

On Incorporating Fire into Our Thinking about Natural Ecosystems: A Response to Saha and Howe

Jon E. Keeley^{1,2,*} and William J. Bond^{3,†}

1. Department of Organismic Biology, Ecology, and Evolution, University of California, Los Angeles, California 90095;

2. U.S. Geological Survey, Western Ecological Research Center, Sequoia National Park, Three Rivers, California 93271;

3. Department of Botany, University of Capetown, Rondebosch, 7700 South Africa

Submitted January 12, 2001; Accepted July 3, 2001

Keywords: bamboo, critique, delayed reproduction, fuels, India, mass flowering, monocarpic, seedling recruitment, wildfire.

Ecologists long have had a fascination with fire impacts, although they have been slow to incorporate this ecological factor into serious thinking about the structure of communities and evolution of species (Bond and van Wilgen 1996). The remarks by Saha and Howe (2001, in this issue) illustrate some of the problems ecologists have in trying to apply fire to their thinking about natural ecosystems. Fire is commonly perceived qualitatively in terms of presence or absence, and the variation in frequency and intensity, as well as other components of the fire regime (e.g., fig. 1), is ignored. Often not considered is the fact that plant life histories are fine-tuned to particular fire regimes, and in this regard, landscapes present a range of selective peaks and valleys, both figuratively and literally. Because landscape patterns affect the propagation of natural fires, it is imperative that the degree of human disturbance be considered (e.g., Marsh [1864] 1965; Gadgil and Guhu 1993) and the limitations of basing evolutionary arguments on anthropogenically derived landscapes be recognized (e.g., Janzen and Martin 1982).

Saha and Howe's critique of the bamboo fire model (Keeley and Bond 1999) centers on the argument that fire could never have been an evolutionary force in tropical and subtropical monsoon forests. The basis for their crit-

icism is that other plant species in these forests lack "hallmark" traits reported from "fire-adapted" communities and it is not possible for fire to select for traits in a single species or guild and that lightning does not ignite fires in monsoon forests, and therefore, in the absence of people, there would be no natural fires.

Fire Adaptations

Saha and Howe state that they "do not see evidence that other plant taxa are fire adapted in habitats where mast-flowering, monocarpic bamboos thrive" (p. 659). This may be true, but others who have studied monsoon forests of Southeast Asia would seem to disagree (Stott 1988; Goldammer 1993; Hegde et al. 1998; Kikim and Yadava 1998; Sidhu and Thakur 1998). Regardless, there are well-documented examples of fire-adapted species (e.g., lodgepole pine in the Rocky Mountains or pitch pine in the Appalachian Mountains, species with fire-dependent reproduction), in communities where other species show little evidence of having had their reproductive biology altered by fire.

Saha and Howe comment that in the monsoon forests, "there is no evidence of serotiny, postfire-obligate seeding, or other hallmarks of fire-adapted ecosystems" (p. 660). These traits, however, are not the ecological litmus test for fire having been an important disturbance factor over geological time. These two reproductive traits are unique to particular fire regimes (moderately frequent stand-replacing fires; fig. 1) and seldom are present under other fire regimes (Keeley and Zedler 1998). For example, moderately frequent low-intensity stand-thinning fires (fig. 1) have been a natural feature of coniferous forests in the Sierra Nevada in California (Swetnam 1993), but these forests generally lack serotinous or postfire-obligate seeding species. Different fire regimes select for different traits. Zedler (1995) presents an interesting case in contrasting the very thick bark of savanna oaks in California (where frequent surface fires are thought to be involved in selection for bark thickness) with oaks in the adjacent shrubland that have very thin bark. Using Saha and Howe's approach, one might conclude that chaparral is not a fire-

* E-mail: jon_keeley@usgs.gov.

† E-mail: Bond@botzoo.uct.ac.za.

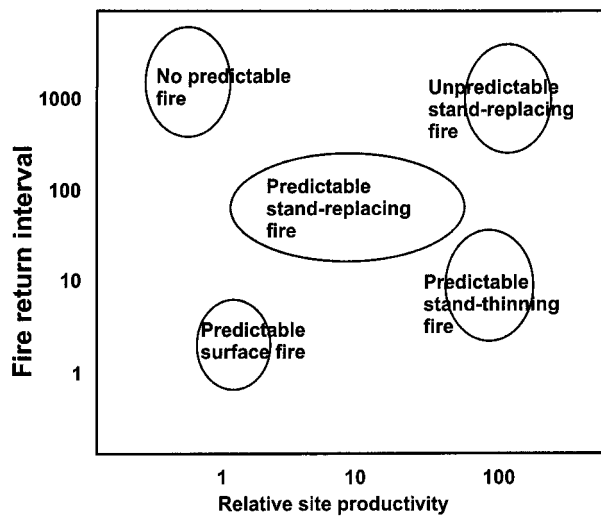


Figure 1: Fire regimes predicted by patterns of site productivity and fire recurrence interval (Keeley and Zedler 1998).

prone environment; however, Zedler concludes that the thin bark is a result of the high-intensity crown fire regime (fig. 1) in chaparral, which makes resisting fire an exercise in futility, and thus, there has not been selection for thick bark.

Saha and Howe emphasize that resprouting is not an adaptation to fire. With the exception of conifers (Keeley and Zedler 1998), we have expressed that opinion repeatedly over the years (e.g., Keeley 1981, 1986; Bond and van Wilgen 1996) and did not invoke the idea in Keeley and Bond (1999).

Natural Fires in Monsoon Forests

Saha and Howe contend that lightning is rare in Southeast Asia and is accompanied by rain and therefore has never been an important source of natural ignition. They say, "If lightning existed, there would be something to ignite and many people to witness the ignition" (p. 660). They continue "Lightning unaccompanied by heavy rain is unknown in habitats that are home to a high diversity of synchronous, monocarpic bamboos" (p. 660). They further argue that "if cyclical weather patterns are necessary to provide cycles of lightning strikes, there is no evidence of them" (p. 662). We believe these comments are not evidence of a lack of natural fires in tropical and subtropical forests for the following reasons:

Saha and Howe assert that lightning is rare in Southeast Asia. Figure 2 shows the global distribution of lightning for the period March–May 1987 (Goodman and Christian 1993). We selected this period because it is the dry season

for monsoon forests and follows 3–6 mo of drought. Clearly, there is substantial lightning activity in Southeast Asia during the dry season (fig. 2), and this period is considered a time of extreme fire danger (Sidhu and Thakur 1998). Joshi (1980) warned Indian foresters that "there is a danger of fire of great severity breaking out due to prevailing high velocity winds, high temperature and low humidity in the atmosphere during these months [May–June]" (p. 268). More specific to bamboo, Kadambi (1949), an Indian forester writing on the ecology of bamboo-dominated forests, noted that occasional thunder storms occur in April and May, which is near the end of the dry season but prior to the monsoon season. Not only is lightning common in the dry season, but it is even more frequent during much of the rest of the year. Across Southeast Asia there are 20–140 thunderstorm days each year, which is not unlike the density observed throughout North America or most other parts of the world (Goodman and Christian 1993).

Saha and Howe seem to suggest that electrical storms in Southeast Asia are qualitatively different from other parts of the world because lightning is accompanied by rain. However, globally, precipitation is a predictable feature of lightning storms, even in regions where the predominant source of wildfire ignition is lightning (Goodman and Christian 1993; Gosz et al. 1995). The reason lightning ignitions accompanied by rain can generate wildfires is because natural fires commonly have ignition and fire spread separated in time. Lightning ignites fires, and these fires hold over for days or even weeks until weather conditions are more conducive to fire spread. Indeed, this disjunct between time of ignition and time of fire spread is one of the reasons why, in regions where lightning is still the dominant ignition source (e.g., coniferous forests of the southwestern United States), fire suppression has been able to effectively exclude fire during most of the last century. In the monsoon forests of Southeast Asia, Stott (1986, p. 347) has documented that, "despite heavy overnight rains," logs will continue to smolder at temperatures over 700°C. Fuels in such tropical forests will ignite and spread fire with less than a week of rainless days (Uhl et al. 1988). Stott et al. (1990, p. 35) concluded that a common cause of fires in monsoon forests is lightning strikes and, "although an immediate outbreak of fire is often prevented by the accompanying rain, the tree can continue to smolder within, leading to fire after the storm has passed."

Other monsoon climates are well-documented fire-prone environments. For example, northern Florida has a climate remarkably similar to parts of India and is well known for its lightning-fire regime (Christensen 1985). Coniferous forests in the Southwest are fire-prone environments where the peak fire season occurs between the

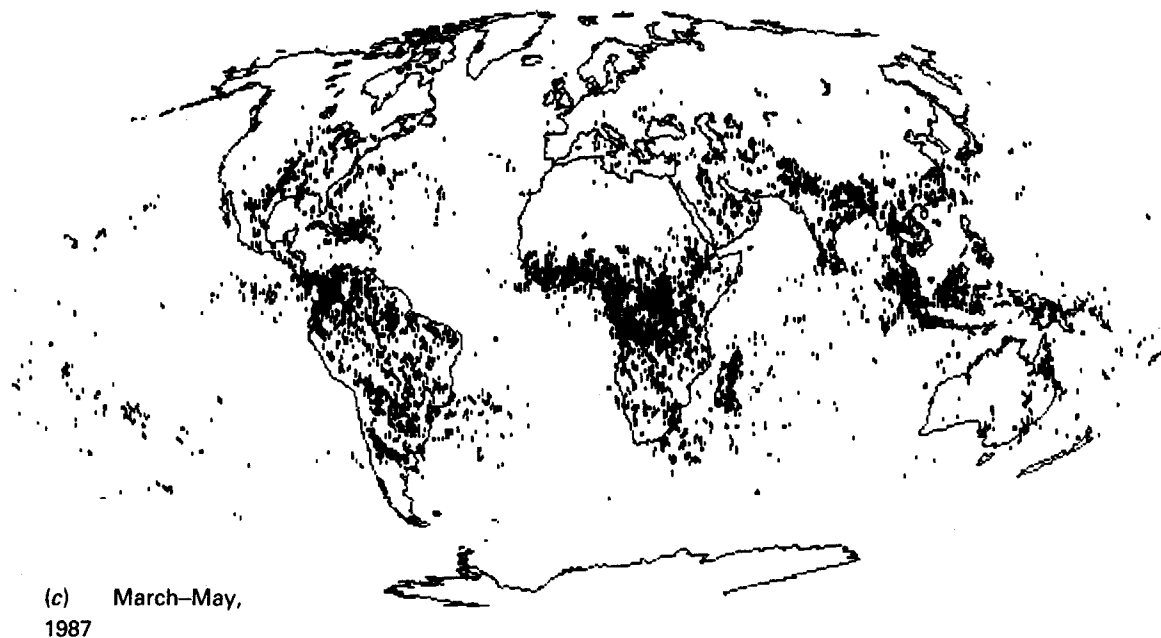


Figure 2: Global distribution of lightning at midnight for the period March to May 1987 (Goodman and Christian 1993)

end of the dry season and the beginning of the monsoons (Swetnam and Baisan 1996). Lightning-strike data do not indicate any greater concentration in these regions than in India (fig. 2). However, in both of these North American monsoon regions, anthropogenic impacts on the landscape, and on the fire regime, have been brief and minor compared to India.

The anthropogenically altered landscape throughout Southeast Asia may account in part for why villagers fail to observe lightning fires. For more than 3,000 yr, shifting cultivation has created a landscape that has left only isolated fragments of intact forest throughout much of the region (Wharton 1966; Gadgil and Guhu 1993; Zhang and Cao 1995). Such fragmentation alters fuels in ways that inhibit both the ignition and the spread of lightning fires. Occurrence of natural fires is also limited by the fact that humans currently are the predominant source of fire ignition in both monsoon and evergreen forests throughout tropical and subtropical latitudes. In India, 55% of the forests are affected by frequent or occasional anthropogenic fires, and fires are most abundant in moist monsoon forests (Rai and Saxena 1997).

The fact that villagers are unaware of lightning fires is not reliable evidence of a lack of such natural fires. One of us (J.E.K.) has made a comprehensive study of historical documents pertaining to fire in the Sierra Nevada of California, and it is striking that, based on reports of early settlers, it would seem that almost all fires prior to the

twentieth century were caused either by “Indians” or “shepherders.” Today, we know that lightning is responsible for the majority of fires in these coniferous forests (Parsons 1981); however, the early settlers were not predisposed to see this as a source of ignition and thus assumed a different source for most fires. Recently Baker (2000) reported the same phenomenon from historical documents pertaining to fire in the Rocky Mountains. The fact that there is typically a time delay of days or weeks between lightning ignitions and fire spread likely accounts for the failure of North American settlers and Asian villagers to perceive the link between lightning and subsequent fires. In short, the fact that villagers in India do not appreciate lightning as an important source of ignition is not evidence that in the absence of a human presence in Southeast Asia this source of ignition did not exist.

Many researchers studying tropical forests report the occurrence of natural lightning-ignited fires (Batchelder 1967; Vogl 1969; Stott 1986; Goldammer and Seibert 1990; Stott et al. 1990; Middleton et al. 1997; Sidhu and Thakur 1998; Roberts 2000). Natural fires occur in a range of forest and woodland types, being common in seasonal monsoon forests and uncommon in wet rain forests. Consistent with our model is the fact that mast-flowering bamboo species are largely in seasonal environments (Janzen 1976; Gadgil and Prasad 1984) and the bamboos indigenous to the forest types at the wettest end of the gradient are not mast flowering (McClure 1966; Holtum 1967).

Saha and Howe assume that in order for lightning-ignited fires to be evolutionarily important they had to be frequent. We know from other fire-prone communities that this is not the case. Take, for example, a well-known fire-prone vegetation such as chaparral shrublands in coastal California. Perhaps 20% or more of the species show some level of fire dependency in their reproductive biology (Keeley 2000), yet the natural fire regime was apparently one of infrequent crown fires, perhaps once or twice a century (Keeley and Fotheringham 2001). In Southeast Asia, the contemporary fire regime of frequent low-intensity surface fires is an anthropogenic artifact (Goldammer 1993) and the natural fire regime was likely one with a "long-term cycle" (Stott et al. 1990, p. 33). As the interval between fires increases, the propensity for high-intensity crown fires increases (fig. 1). A long fire-return interval is a necessary component of the bamboo fire cycle model and is predicted by the very long masting cycle of bamboos (Keeley and Bond 1999).

Papers on response of bamboos and forest to fire report widespread bamboo recruitment after fires as stated in Keeley and Bond (1999). Saha and Howe seem to object that these were not lightning fires. However, research on the fire biology of plants in well-studied systems such as chaparral are very seldom based on natural lightning fires. Anthropogenic fires preempt lightning fires in many fire-prone landscapes. Saha and Howe further contend that, with respect to the literature we cited (Keeley and Bond 1999), "to support the wildfire hypothesis in Indian monsoon forests, ... most do not mention fire." This is not true; all papers we cited in the section referred to above (Brandis 1899; Kadambi 1949; Yadav 1963; Joshi 1975, 1980; Rao and Ramakrishna 1987; Sharma and Rikhari 1997) make specific references to fires in Indian forests and several describe the linkage between bamboo mortality and wildfires. Episodes of bamboo mortality have erupted in serious crown fires in India (e.g., Bourdillon 1895; Brandis 1899; Kwe-Tu-Wet-Tu 1903; Kadambi 1949; Gadgil and Prasad 1984), in Africa (Henkel 1927), in North America (Platt and Brantley 1997), and in South America (Kitzberger et al. 1997)

Saha and Howe are very critical of the fact that we have not provided clear-cut examples of where lightning-ignited fires have resulted in bamboo seedlings that "have a better chance of recruiting than in unburned forests; none is given and none is cited." This criticism goes beyond their initial premise, which was that our hypothesis is implausible. The type of proof they are demanding would require experimental studies of which none are available. There are, however, papers describing abundant bamboo recruitment following mast mortality and fire (Brandis 1899; Henkel 1927; Kadambi 1949), and recruitment occurs either from seeds that survive fire or from seedlings that

resprout (Keeley and Bond 1999). In addition, there are reports of better seedling recruitment by mast-flowering bamboos in areas that burned after mast mortality, relative to unburned areas (Win 1951; Prasad 1985).

Fossil Record

Saha and Howe present observations on the geological history of the Indian subcontinent but fail to appreciate that similar changes have occurred over the same time in other parts of the globe, which today have what even they would accept as "fire-type" communities (Graham 1999). Indeed, the Miocene floras of California comprised summer-rain humid forests with genera such as *Nyssa*, *Liquidambar*, *Ulmus*, *Juglans*, *Carya*, and *Betula* and many other taxa that presently are not associated with fire (Axelrod 1989). These fossil floras provide little suggestion that one day they would be replaced by highly flammable chaparral. Cladistic analysis suggests that some of the most specific fire-related attributes in chaparral species (such as smoke-stimulated seed germination) are relatively old and likely predate the Quaternary (Fotheringham and Rundel 2000), yet the Tertiary fossil flora in California could be used to make very different predictions about the timing of fire-adapted traits.

The primary problem with using the fossil record to make inferences about landscape processes is that it is not a random sample of the past. Those arid portions of the landscape where fire may have been important are poorly or not at all represented in the fossil record (Graham 1999). For example, *Adenostoma fasciculatum* (Rosaceae), which today is the most ubiquitous and dominant fire-type chaparral shrub distributed from Oregon to Baja California, is not represented in any fossil flora (Axelrod 1989). Chaparral taxa represented in Early Tertiary fossil floras include species of *Ceanothus* (Rhamnaceae) and *Arctostaphylos* (Ericaceae), yet all of the contemporary species in these genera have fire-dependent seedling recruitment. Either Early Tertiary landscapes were a mosaic of mesic and arid (fire-prone) habitats or fire-dependent recruitment evolved more recently in these modern taxa. The same arguments apply to the evolution of mast flowering and monocarpy in bamboo.

The primary weakness in the argument posed by Saha and Howe is that we do not know when mast flowering evolved (Clark 1997). Molecular studies suggest bamboo origins lie in the herbaceous species of the lowland Neotropics (Kobayashi 1997), and based on other traits, these have long been considered to be the more primitive taxa (Soderstrom and Calderon 1974). A few of these herbaceous species of the lowland Neotropics (e.g., the Tribe Olyreae) are monocarpic, but apparently none are mast flowering (Judziewicz et al. 1999). Presently the molecular

data are equivocal with respect to the phylogenetic position of the woody mast-flowering bamboos (Clark 1997). Among the American woody bamboos, diversification has largely been in montane forests rather than the lowland tropical rainforests (Clark 1995).

Life History

Saha and Howe suggest that the death of bamboo clones provides sufficient disturbance to maintain bamboo populations by providing suitable regeneration conditions. On the contrary, by dying, bamboos increase the risk of losing space to competitors by enhancing recruitment opportunities of forest tree seedlings (Keeley and Bond 1999).

Saha and Howe also argue that predator satiation is a well-supported hypothesis. We agree with them, for woody plants and other grass species but not for bamboo. The problem for proponents of predator satiation for bamboo life histories is why flowering episodes are so far apart (15–120 yr vs. 4 or 5 yr for trees and grasses) and why the plants die after flowering. *Chionochloa* species, long-lived grass species from New Zealand, flower every 3 to 4 yr and do not die after flowering despite massive investment into reproduction (Kelly et al. 2000). The long intervals between flowering events in bamboo and the subsequent mass mortality are quite different from the patterns seen in *Chionochloa* grasses.

Finally, Saha and Howe suggest that bamboo seeds and seedlings are likely to be damaged by burning. We refer the reader to Keeley and Bond (1999) for verbatim quotes on the highly effective recruitment of bamboo after fires. Like most perennial grasses, bamboo seedlings are very good at surviving fires and at recovering rapidly from underground rhizomes. In addition, seeds of some mast-flowering bamboo species have extended dormancy (see Keeley and Bond 1999).

In conclusion, the importance of fire as a selective agent is still very poorly explored, and the response of Saha and Howe is not unexpected. We think the challenge lies more in identifying and testing putative adaptive traits, vegetative and reproductive, than in arguments over prehuman fire regimes in areas that experience predictable fires. The fire cycle hypothesis for mass-flowering, mass-dying bamboos makes testable assumptions and predictions (see Keeley and Bond 1999). Here are some:

Monocarpic should be rare in forests that are too wet to burn or are unlikely to burn for other reasons (e.g., on small islands). Keeley and Bond (1999) noted the scarcity of monocarpic in Malay and Neotropical wet forests. They also predicted that monocarpic should be rare where other forms of forest gap-creating disturbance are common (landslides, flooding, avalanche, etc). Data on patterns of bamboo monocarpic and mass flowering in different parts

of the world are still too patchy and incomplete to test these predictions.

Bamboos evolved first in wet forests, thus monocarpic should first have appeared as forests began to dry, and burn, late in the Tertiary. If Late Tertiary dispersal among continents can be discounted, this implies monocarpic evolved independently on separate continents. As the resolution of bamboo phylogenies increase, we should be able to test this idea.

Since we argue that monocarpic in bamboo increases the severity of forest fires, creating canopy gaps, we predict that in regions with minimal anthropogenic impact, crown fires that destroy forest canopies and open up forests will be significantly more common in the first few years after a mass-flowering bamboo event than at other times. Though fires might occur at other times, their severity should be significantly less.

Since we argue that fire promotes bamboo populations by opening forest canopy gaps, we would predict that the monocarpic life history should be more common in high-light-requiring species.

A major difficulty rectifying masting in bamboo with the predator-satiation hypothesis is explaining mass mortality after flowering. Predator satiation can only explain semelparity by positing that mast flowering exhausts carbohydrate reserves in the rhizomes and this lack of reserves is lethal to adventitious buds.

One could falsify this prediction by demonstrating that, in nonflowering clones, artificial exhaustion of rhizome carbohydrates to the level found after flowering will preclude bud initiation and growth. Another test of this hypothesis would require a naturally flowering population in which the flowers are artificially prevented from setting seed, and this should result in the rhizomes not being depleted of carbohydrates and the clones avoiding mortality.

Acknowledgments

We thank C. J. Fotheringham, H. Howe, S. Saha, and two anonymous reviewers for helpful comments on an earlier version.

Literature Cited

- Axelrod, D. I. 1989. Age and origin of chaparral. Pages 7–19 in S. C. Keeley, ed. *The California chaparral: paradigms reexamined*. Science Series, no. 34. Natural History Museum of Los Angeles County, Los Angeles.
- Baker, W. L. 2000. Indians and fire in the U.S. Rocky Mountains. *Ecological Society of America 85th Annual Meeting Abstracts*.
- Batchelder, R. B. 1967. Spatial and temporal patterns of

- fire in the tropical world. Proceedings Tall Timbers Fire Ecology Conference 6:171–190.
- Bond, W. J., and B. van Wilgen. 1996. Plants and fire. Chapman & Hall, New York.
- Bourdillon, T. F. 1895. Seeding of the thorny bamboo. Indian Forester 21:228–229.
- Brandis, D. 1899. Biological notes on Indian bamboos. Indian Forester 25:1–25.
- Christensen, N. L. 1985. Shrubland fire regimes and evolutionary consequences. Pages 85–100 in S. T. A. Pickett and P. S. White, eds. The ecology of natural disturbance and patch dynamics. Academic Press, New York.
- Clark, L. G. 1995. Diversity and distribution of the Andean woody bamboos (Poaceae: Bambusoideae). Pages 501–512 in S. P. Churchill, H. Balslev, E. Forero, and J. L. Luteyn, eds. Biodiversity and conservation of Neotropical montane forests. New York Botanical Garden, Bronx.
- . 1997. Bamboos: the centrepiece of the grass family. Pages 237–248 in G. P. Chapman, ed. The bamboos. Academic Press, London.
- Fotheringham, C. J., and P. Rundel. 2000. Comparative seed germination of chaparral and desert annuals. Ninth MEDECOS Meeting Abstracts, Stellenbosh, South Africa.
- Gadgil, M., and R. Guhu. 1993. This fissured land: an ecological history of India. University of California Press, Berkeley.
- Gadgil, M., and S. N. Prasad. 1984. Ecological determinants of life history evolution of two Indian bamboo species. Biotropica 16:161–172.
- Goldammer, J. G. 1993. Historical biogeography of fire: tropical and subtropical. Pages 297–314 in P. J. Crutzen and J. G. Goldammer, eds. Fire in the environment: the ecological, atmospheric, and climatic importance of vegetation fires. Wiley, New York.
- Goldammer, J. G., and B. Seibert. 1990. The impact of droughts and forest fires on tropical lowland rain forest of East Kalimantan. Pages 11–31 in J. G. Goldammer, ed. Fire in the tropical biota: ecosystem processes and challenges. Springer, New York.
- Goodman, S. J., and H. J. Christian. 1993. Global observations of lightning. Pages 191–219 in R. J. Gurney, J. L. Foster, and C. L. Parkinson, eds. Atlas of satellite observations related to global change. Cambridge University Press, Cambridge.
- Gosz, J. R., D. I. Moore, G. A. Shore, and H. D. Grover. 1995. Lightning estimates of precipitation location and quantity on the Sevilleta LTER, New Mexico. Ecological Applications 5:1141–1150.
- Graham, A. 1999. Late Cretaceous and Cenozoic history of North American vegetation. Oxford University Press, Oxford.
- Hegde, V., M. D. S. Chandran, and M. Gadgil. 1998. Variation in bark thickness in a tropical forest community of Western Ghats in India. Functional Ecology 12: 313–318.
- Henkel, J. S. 1927. *Oxytenanthera*, occurrence, gregarious flowering and natural regeneration S.R. South African Journal of Science 24:224.
- Holtum, R. E. 1967. The bamboos of New Guinea. Kew Bulletin 21:263–292.
- Janzen, D. H. 1976. Why bamboos wait so long to flower. Annual Review of Ecology and Systematics 7:347–391.
- Janzen, D. H., and P. Martin. 1982. Neotropical anachronisms: what the gomphotheres ate. Science (Washington, D.C.) 215:19–27.
- Joshi, H. B. 1975. Troup's "The silviculture of Indian trees." Vol. 1. Forest Research Institute, Delhi.
- . 1980. Troup's "The silviculture of Indian trees." Vols. 1 and 2. Forest Research Institute, Delhi.
- Judziwicz, E. J., L. G. Clark, X. Londoño, and M. J. Stein. 1999. American bamboos. Smithsonian Institution, Washington, D.C.
- Kadambi, K. 1949. On the ecology and silviculture of *Dendrocalamus strictus* in the bamboo forests of Bhadravati Division, Mysore State, and comparative notes on the species *Bambusa*, *Arundinacea ochladra travancorica*, *Oxytenanthera monostigma* and *O. stocksii*. Indian Forester 75:289–299.
- Keeley, J. E. 1981. Reproductive cycles and fire regimes. Pages 231–277 in H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners, eds. Proceedings of the conference Fire Regimes and Ecosystem Properties. USDA Forest Service, General Technical Report WO-26, Washington, D.C.
- . 1986. Resilience of Mediterranean shrub communities to fire. Pages 95–112 in B. Dell, A. J. M. Hopkins, and B. B. Lamont, eds. Resilience in Mediterranean-type ecosystems. Junk, Dordrecht.
- . 2000. Chaparral. Pages 203–253 in M. G. Barbour and W. D. Billings, eds. North American terrestrial vegetation. Cambridge University Press, Cambridge.
- Keeley, J. E., and W. J. Bond. 1999. Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. American Naturalist 154:383–391.
- Keeley, J. E., and C. J. Fotheringham. 2001. The historic fire regime in southern California shrublands. Conservation Biology, in press.
- Keeley, J. E., and P. H. Zedler. 1998. Evolution of life histories in *Pinus*. Pages 219–251 in D. M. Richardson, ed. Ecology and biogeography of pines. Cambridge University Press, Cambridge.
- Kelly, D., A. L. Harrison, W. G. Lee, I. J. Payton, P. R. Wilson, and E. M. Schaubert. 2000. Predator satiation

- and extreme mast seeding in 11 species of *Chionochloa* (Poaceae). *Oikos* 90:477–488.
- Kikim, A., and P. S. Yadava. 1998. Impact of fire on regeneration of dominant tree species in a secondary subtropical forest of north-eastern India. *International Journal of Ecology and Environmental Sciences* 24: 81–93.
- Kitzberger, T., T. T. Veblen, and R. Villalba. 1997. Climatic influences on fire regimes along a rain forest-to-xeric woodland gradient in northern Patagonia, Argentina. *Journal of Biogeography* 24:35–47.
- Kobayashi, M. 1997. Phylogeny of world bamboos analyzed by restriction fragment length polymorphisms of chloroplast DNA. Pages 227–236 in G. P. Chapman, ed. *The bamboos*. Academic Press, London.
- Kwe-Tu-Wet-Tu. 1903. The flowering of *Bambusa polymorpha*. *Indian Forester* 29:513–516.
- Marsh, G. P. (1864) 1965. *Man and nature; or, physical geography as modified by human action*. Belknap, Cambridge, Mass.
- McClure, F. A. 1966. *The bamboos*. Harvard University Press, Cambridge, Mass.
- Middleton, B. A., E. Sanchez-Rojas, B. Suedmeyer, and A. Michels. 1997. Fire in a tropical dry forest of Central America: a natural part of the disturbance regime? *Biotropica* 29:515–517.
- Parsons, D. J. 1981. The historical role of fire in the foothill communities of Sequoia National Park. *Madroño* 28: 111–120.
- Platt, S. G., and C. G. Brantley. 1997. Canebrakes: an ecological and historical perspective. *Castanea* 62:8–21.
- Prasad, S. N. 1985. Impact of grazing, fire and extraction on the bamboo (*Dendrocalamus strictus* and *Bambusa arundinacea*) populations of Karnataka. *Agriculture Ecosystems and Environment* 14:1–14.
- Rai, S. N., and A. Saxena. 1997. The extent of forest fires, grazing and regeneration status in inventoried forest areas of India. *Indian Forester* 123:698–702.
- Rao, K. S., and P. S. Ramakrishnan. 1987. Comparative analysis of the population dynamics of two bamboo species, *Dendrocalamus hamiltonii* and *Neohouzeua dulloa*, in a successional environment. *Forest Ecology and Management* 21:177–189.
- Roberts, S. J. 2000. Tropical fire ecology. *Progress in Physical Geography* 24:281–288.
- Saha, S., and H. F. Howe. 2001. The bamboo fire cycle hypothesis: a comment. *American Naturalist* 158: 659–663.
- Sharma, S., and H. C. Rikhari. 1997. Forest fire in the central Himalaya: climate and recovery of trees. *International Journal of Biometeorology* 40:63–70.
- Sidhu, D. S., and A. Thakur. 1998. Forest fire and their control in India. Pages 191–201 in D. X. Viegas, ed. *Third International Conference on Forest Fire Research, Fourteenth Conference on Fire and Forest Meteorology*. Vol. 1. University of Coimbra, Coimbra, Portugal.
- Soderstrom, T. R., and C. E. Calderon. 1974. Primitive forest grasses and evolution of the Bambusoideae. *Biotropica* 6:141–153.
- Stott, P. 1986. The spatial pattern of dry season fires in the savanna forests of Thailand. *Journal of Biogeography* 13:345–358.
- . 1988. The forest as Phoenix: towards a biogeography of fire in mainland South East Asia. *Geographical Journal* 154:337–350.
- Stott, P. A., J. G. Goldammer, and W. L. Werner. 1990. The role of fire in the tropical lowland deciduous forests of Asia. Pages 32–44 in J. G. Goldammer, ed. *Fire in the tropical biota: ecosystem processes and challenges*. Springer, New York.
- Swetnam, T. W. 1993. Fire history and climate change in giant sequoia groves. *Science (Washington D.C.)* 262: 885–889.
- Swetnam, T. W., and C. H. Baisan. 1996. Fire histories of montane forests in the Madrean Borderlands. Pages 15–36 in P. F. Ffolliott, L. F. DeBano, M. B. Baker, G. J. Gottfried, G. Solis-Garza, C. B. Edminster, D. G. Neary, L. S. Allen, and R. H. Hamre, eds. *Effects of fire on Madrean Province ecosystems: a symposium proceedings*. General Technical Report RM-GTR-289, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.
- Uhl, C., J. B. Kauffman, and D. L. Dummings. 1988. Fire in the Venezuelan Amazon. 2. Environmental conditions necessary for forest fires in the evergreen rainforest of Venezuela. *Oikos* 53:176–184.
- Vogl, R. J. 1969. The role of fire in the evolution of the Hawaiian flora and vegetation. *Proceedings Tall Timbers Fire Ecology Conference* 9:5–60.
- Wharton, C. H. 1966. Man, fire and wild cattle in North Cambodia. *Proceedings Tall Timbers Fire Ecology Conference* 5:23–65.
- Win, U. N. 1951. A note on kyathaung (*Bambusa polymorpha*) flowering in Pinyinana Forest Division. *Burmese Forester* 1:52–56.
- Yadav, J. S. P. 1963. Site and soil characteristics of bamboo forests. *Indian Forester* 89:177–193.
- Zedler, P. H. 1995. Are some plants born to burn? *Trends in Ecology & Evolution* 10:393–395.
- Zhang, J., and M. Cao. 1995. Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. *Biological Conservation* 73:229–238.