




Evolution of Postfire Seedling Recruitment

Jon E. Keeley
 U.S. Geological Survey
 Western Ecological Research Center
 &
 UCLA
 Department of Ecology & Evolutionary Biology




Paleozoic

Silurian Charred remains of low-growing vegetation of the (440 Ma) earliest stomatal bearing plants, plus charred coprolites, indicate a low-temperature surface fire (Glasspool et al. 2004)




Devonian Pro-gymnosperm forests persisted with (395 Ma) frequent fires that burned shrubs desiccated during the dry season (Cressler 2001)





Carboniferous (345 Ma) Laminated deposits record fires 3-35 yrs in pro-gymnosperm communities under a monsoonal climate

Wetland lepidodendron forests with fires 105-1585 yrs, charred apices indicate crown fires (Falcon-Lang 2000)



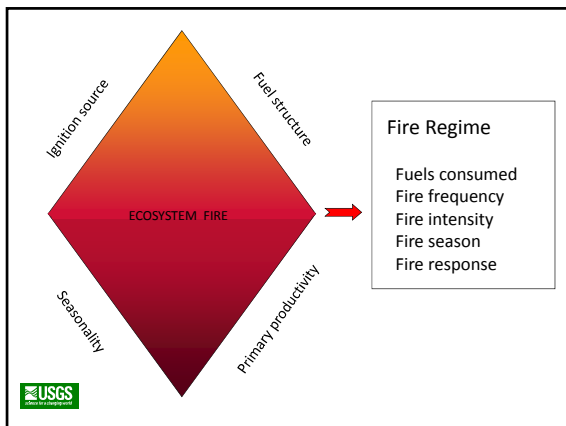
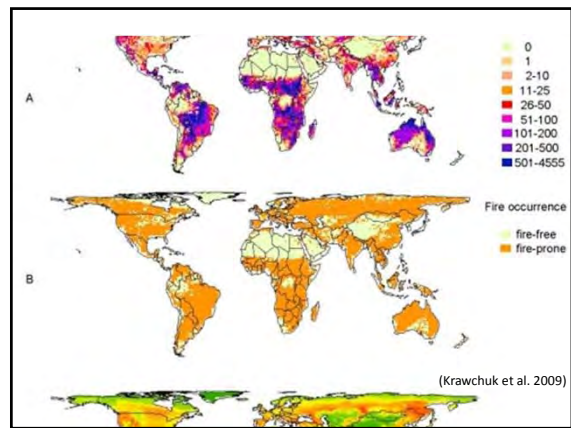
Mesozoic

Jurassic Gymnosperm forests with tree ring patterns (195 Ma) of a mediterranean climate – mild winter rain and summer drought, charred fragments provide evidence of light surface fires (Francis 1984)

Allen (1998): Cretaceous landscapes with "chaparral-like shrublands" (conifers, cycads, ferns) that supported diverse dinosaur faunas and with abundant evidence of periodic fires.

Charred remains interpreted as fire adaptations, including serotinous cones, fire-stimulated hard seeds, and highly sclerotic fern indusia that were dropped when heated by fire.



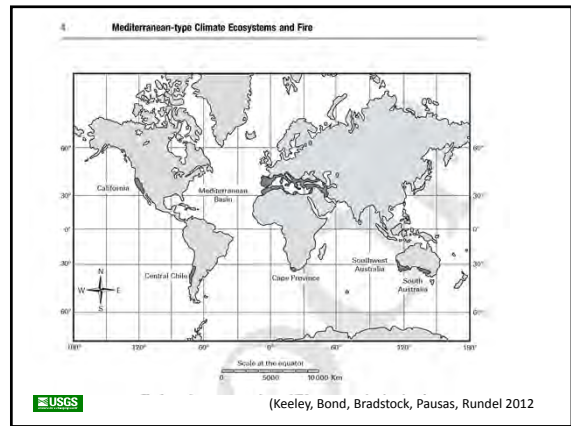

Mixed conifer / surface-fire regime

Pine savanna surface-fire regime

Chaparral crown-fire regime


Grassland surface-crown fire regime






Recruitment on fire-prone landscapes

— Q1: Continuous vs delayed recruitment
e.g. *Rhamnus* vs *Ceanothus*



No postfire recruitment
(postfire obligate resprouters)



Pulse of postfire seedlings
(postfire seeders)

USGS

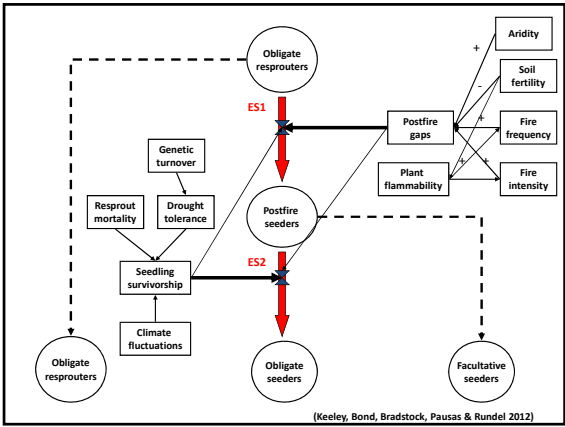
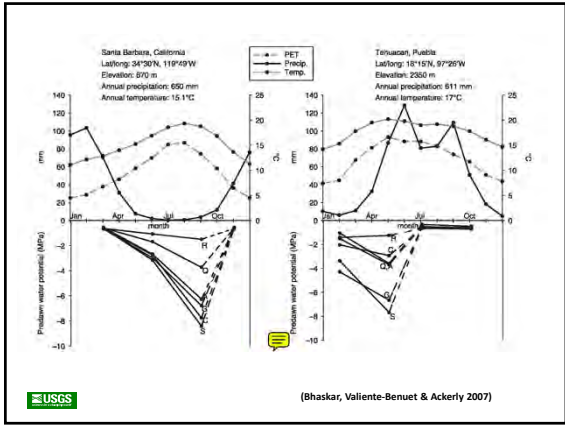
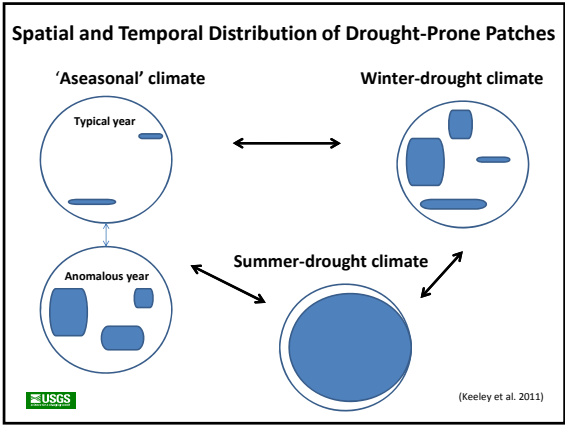
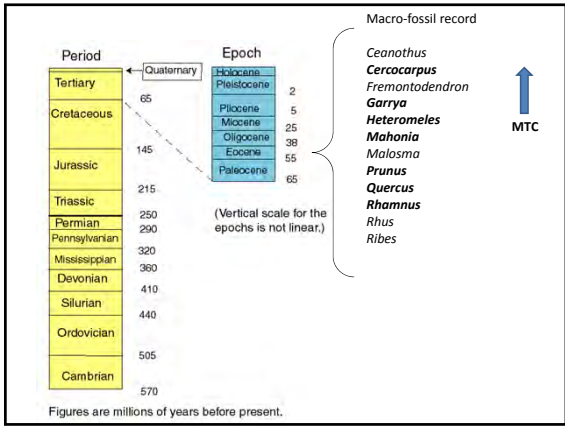


Recruitment on fire-prone landscapes

– Q1: Continuous vs delayed recruitment

Many theories:


- 1) Lack of postfire seeding is a reflection of pre-MTC origins, i.e., “non-adaptive ...ecological phantoms...unchanged in the face of changing ecological conditions”
- 2) Fire-prone landscapes provide multiple selective peaks favoring both continuous and delayed reproduction






Stresses or traits	Obligate resprouters (see Table 3.1)	Obligate seeders (see Table 3.4)
Water stress mode:	Avoiders (anisohydric)	Tolerators (isohydric)
Mechanism:	morphological (deep roots)	anatomical physiological
Potential drought-induced mortality:		
-- Adults:	very low	moderate
-- Seedlings:	very high	moderate
Recruitment mode:	disturbance-free	disturbance-dependent
Safe sites:	under canopy	burned sites
Availability:		
-- In time:	1 yr	10 - 100 yr
-- In space:	limited	extensive
Seed dormancy:	weak/no	deep
Seed bank:	transient (< 1 yr)	persistent (10 - 100 yr)
Germination cues*:	none	heat shock or chemicals from char or smoke
Dispersal strategy:		
-- Mode:	spatial vertebrates	temporal passive or invertebrates
-- Shadow:	wide	narrow
-- Season:	fall-winter	spring-summer
Seed size:	large	small
Ecological pattern:		
-- Niche width:	wide	narrow
Biogeographical distribution:	widespread	localized
Origin:	early Tertiary	early Tertiary - Quaternary


* many species from both life histories may have a cold stratification requirement

 (Keeley, Bond, Bradstock, Pausas & Rundel 2012)

Recruitment on fire-prone landscapes

– Q2: **Facultative vs obligate seeding**
e.g. *Ceanothus* subg vs *Cerastes* subg






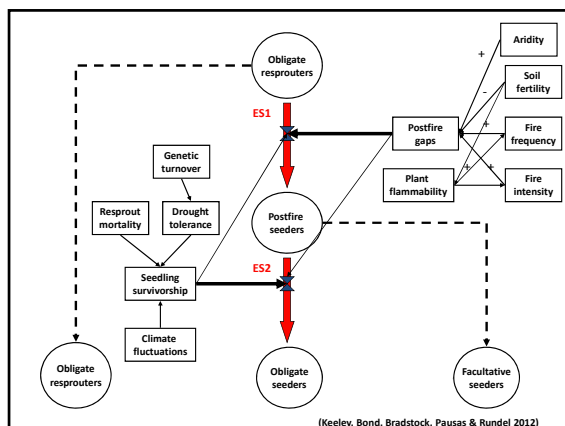
Recruitment on fire-prone landscapes

– Q2: **Facultative vs obligate seeding**

Factors selection for obligate seeding
Analogous to tradeoffs between semelparity and iteroparity (where fire cycles ~ annual)
Charnov & Shaffer (1973) iteroparity selected for when $P/C \gg 1$


- Resprouting success is high and/or
- Seedling recruitment success is low





Recruitment on fire-prone landscapes

– Q3: **Soil storage vs canopy storage**
e.g. *Adenostoma* vs *Protea*



Recruitment on fire-prone landscapes

– Q3: Soil storage vs canopy storage

Why the discrepancy in distribution of serotiny between northern and southern hemispheres?

Many theories:

- 1) Higher rainfall predictability favors serotiny
- 2) Higher surface seed predation favors serotiny

Species	Total seedling recruitment for all 5 years (n/ha)						Percentage by year				
	Chaparral			Sage scrub							
	Life form ¹	# sites	$\bar{X} \pm \text{S.E.}$	# sites	$\bar{X} \pm \text{S.E.}$	1	2	3	4	5	
Obligate Seeders											
<i>Quercus emoryi</i>	s	10	42,100 ± 17,800	2	1,200 ± 800	99	1	0	0	0	
<i>C. canadensis</i>	s	1	14,000	2	9,800 ± 9,800	97	3	0	0	0	
<i>C. greggii</i>	s	8	18,500 ± 18,500	1	1,000	100	0	0	0	0	
<i>C. macrocarpa</i>	s	9	55,700 ± 24,200	2	11,000 ± 7,000	96	4	0	0	0	
<i>C. algarhica</i>	s	6	103,900 ± 85,500	0	-	100	0	0	0	0	
<i>C. tomentosa</i>	s	2	56,500 ± 7,500	0	-	99	1	0	0	0	
<i>Dendromecon rigida</i>	ss	1	53,000	0	-	95	5	0	0	0	
<i>Rhus microbotrys</i>	ss	12	33,500 ± 17,500	3	109,200 ± 75,200	73	13	7	0	7	
<i>Larrea tridentata</i>	ss	39	46,800 ± 8,400	43	77,600 ± 31,900	72	9	2	1	16	
Facultative Seeders											
<i>Adenostoma fasciculatum</i>	s	31	104,500 ± 22,800	11	23,700 ± 12,700	94	3	0	0	3	
<i>Artemisia californica</i>	ss	12	11,600 ± 4,800	41	31,500 ± 10,600	41	42	13	1	4	
<i>Callitriche macrocarpa</i>	ss	25	49,700 ± 12,100	34	38,600 ± 7,200	92	5	2	0	1	
<i>Quercus spinescens</i>	s	9	36,600 ± 25,100	1	2,000	92	3	0	0	5	
<i>Eucalyptus fortunei</i>	ss	0	-	8	21,100 ± 8,500	19	19	18	0	53	
<i>Brodiaea spinescens</i>	ss	4	3,100 ± 800	1	1,000	52	24	19	12	2	
<i>Dryophyllum confertiflorum</i>	ss	25	168,700 ± 42,900	30	24,000 ± 8,500	20	33	24	10	13	

(Keeley, Fotheringham & Keeley 2006)

