

Fig. 3. Relationship between \log_{10} searching efficiency (A) and \log_{10} parasitoid abundance (P): $Y = -0.1620 - 0.5647 \cdot X$, $r^2 = .16$, P < .07.

3). Hassell (1985) has already pointed out that such declines in parasitoid searching efficiencies can be stabilizing. It remains to be seen how common these sorts of patterns are, and what behavioral mechanisms underlie reduced parasitoid efficiency with increasing numbers of parasitoids per host.

Literature Cited

Arditi, R., and L. R. Ginzburg. 1989. Coupling in predatorprey dynamics: ratio-dependence. Journal of Theoretical Biology 139:311–326.

Dempster, J. P. 1983. The natural control of populations of butterflies and moths. Biological Reviews **58**:461–481. Doutt, R. L., and J. Nakata. 1973. The *Rubus* leafhopper and its egg parasitoid: an endemic biotic system useful in

grape-pest management. Environmental Entomology 2:381–386.

Getz, W. M. 1984. Population dynamics: a per capita resource approach. Journal of Theoretical Biology 108:623–643.

Hassell, M. P. 1985. Insect natural enemies as regulating factors. Journal of Animal Ecology 54:323–334.

Lessels, C. M. 1985. Parasitoid foraging: should parasitism be density dependent? Journal of Animal Ecology **54**:27–41.

Moratorio, M. S. 1977. Aspects of the biology of *Anagrus* spp. (Hymenoptera: Mymaridae), with special reference to host-parasitoid relationships. Dissertation. University of London, London, England.

Morrison, G. 1986. Stochastic aggregative responses and spatial patterns of parasitism in patchy host–parasitoid interactions. Oecologia (Berlin) **70**:402–410.

Morrison, G., and D. R. Strong, Jr. 1980. Spatial variations in host density and the intensity of parasitism: some empirical examples. Environmental Entomology 9:149–152.

Price, P. W. 1988. Inversely density-dependent parasitism: the role of plant refuges for hosts. Journal of Animal Ecology 57:89–96.

Stiling, P. D. 1987. The frequency of density dependence in insect host-parasitoid systems. Ecology **68**:844–856.

Stiling, P. D., and D. R. Strong, Jr. 1982. Egg density and the intensity of parasitism in *Prokelism marginata* (Homoptera: Delphacidae). Ecology **63**:1630–1635.

Williams, D. W. 1981. Ecology of the blackberry leafhopper, Dikrella californica (Lawson), and its role in California grape agro-ecosystems. Dissertation. University of California, Berkeley, California, USA.

—. 1984. Ecology of a blackberry-leafhopper-parasite system and its relevance to California grape agroecosystems. Hilgardia 52(4).

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EARLY 19TH-CENTURY FIRE DECLINE FOLLOWING SHEEP PASTURING IN A NAVAJO PONDEROSA PINE FOREST

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Pattern in ponderosa pine (*Pinus ponderosa* Laws.) forests in the American Southwest is significantly influenced by fire (Cooper 1960). The fire-scar record in

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tree rings reveals that the occurrence of fire has been greatly reduced throughout the region in the past century (Swetnam, *in press*). Many authors have argued that this decline was caused by dramatic land-use changes associated with European settlement in the last two decades of the 19th century (Weaver 1951, Cooper 1960, Biswell et al. 1973, Dieterich 1980a, Madany 1981). Herd numbers of domestic grazing animals, particularly sheep, rose steeply in the Southwest at that time (Bailey and Bailey 1986). Intense grazing removed the grass that had fueled light, episodic surface fires. After grazing herds dwindled in the 20th century, active fire-suppression policy maintained low fire frequency.

A second thesis, that reduced fire frequency at the turn of the century is responsible for major structural changes in ponderosa pine communities, has been postulated by a long lineage of studies (Arnold 1950, Weaver 1951, Cooper 1960, Biswell et al. 1973, Wright 1978, Allen 1989). In the early decades of the 20th

Table 1. Fire chronologies from *Pinus ponderosa* forests in the United States Southwest. Mean fire intervals (MFIs) are the mean of periods between fires that scarred ≥10% of the sample trees. MFIs are generally calculated for one to two centuries prior to a decline in fire frequency.

Author	Date of publication	Location	Tree sample size	Mean fire interval, yr	Date of decline
Dieterich	1980 <i>a</i>	Fort Valley Exp. Forest,	7	2.5	1876
Dieterich	1980 <i>b</i>	Long Valley Exp. Forest, north central Arizona	10	2.9	1898
Swetnam and Dieterich	1985	Gila Wilderness, southwestern New Mexico	18	5.1	1892
Dieterich and Hibbard	In press	Prescott National Forest northern Arizona	6	1.9	1874
Allen	1989	Jemez Mountains, central New Mexico	12	6.4	1893
Savage and Swetnam	This paper	Chuska Mountains, northeastern Arizona	16	4.2	1829

century, significant increases in establishment and survival of ponderosa pine in the region caused a shift from an open forest to an increasingly young, dense, and even-aged forest. Explanations for this regeneration pulse cite anthropogenic causes, in particular, elimination of frequent fires by livestock grazing, and subsequent fire-suppression activities. Low-intensity fires thin ponderosa stands by killing seedlings and saplings in a patchy manner (Cooper 1960). In addition, grazing may favor pine recruitment by reducing competition from grass and exposing a mineral seedbed (Wright 1978).

Severe grazing pressure may also suppress regeneration of trees by trampling and browsing seedlings. Considerable concern was expressed early in the century over the paucity of regeneration in southwestern pine forests due to this effect (Pearson 1923). The sharp reduction of livestock numbers in the 1920s and 1930s has been suggested as a mechanism for a regenerational release at that time (Pearson 1950).

Climate variation also plays an important role in the development of ponderosa pine forest structure. The coordination of a good seed-production year with adequate and timely precipitation is required for germination and establishment (Schubert 1970).

The objective of this study is the documentation and interpretation of an unusual fire history in a Southwest ponderosa pine community. The fire-scar record from the Chuska Mountains shows an abrupt and persistent reduction in fire frequency at least four decades earlier than in other parts of the Southwest (Table 1). Yet dense, even-aged cohorts were established in the Chuskas at the same time as others in the Southwest, in the 1910s, 1920s, and early 1930s (Savage 1989). The difference in land-use history offers an opportunity (1) to assess the strength of the hypothesis that grazing impacts caused fire-frequency decline in the Southwest,

and (2) to assess the relationship between fire decline and shifts in forest structure that occurred soon after.

Methods

Data were collected in a ponderosa pine forest at 2700 m elevation on a gently rolling plateau on the Arizona–New Mexico border at $\approx 36^{\circ}$ N and 108° W. Ponderosa pine occurs in nearly pure stands on the relatively homogeneous and mesic habitat of the plateau top.

Fire history was documented from partial cross sections taken 20–30 cm above the ground from scarred stumps of 16 ponderosa pine in an area of ≈ 6500 ha. Sampling procedure followed Kilgore and Taylor's (1979) technique of collecting small clusters of stumps, which, because of the patchiness of these fires and the variability of fire scarring among trees, provides a more complete record than isolated stumps. Six clusters of 2–3 stumps and two isolated stumps were analyzed.

Specimens were surfaced and crossdated and fire scars identified. Crossdating the scars allowed accurate assignment of scars to a calendar date (Dieterich and Swetnam 1984). In 15 cases it was unclear in which of two years a fire occurred, and the fire was assigned to the later date for computational purposes. Fire scars were identified on the basis of three criteria: (1) the presence of a gap within a ring or along a ring boundary, (2) charred wood within the gap, and (3) subsequent overlapping growth over the gap (Dieterich and Swetnam 1984).

Results

A total of 174 fire scars were recorded on 16 stumps (Fig. 1). Fires were recorded in 95 yr over a period of 594 yr. Mean fire intervals (MFIs), or the mean of the number of years between fires, were calculated for the entire record and for three historical periods. The MFI

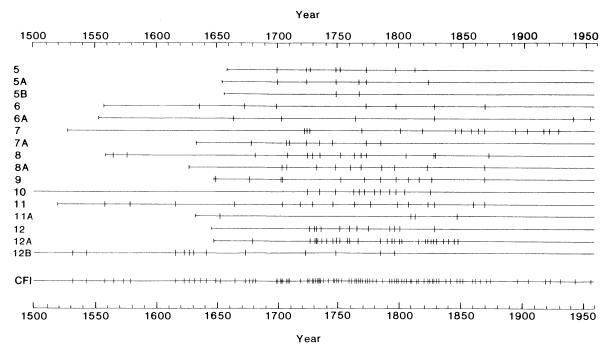


Fig. 1. Master fire chronology for the Chuska Mountains, Arizona and New Mexico, from 1500 to 1960. Horizontal lines represent life spans of 16 individual trees; vertical tick marks on life lines indicate dates of fire scars in each tree. CFI (Composite Fire Interval) reflects entire fire-scar record in the remaining stumps of the sample trees.

from the date when all sample trees were established, 1660, to 1986, is 3.7 yr (sp = 3.9 yr, Range [R] = 1-22 yr, number of fire years = 80), comparable to the fire frequency in similar habitats of the Southwest (Table 1).

Fires were frequent in the Chuskas until ≈ 1830 . Based on Navajo pastoral history and a subjective assessment of fire frequency, the record can be divided into three periods, an early period when sheep herds were building, a pastoral period when sheep numbers were erratic but usually high, and a modern period, when fire supression was active. The MFI for the Navajo forest from 1660 to 1830 is 2.8 yr (sD = 2.7 yr, R = 1–18 yr, fire years = 61). From 1830 to 1930 the MFI was 6.1 yr (sD = 5.5 yr, R = 1–22 yr, fire years = 17), and for the period 1930, when effective fire suppression was instituted, to 1986, the MFI was 13 yr (sD = 0.7 yr, R = 12–13 yr, fire years = 2).

In fact, the decline after 1830 was more pronounced than these figures imply. For the period from 1830 until 1930, 62% of the fires were recorded on 2 of the 16 trees, both of which were located next to a large lake and may have received scars from small fires associated with camps and dwellings. Moreover, only three fires were recorded after 1930, and they were bunched in time, resulting in a low MFI estimate. To eliminate

such exceptional coincidence, MFI may be calculated based only on fire scarring of $\geq 10\%$ of trees. Using this criterion, the MFI for the period 1700–1830 in the Chuskas is 4.2 yr. After 1830, fire scars were recorded in >10% of the sampled trees in only two years, 1846 and 1870.

Discussion

The coincidence of fire decline and early sheep herding on the Navajo Reservation, 45–70 yr before the same association in the rest of the region, lends strong support to the hypothesis that heavy livestock grazing played a significant role in reducing fire frequency in ponderosa pine forests.

In the great river basins of New Mexico a thriving livestock trade had developed in the early 1700s (Denevan 1967). Navajos became adept at raiding Hispanic settlements for sheep and goats, and favored the Chuskas as a refuge and summer pasture for their growing herds from as early as 1740 (Kemrer and Lord 1984). Huge flocks of sheep in New Mexico, estimated to total 3 000 000 animals by 1820, allowed the Navajo to accumulate herds, slowly at first, but at an accelerating pace as both Navajo and livestock populations grew. This trend intensified after 1800, when raiding of Hispanic flocks increased. Bailey (1980) estimates

Navajo population in 1700 at \approx 1000, and cites a Hispanic observer reporting in 1743 only "few small flocks." By 1850 the Navajo population probably exceeded 10 000, and written descriptions of the area by travellers and United States military expeditions recorded huge sheep herds and signs of severe grazing impacts in the 1840s (Bailey and Bailey 1986).

Fire became rare in the Chuskas around 1830. The impact of grazing by ever-greater herd numbers was compounded at this time by climate conditions. An extremely wet episode in the 1830s and early 1840s, reflected in tree-ring widths of the region (Schulman 1956, Dean and Robinson 1977), probably enhanced the abruptness of the fire decline as well as supporting larger sheep herds.

The Anglo and Hispanic settler livestock industry in the Southwest was delayed until the end of the 19th century by Indian presence and lack of railroad transportation to a market. For most southwestern ponderosa pine forests, the decline in fire frequency occurred in the last decades of the century, coinciding with the steep rise of grazing herds, but preceding organized fire suppression efforts by at least one to two decades. These observations, together with the association of grazing and early fire decline in the Chuska Mountains, suggest that grazing may have been the most important factor in the ending of episodic fire regimes in ponderosa pine forests.

The unusual fire history in the Chuskas, however, does not support the thesis that reduced fire occurrence by itself, or even a combination of grazing and fire decline, can fully account for dramatic structural shifts in the ponderosa forest. If so, a similar response should have followed grazing and fire decline in the Chuskas before the mid-19th century. Instead, the regeneration pulse in the Chuskas was synchronous with that of other ponderosa pine forests in the Southwest, for the forest today exhibits dense, even-aged cohorts that established in the early decades of the 1900s (Savage 1989).

It is difficult to interpret the effect that fluctuating levels of grazing in the 1900s may have had on pine regeneration. Whereas the non-Indian livestock industry in the Southwest depended on Eastern markets, and declined rapidly after World War I, remaining depressed through the 1920s, Navajo sheep herds were never kept primarily for commercial reasons, except for rug wool. Livestock numbers generally remained high from 1880 until 1930, when federal government policies reduced herd numbers by force for conservation reasons (Bailey and Bailey 1986). By then much of the pine regeneration pulse in the Chuskas was past (Savage 1989). A respite from severe grazing pressure, then, could not have been an important factor in forest structure shifts in the Chuskas.

The complex history of forest development in the Chuskas over several centuries suggests that anthropogenic impacts on fire and grazing regimes were not sufficient by themselves to cause a major regeneration pulse in pine. On the other hand, climatic factors appear to be quite important in controlling ponderosa regeneration. Schubert (1970) documents the importance of coordination of a good seed supply with timely temperature and precipitation patterns. Specifically, ponderosa seeds appear to need continually moist conditions for at least 7 d at temperatures >13° C to germinate. Apparently, such conditions were unusually common during the 1910s, 1920s, and early 1930s in the Chuskas. Exceptionally favorable climate conditions, that is, anomalously warm and wet, are documented in the Southwest for many years in the early decades of this century (Sellers 1960, Dean and Robinson 1977, Bradley et al. 1982).

The Chuska forest history suggests that insufficient attention has been given to the role of climate variation in the interpretation of southwestern pine-forest shifts in this century. The influence of favorable climate conditions on regeneration of forest species appears to have been masked by dramatic land-use changes occurring about the same time. The Chuska fire history suggests that major structural alteration of the forest landscape in this century must have been produced by anthropogenic disturbance coupled with a period of highly favorable climate conditions.

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Literature Cited

Allen, C. D. 1989. Changes in the landscape of the Jemez Mountains, New Mexico. Dissertation. University of California, Berkeley, California, USA.

Arnold, J. F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. Journal of Forestry 48:118–126.

Bailey, G., and R. G. Bailey. 1986. A history of the Navajos: the reservation years. School of American Research, Santa Fe, New Mexico, USA.

Bailey, L. R. 1980. If you take my sheep... the evolution and conflicts of Navajo pastoralism, 1630-1868. Westernlore Publications, Pasadena, California, USA.

Biswell, H. H., H. R. Kallander, R. Komarek, R. J. Vogl, and H. Weaver. 1973. Ponderosa fire management. Miscellaneous Publications Number 2. Tall Timbers Research Station, Tallahassee, Florida, USA.

- Bradley, R. S., R. G. Barry, and G. Kiladis. 1982. Climatic fluctuations of the western United States during the period of instrumental records. Contribution Number 42. University of Massachusetts, Amherst, Massachusetts, USA.
- Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecological Monographs 30:129-164.
- Dean, J. S., and W. J. Robinson. 1977. Expanded tree-ring chronologies for the southwestern United States. Chronology Series III. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, USA.
- Denevan, W. M. 1967. Livestock numbers in nineteenth-century New Mexico, and the problem of gullying in the southwest. Annals of the Association of American Geographers 57:691–703.
- Dieterich, J. H. 1980a. Chimney Springs forest fire history. General Technical Report RM-220. United States Forest Service, Fort Collins, Colorado, USA.
- Dieterich, J. H. 1980b. The composite fire interval—a tool for more accurate interpretation of fire history. Pages 8–14 in M. A. Stokes and J. H. Dieterich, technical coordinators. Fire history workshop: proceedings of a technical conference, October 1980, Tucson, Arizona. General Technical Report RM-81. United States Forest Service, Fort Collins, Colorado, USA.
- Dieterich, J. H., and A. R. Hibbert. *In press.* Fire history in a small ponderosa pine stand surrounded by chaparral. *In J. S. Krammes, M. J. Zwolinski, and W. W. Covington, technical coordinators. Proceedings of the symposium on effects of fire in management of southwestern natural resources, 15–17 November 1988, Tucson, Arizona. General Technical Report. United States Forest Service, Fort Collins, Colorado, USA.*
- Dieterich, J. H., and T. W. Swetnam. 1984. Dendrochronology of a fire-scarred ponderosa pine. Forest Science 30: 238–247.
- Kemrer, M. F., and K. J. Lord. 1984. Cultural resources overview for the Navajo Forest. United States Bureau of Indian Affairs, Window Rock, Arizona, USA.
- Kilgore, B. M., and D. Taylor. 1979. Fire history of a sequoia–mixed conifer forest. Ecology **60**:129–142.
- Madany, M. H. 1981. Land use-fire regime interactions with vegetation structure of several montane forest areas of Zion National Park. Thesis. Utah State University, Logan, Utah, USA
- Pearson, G. A. 1923. Natural reproduction of western yellow

- pine in the Southwest. Department of Agriculture Bulletin 1105. United States Department of Agriculture, Washington, D.C., USA.
- ——. 1950. Management of ponderosa pine in the Southwest. Department of Agriculture Monograph 6. United States Department of Agriculture, Washington, D.C., USA.
- Savage, M. 1989. Structural dynamics of a pine forest in the American Southwest under chronic human disturbance. Dissertation. University of Colorado, Boulder, Colorado, USA.
- Schubert, G. H. 1970. Ponderosa pine regeneration problems in the Southwest. Pages 1–4 *in* R. K. Hermann, editor. Regeneration of ponderosa pine. Paper 681. School of Forestry, Oregon State University, Corvallis, Oregon, USA.
- Schulman, E. 1956. Dendroclimatic changes in semiarid America. University of Arizona Press, Tucson, Arizona, USA
- Sellers, W. D. 1960. Precipitation trends in Arizona and western New Mexico. Pages 81–94 *in* Proceedings of the 28th Western Snow Conference, 12–14 April 1960, Santa Fe, New Mexico. Colorado State University Press, Fort Collins, Colorado, USA.
- Swetnam, T. W. *In press*. Fire history and climate in the southwestern United States. *In J. S. Krammes, M. J. Zwolinski, and W. W. Covington, technical coordinators. Proceedings of the symposium on effects of fire in management of southwestern natural resources, 15–17 November 1988, Tucson, Arizona. General Technical Report. United States Forest Service, Fort Collins, Colorado, USA.*
- Swetnam, T. W., and J. H. Dieterich. 1985. Fire history of ponderosa pine forests in the Gila Wilderness, New Mexico. Pages 390–397 in J. E. Lotan, B. M. Kilgore, and R. W. Mutch, technical coordinators. Proceedings of the symposium and workshop on wilderness fires, 15–18 November 1983, Missoula, Montana. General Technical Report INT-182. United States Forest Service, Ogden, Utah, USA.
- Weaver, H. 1951. Fire as an ecological factor in the southwestern ponderosa pine forests. Journal of Forestry **49**:93–98.
- Wright, H. A. 1978. The effect of fire on vegetation in ponderosa pine forests: a state wildlife information series number 2. College of Agricultural Science Publications, Lubbock, Texas, USA.

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