is more than enough to explain dominance of the region by fire-dependent ecosystems



VAISALA

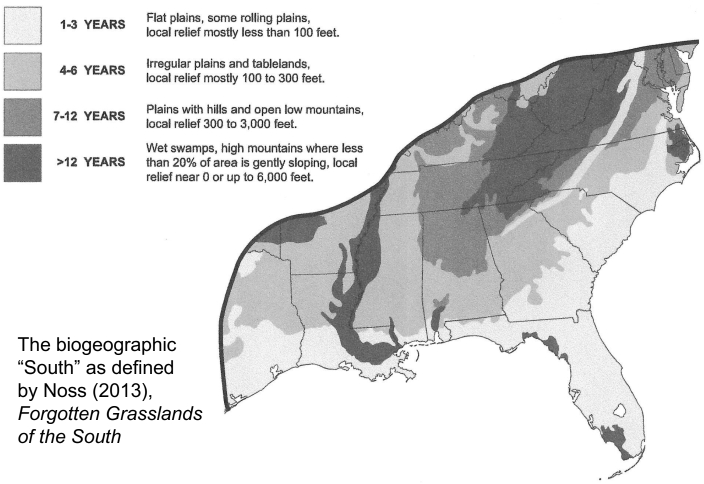
What do evolutionary history, patterns of endemism, fire-adaptive traits, and fire-dependent ecosystems have to do with the management question of "How often and during what times of the year should I burn the lands I am responsible for managing?"

Everything!

(if we care about maintaining and restoring native biodiversity)

Species are not adapted to fire per se, but to a particular fire regime (Keeley et al. 2011)

Presettlement Fire Regimes (for most fire-exposed portions of the landscape)
Adapted from Frost (1995, 1998, 2006, pers. comm.)



The biogeographic "South" as defined by Noss (2013), *Forgotten Grasslands of the South*

Huffman (2006, dissertation): *Historical fire regimes in southeastern pine savannas*

"There was a 2-3 year fire return interval between 1679 and 1868. Variability in fire return intervals was low, with 92% of all fires occurring at < 5 yr intervals."

Active and Passive Fire Exclusion Has Reduced Fire Frequency

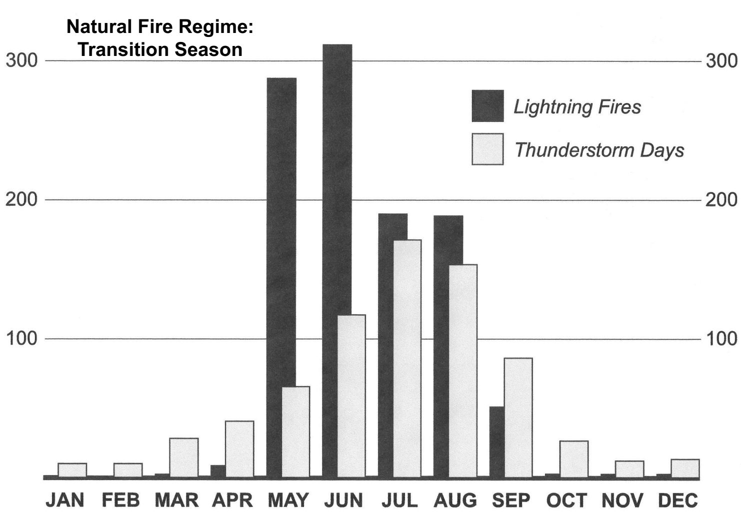
That fires no longer burn as frequently as they once did in Florida is a consequence of two kinds of fire exclusion:

1. Active fire exclusion and suppression
2. Passive fire exclusion by landscape fragmentation, which prevents fire from flowing as it once did across huge areas

Fire Seasonality Hypothesis

If fire is an important agent of selection, and if fires during the evolution of species in a region were concentrated in a particular season, then species should have evolved mechanisms of growth and reproduction that are timed to respond to seasonal cues.

They also should experience greater fitness when burned during this season than in seasons largely outside of their evolutionary experience.



Adapted from Komarek (1964; data from Florida, 1962-63)

Lightning season fires were the only fires recorded in the annual rings of pines at the St. Joseph Bay savanna between 1592 and 1830

From Huffman (2006)

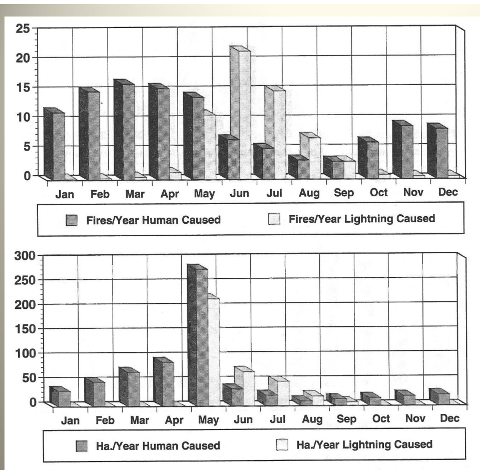


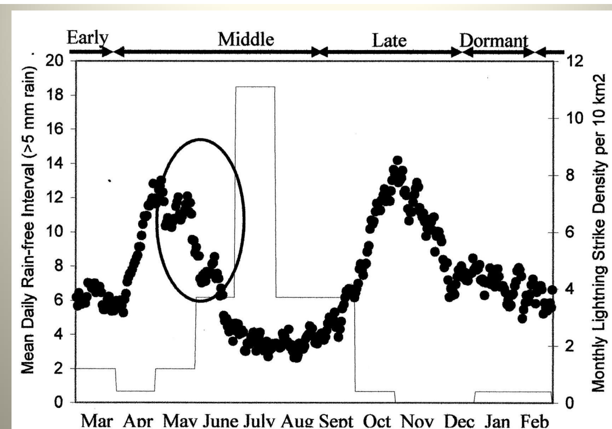
Figure 2. Yearly distribution of lightning- and human-caused wildfires in the National Forests in Florida, 1968-1987 (compiled from USDA Forest Service fire records). Human-caused wildfires occur throughout the year, but a greater number are ignited during the dormant season. Lightning fires occur year-round, but the vast majority occur during the growing season. In either case, the important statistic is not occurrence but rather area burned. Regardless of ignition source, the greatest area burned occurs in May—the height of the spring drought.

Yearly distribution of lightning- and human-caused fires in Florida's national forests, 1968-1987

"…**the important statistic is not occurrence but rather area burned**. Regardless of ignition source, the greatest area burned occurs in May…"

Authors acknowledge that small lightning fires are often unreported, and area burned means the area before suppression (not what might have burned).

Robbins and Myers (1992)



Monthly lightning strike density per 10 km2 (vertical bars) and mean number of days since last recorded precipitation >5 mm (dots) in Apalachicola, Florida. Lightning: 1986-1995, Rain-free periods: 1931-1993. **Circled area indicates when long rain-free intervals and an abundance of lightning strikes coincide** and lightning fires are most likely. From Huffman (2006).

A clear definition of the lightning fire season in Florida:

PLOS | ONE

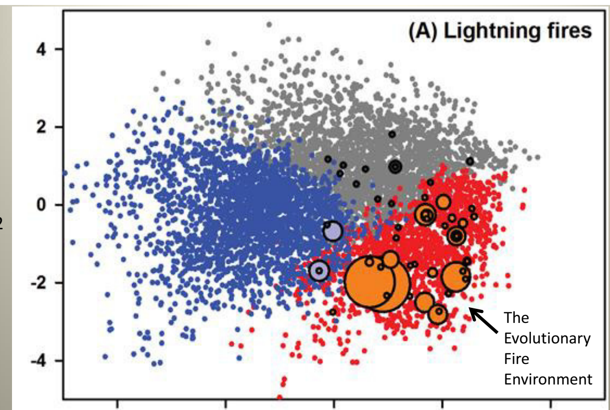
2015

RESEARCH ARTICLE

Seasonality of Fire Weather Strongly Influences Fire Regimes in South Florida Savanna-Grassland Landscapes

William J. Platt[1]*, Steve L. Orzell[2], Matthew G. Slocum[1a]

Discriminant function analysis of 13 years of daily weather data determined a lightning fire season characterized by drought, intense solar radiation, low humidity, and warm air temperatures.



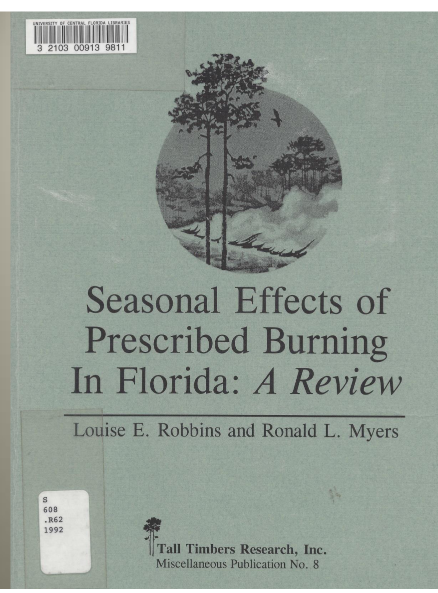
DF 2

DF 1

Relationship between lightning fires and climate at APAFR. Blue dots = dry season; red dots = transition season ("fire season"); gray dots = wet season. Bubbles are lightning fires (size proportioned). From Platt et al. (2015, *PLOS ONE*).

Evidence and logic in support of the biological importance of fire seasonality in Florida and surroundings

- Species have evolved adaptations to fire, and if fire varies seasonally, such adaptations should include responses to seasonality of fire
- A distinct lightning fire season (early growing or "transition" season) exists in Florida and presumably has for a long time
- Many species characteristic of southeastern pine savannas respond to fire most positively in the lightning fire season than in any other particular season
- Fires outside the lightning fire season have less beneficial effects, and sometimes negative effects (less control of woody understory or midstory) on native natural communities and species of conservation concern
- Typically only lightning season fires burn across wetlands, preventing woody encroachment and maintaining open water

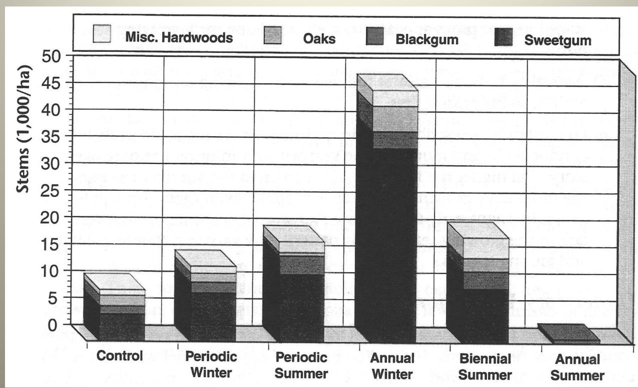


"…nothing is known about the effect of fire season on a number of species or communities, and the data we do have are, in many cases, incomplete or unreliable."

1992

Santee Fire Plots, SC

Waldrop et al. (1987; *USDA Gen Tech Rep SE-45*)



Number of understory hardwood stems < 2.5 cm dbh after 30 years of prescribed burning in a loblolly pine plantation. Annual winter fires led to a proliferation of hardwood stems. Annual summer burns were most effective in reducing hardwood stem density.

Enhanced flowering of grasses and forbs in response to growing season fire (St. Marks studies)

- Streng et al. (1993; *Proc Tall Timbers Fire Ecol Conf*): high rates of topkill and complete kill of midstory oaks; large positive effect on flowering and presumably seed production of dominant grasses and some forbs, no overall negative impact on pines.
- Brewer and Platt (1994; *J Ecology*): For *Pityopsis graminifolia*, floral induction and fecundity greater following May and August fires than following January fire; seedling emergence highest in May-burned plots, intermediate in August-burned plots, and lowest in January-burned plots.

Oecologia (2014) 174:765–776
DOI 10.1007/s00442-013-2823-4

POPULATION ECOLOGY - ORIGINAL RESEARCH

Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities

Kevin M. Robertson · Tracy L. Hmielowski

Confirms previous studies suggesting that resprouting of woody plants is less vigorous during seasons when carbohydrate reserves are low – i.e., the transition (lightning fire) season in Florida!

"Plants burned in the late dormant season (February–March) had a greater positive Δ growth rate than those burned in the early growing season (April-June), consistent with the presumption that **root carbohydrates are depleted and thus limiting during spring growth**."

esa
ECOSPHERE
2012

The reproductive response of an endemic bunchgrass indicates historical timing of a keystone process

JENNIFER M. FILL,† SHANE M. WELCH, JAYME L. WALDRON, AND TIMOTHY A. MOUSSEAU

"…We used the observed allocation of wiregrass reproductive effort to sexual reproduction as the response variable to examine reproductive response to fire season.

…The temporal link between fire and flowering indicates this allocation was optimized to the historical fire regime through selection.

…Plants burned during early summer (May–June) produced a greater proportion of inflorescences than did those burned in early spring (March–April) or in late summer (August)."

Important point from Streng, Glitzenstein, and Platt (1993)

Recruitment into the groundcover from seed occurs infrequently in pine savannas; thus, **changes in species composition related to season of burns will be apparent only after many years of burning within the same season.**

Evidence and arguments in support of the alternative hypothesis that fire season is not important or is much less important than frequency or other variables of the fire regime

- Lack of strong differences in response of many species between lightning-season fires and fires in other seasons, at least if the latter are as frequent or as intense
- Evidence of negative effects of lightning-season fire on particular species (e.g., pines [40-50% mortality at some sites; K. Hiers, pers. comm.], game species, imperiled species), air quality, or other resources
- Legal requirements (e.g., ESA, Clean Air Act, burn bans) that discourage burning during the lightning season
- Other practical considerations (e.g., manageability, liability, fire crew safety and comfort, politics, agency culture or tradition)

Oecologia (2000) 125:521–530
DOI 10.1007/s004420000469

J. Kevin Hiers · Robert Wyatt · Robert J. Mitchell

The effects of fire regime on legume reproduction in longleaf pine savannas: is a season selective?

"Contrary to the conventional paradigm, we found a wide range of reproductive responses among dominant legumes in response to the season of burn treatments, suggesting that **a variable fire season, rather than a single season of burn, is appropriate to maintain a greater variety of native species."**

"This study suggests that, if short-term reproductive success is vital to the maintenance of legumes in the ecosystem, then either (1) lightning-season fires have not exerted strong selection pressure on this group of species or (2) legumes have adapted to a wider range of fire seasons."

Scrub studies by Eric Menges and colleagues, Archbold Biological Station

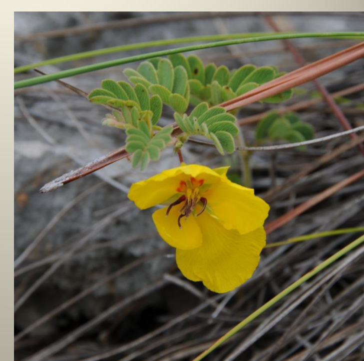
- Hotter fires in winter than summer
- No differences in survival or resprouting of shrubs after 6 months, 1 year, or 2 years following winter vs. summer fires
- Season affected subsequent resprouting growth for 6 months, but not for 1 year (Maguire and Menges 2011, *Fire Ecology*)
- No evidence of starch depletion with frequent fire or clipping
- Resprouting shrubs not very sensitive to extremely frequent fires and not sensitive to fire intensity
- Wiregrass will flower and produce viable seed as early as February on the Lake Wales Ridge

An exception that proves the rule?

Chamaecrista keyensis

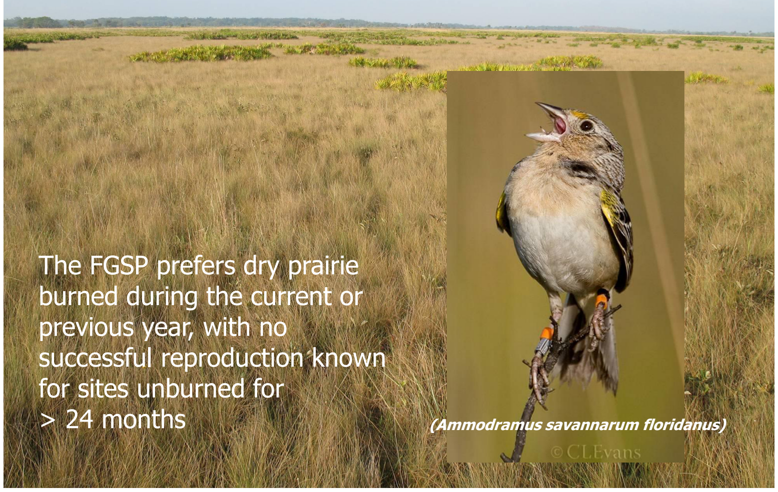
- Endemic to Lower FL Keys
- Winter fires promote greater vital rates than hotter summer fires
- However, after 3 years effects were reversed, with plants in summer-burned plots showing greatest survival
- May have evolved under a fire regime that included both lightning and human ignitions
- Keys are geologically young (ca. 6,000 yrs) – so, humans probably present at time of divergence

Liu and Menges (2005, *Ecology*)
Liu, Menges, and Quintana-Ascencio (2005, *Ecol Appl*)



Big Pine Partridge Pea

Fire management for the Florida Grasshopper Sparrow



The FGSP prefers dry prairie burned during the current or previous year, with no successful reproduction known for sites unburned for > 24 months

(Ammodramus savannarum floridanus)

Fire Management for Florida Grasshopper Sparrow (Nov. 2014 workshop notes compiled by Jim Cox)

From Appendix 2. FGSP Habitat Management Recommendations from current research on TLWMA (Erin Ragheb):

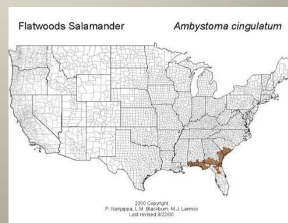
Burn Strategically

- Growing season burns (Apr-Sept) destroy active nests and young fledglings at the time of the burn and delay re-nesting initiation by at least 33 days post burn. This delay could push nesting into less ideal conditions (wet).
- Avoid burning in Apr-Jul if you know there could be territorial males in that unit. Plan ahead and provide Feb-Mar burns in areas containing males the previous season.
- Growing season burns are still important, but should they only be used to create new sparrow habitat in areas no longer supporting territorial males, at least until the populations are robust enough to support nest loss.

Frosted flatwoods salamander (*Ambystoma cingulatum*)

Reticulated flatwoods salamander (*Ambystoma bishopi*) – **west of Apalachicola River**

Breeding behavior of flatwoods salamanders (migration into and out of ponds) constrains burning usually in November (October-January) and March-April, when metamorphs emerge. Requires lightning-season fire to maintain grassy habitat!



Split by Pauly et al. (2007, *Molecular Ecology*)

Other arguments in favor of a variable fire regime

- Climate and communities have been in constant flux; the longleaf pine ecosystem became established in the Atlantic Coastal Plain only 7,000 BP (Hiers et al. 2000 and others). **No.**
- Indigenous people influenced season of burn and plant responses; humans exerted significant control over fire regimes within time frames capable of influencing natural selection (Hiers et al. 2000, citing others). **Maybe.**
- **"Variation in amount of fuel, fuel moisture, wind speed, etc., may obscure or accentuate seasonal differences"** (Robbins and Myers 1992). **Yes.**
- Intensity is more important than seasonality. A good fire manager can burn at virtually any time of year and mimic a lightning season fire (K. Hiers, pers. comm.). **Maybe.**
- Winter fires are critical for adding burn days, keeping fire on the ground. **Yes.**

MESIC

3F	3V	9S	7V	4F	2S	4F	9S	3V	2V	6S	3F	2S	1W
8V	2W	8S	5V	6F	9F	1V	1S	8S	4W	7V	2V	2F	10S
3S	3S	9S	6V	3F	8W	4F	7F	4F	7S	4W	7V	6F	6S
2F	6S	8F	9W	4S	8W	9W	1W	5V	2S	8F	5F	8V	9S
2V	4S	2F	4S	1S	1S	8V	10V	4F	1W	1S	10F	9V	4V
4V	9W	3V	1S	7V	1V	3F	2V	6S	6S	4S	9S	3S	1V
3V	8S	8S	2F	6F	7F	3W	10S	9S	2V	4S	2F	4S	1V
4S	2F	7V	4V	7S	4V	2V	4V	1V	9S	2W	1V	6W	8F
9S	9S	4F	10S	2W	10W	10V	3V	2S	1S	10S	6V	3V	4V
4S	1V	3V	1V	9S	2S	4W	4S	5F	3S	4F	6V	5W	2S
3V	3V	10V	2W	2S	3S	2V	5F	2S	1V	2S	2V	6V	1W
2S	9S	10S	2V	5V	8V	4F	9V	3W	6S	1F	1S	4F	2V
4S	5V	1V	3F	8W	1V	7V	9S	2S	1F	3V	3S	4S	5V
7V	6F	2S	4S	1S	8V	2V	7F	4V	1W	6F	1V	4F	2S
6S	1V	10F	1V	7W	7F	6S	4V	2V	9V	2V	2S	5V	4S
8F	6S	6S	1S	3S	9V	9S	2V	4F	1W	4S	2S	4F	8V
1W	2S	1S	10V	10W	1V	7V	2S	10V	7F	2W	4S	2V	10V
10V	6V	10W	3F	4S	4S	1S	3S	1V	3V	5V	8V	3V	6W
1W	3S	10F	10V	3V	5S	5S	7W	10S	10S	4S	3V	3S	2S
10S	8W	7S	6F	6V	2S	3W	6V	1S	1V	4W	8V	3W	7W
4V	3W	8V	6S	7V	3V	2V	4S	3F	10V	3V	3S	5V	4W
3S	2F	1W	5V	5V	4W	3S	3V	9W	10W	2S	8V	4V	2S
1S	3W	9V	2V	2W	3S	1S	4F	4F	2S	3V	7S	5W	10S
10V	4F	3V	3V	3F	6W	4S	2V	6V	3F	3F	8V	1S	1F
2S	1S	4F	2S	10W	4V	1W	9V	8S	5S	10V	1S	2V	2F
4F	7F	5S	4F	1W	10V	1W	3W	9S	2V	7F	4S	10W	2V
4V	2V	2F	6W	4F	4S	5V	9F	10S	3W	7V	9S	7V	10V
8S	7V	9V	7V	8F	5S	7V	7V	5W	7V	1W	9V	4W	6S
9S	4S	5W	3V	1S	2V	4S	9S	8S	4V	1W	7S	6S	2S
3W	3S	2W	4S	1S	4W	2S	10F	8S	10V	5V	3W	9V	4V
3S	4S	9V	10S	9V	2V	8S	4S	8V	6W	[illegible]	5V	3S	5W

Pyrodiversity? Not if outside evolutionary experience!

Burn schedule for mesic upland Longleaf pine-wiregrass community. Numbers (fire intervals) assigned randomly but with lower numbers having twice the probability of being generated, and with season of burn weighted such that spring and summer are twice as likely to appear as fall or winter.

Select random point (e.g., red circle), then pick new random point each interval or proceed vertically down the column.

From Robbins and Myers (1992)

Implications for Management

- **Frequency usually trumps seasonality**, but not always, especially over the long term (e.g., as woody plants become increasingly dense)
- Many years of regularly burning outside the lightning season may have cumulative negative effects that are not evident in short term (even decadal) studies
- Although many native species may respond equally well to fires during almost any season, the foundation species of grasslands (incl. pine savannas) in Florida – i.e., wiregrass and other C4 grasses – respond best to early growing season fires
- The objectives of a particular prescribed burn (e.g., restoration vs. maintenance) may dictate burning outside the lightning fire season, as will many practical concerns

Research Priorities

- Need more research attention to other aspects of fire regime (e.g., intensity, severity, patch size, heterogeneity at various spatial scales) that are often correlated with season and frequency of burn, but may be mechanistically more important.
- More attention to the demographic responses of multiple species – and vegetation structural responses – to frequency and seasonality of burning over long time periods.
- More research on policies and educational strategies that might promote greater public acceptance of frequent lightning-season fire.

What to do in the face of uncertainty?

- Follow an ecologically and evolutionarily informed precautionary principle (seek to do no harm).
- To the extent feasible, schedule burns to mimic the frequency and seasonality of the lightning fire regime, but incorporating inter-annual variability rather than attempting to replicate the average seasonal pattern.
- Variability (pyrodiversity) is desirable, but only up to a point – need to establish a modal range of fire frequency, seasonality, etc., that is evolutionarily relevant to the species in the community.

Smoke from Red Hill Fire, Archbold Biological Station, 7 January 2015, drifting above US 27