Phytolith evidence for the absence of a prehistoric grass understory in a Jeffrey pine – mixed conifer forest in the Sierra San Pedro Mártir, Mexico

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Abstract: Phytolith analysis was applied to several sites in a Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) – mixed conifer forest in the Sierra San Pedro Mártir, Baja California, Mexico, to explore the hypothesis that the introduction of livestock in the late 18th century led to overgrazing of a prehistoric grass understory, resulting in changes to the prehistoric fire regime observed in the tree-ring fire-scar record. Stable soils in regions with extensive prehistoric grass cover retain a high concentration of total phytoliths and high percentage of grass phytoliths, regardless of historic vegetation changes. Phytoliths extracted from soil samples collected from several sites in the Sierra San Pedro Mártir revealed total phytolith concentrations in forest soils were generally <0.5% by mass, with most <0.1%, whereas grass phytoliths were generally <10% of the total, values consistent with the interpretation of a forest with sparse grass cover in the understory. Phytolith evidence suggests that there was minimal grass available for grazing in prehistoric Sierra San Pedro Mártir forests; overgrazing a grass understory was probably not a major driver of changes in the prehistoric fire regime.

Résumé : Les phytolithes ont été analysés à plusieurs endroits dans une forêt mixte de conifères dominée par le pin de Jeffrey (*Pinus jeffreyi* Grev. & Balf.) située dans la Sierra San Pedro Mártir, à Baja California au Mexique. L'objectif consistait à examiner l'hypothèse selon laquelle l'introduction du bétail, à la fin du 18e siècle, aurait entraîné le broutage excessif d'un sous-étage préhistorique de graminées, ce qui aurait provoqué des changements dans le régime préhistorique des feux détectés par les cicatrices de feu dans les données de cernes annuels. Les sols stables dans les régions autrefois largement couvertes de graminées conservent une concentration totale élevée de phytolithes et un pourcentage élevé de phytolithes contenant des graminées peu importe les changements survenus dans la végétation. Les phytolithes extraits d'échantillons de sol collectés à plusieurs endroits dans la Sierra San Pedro Mártir ont révélé que la concentration totale de phytolithes était généralement inférieure à 0,5 % (0,1 % dans la plupart des cas) en poids dans les sols forestiers, tandis que les phytolithes contenant des graminées représentaient généralement moins de 10 % du total. Ces valeurs sont cohérentes avec l'interprétation qu'il y avait un couvert clairsemé de graminées en sous-bois. Les résultats fournis par les phytolithes indiquent qu'il y avait peu de graminées disponibles pour brouter dans les forêts préhistoriques de la Sierra San Pedro Mártir. Le broutage excessif des graminées en sous-étage n'a probablement pas été une cause majeure de changements dans le régime préhistorique des feux.

[Traduit par la Rédaction]

Introduction

Tree-ring fire-scar analysis has been used to describe prehistoric fire regimes in many forested regions of western North America (Swetnam 1993; Beaty and Taylor 2001; Brown et al. 2001; Swetnam and Baisan 2002; Fule et al. 2003; Grissino-Mayer et al. 2004). One recent study has examined the prehistoric fire regime in a Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) – mixed conifer forest in the Sierra San Pedro Mártir (SSPM) in north-central Baja California, Mexico (Stephens et al. 2003). Unlike most forests in the western United States that have experienced ~100 years of active fire suppression and extensive timber harvesting, SSPM forests have had minimal timber harvesting and have only experienced minor organized fire suppression since approximately 1970 (Stephens et al. 2003).

Stephens et al. (2003) sampled 105 fire-scarred specimens, mostly live Jeffrey pine, from two 0.8 km² sites ~1.5 km apart near Vallecitos Meadow on the upper plateau in the SSPM. Based on analysis of the tree-ring fire-scar record for the past 300 years (Fig. 1), they described a frequent, low-intensity fire regime. The mean fire return interval, depending on the scale of composite fire chronology used and time period analyzed, was between 3.9 and 23.5 years (Stephens et al. 2003, their table 1).

The tree-ring fire-scar record for these two sites (Fig. 1)

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Fig. 1. Historical fire activity at site 1 (Jeffrey pine – mixed conifer forest) and site 2 (Jeffrey pine forest) in the Sierra San Pedro Mártir, Baja California, Mexico (adapted from Stephens et al. 2003). Each horizontal line is an individual tree and each short vertical line is a dated fire scar. Composites show years when fires scarred at least one available recording tree, 10% of trees, and 25% of trees.
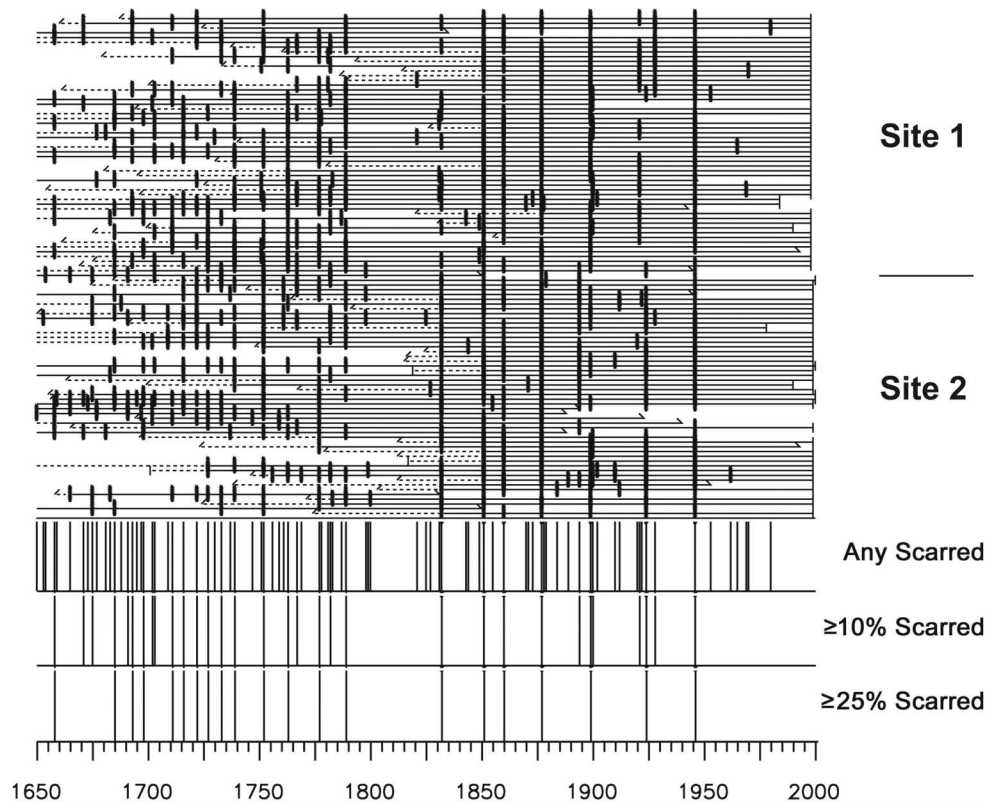
indicated there were substantial changes in the nature of the fire regime over time that can be divided into four distinct periods: (*i*) 1600–1789 (very frequent small fires), (*ii*) 1790–1831 (infrequent small fires), (*iii*) 1832–1946 (frequent larger fires), and (*iv*) 1947–present (infrequent small fires). Tree-ring fire-scar data from sites throughout the SSPM (C. Skinner, USDA Forest Service, Pacific Southwest Research Station, Redding, California, personal communication, 2004) confirmed this general pattern of temporal changes in fire size and frequency extended throughout the mountain range and was not restricted to the sites sampled by Stephens et al. (2003).

The introduction of grazing by livestock has been shown to dramatically increase fire-return intervals in coniferous forests with substantial understory grass cover throughout the southwestern United States (Savage and Swetnam 1990; Swetnam et al. 2001) and has been suggested as a possible factor for similar increases at sites in the southern Sierra Nevada currently lacking a grass understory (Swetnam et al. 1992). The climate and species composition of SSPM forests are much more similar to mixed conifer forests in the Sierra Nevada than to coniferous forests in the monsoonal southwestern United States. However, because the effect of grazing on fire-return intervals was so pervasive in other parts of western North America after the time of European settlement, Stephens et al. (2003) postulated that perhaps there was substantial grass cover in the coniferous forests of the SSPM prior to the introduction of livestock grazing when the SSPM mission was established in 1796. This hypothesis

suggested that overgrazing of forest understory grasses led to the disruption of fuel continuity and the shift from very frequent fires to less frequent fires post-1790. The near absence of fire for 40 years post-1790 and the longer fire-return intervals seen from 1832 to 1946 may have been due to conifer litter (which presumably requires considerably more time to build up to sufficient levels to carry a fire) replacing grass litter as the chief fuel for fire spread.

Currently there is very little grass cover in SSPM forests, but two centuries of overgrazing could have greatly reduced a grass understory. The historical record suggests most grazing in the past focused on several large meadows, where considerable grazing continues today (Minnich and Franco-Vizcaino 1998), but the record provides no information on grazing in the forest understory.

Since the introduction of livestock to the SSPM, there have been several changes in the number and types of animals over time (Henderson 1964; Stephens et al. 2003). After reaching a substantial population by 1820, cattle dominated from the mid-19th century to early 20th century, reaching a peak during a gold rush in the 1870*s*. From 1910 to 1964, there were substantial sheep populations (Minnich and Franco-Vizcaino 1998). Sheep were removed with the creation of San Pedro Mártir National Park in 1964 and replaced with cattle that continue to graze there today. If the prehistoric grass understory hypothesis is correct, changes in fire regime parameters may have mirrored changes in livestock grazing parameters.

To test the prehistoric grass understory hypothesis, we

employed phytolith analysis of the forest soils to determine if there was a grass understory in SSPM forests prior to European contact (Parker 2002). Opal phytoliths are microscopic, mostly silt-sized particles of amorphous silica that are formed in the tissues of certain plants and deposited in the soil when the plant dies (Piperno 2006). Phytoliths are highly resistant to weathering in most environments and can remain in the soil for thousands or even millions of years (Wilding 1967; Strömberg 2004). Grasses produce larger amounts of phytoliths than most plants (Piperno 2006). Short-cell phytoliths, formed in specialized silica accumulator cells, are diagnostic of the Poaceae family and can be used to identify some grasses to the subfamily level (Twiss et al. 1969; Twiss 1992; Mulholland and Rapp 1992).

Soil phytolith content has been used by several investigators to document changes in dominant surface vegetation. Wilding and Drees (1968), working in the prairie peninsula in Illinois, found clear signs of a forest–prairie ecotone based on soil phytolith content. Grass-dominated prairie soils in this region have 3%–5% phytolith content by mass, whereas forest soils in the region have an order of magnitude less. Fisher et al. (1995) used soil phytolith assemblages in Utah to document a shift from grassland to shrubland with the introduction of grazing. Bicknell et al. (1992, 1993) used soil phytolith abundance evidence to aid mapping vegetation prior to European contact in several regions of coastal California; they found areas where major shifts from grassland to forest and vice-versa had occurred after contact. At a ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) – bunchgrass site in northern Arizona, where the modern vegetation differs considerably in species composition but has similar physiognomy to the postulated prehistoric vegetation in the SSPM, the soil phytolith assemblage was extracted and analyzed to determine the long-term stability of the current plant community (Kerns 2001; Kerns et al. 2001, 2003). Soil phytolith content, composed mostly of grass and ponderosa pine phytoliths, was 1.0%–2.5% of the soil dry mass. All of these studies have shown that, if there was grass cover on a site with stable soil for an appreciable time in the past, a large concentration of grass phytoliths will be present in the soil.

Materials and methods

Study area

The study was located in San Pedro Mártir National Park within the SSPM mountain range in north-central Baja California, Mexico, 100 km southeast of Ensenada (Fig. 2). The SSPM, the southernmost extension of the Peninsular Range, is dominated by a sloping plateau with elevations averaging 2600 m in the north, decreasing to 1800 m in the south. Coniferous forests, comprising approximately 40 655 ha (Minnich et al. 2000), dominate the plateau. Major tree species on and near the study sites include the following (from Wiggins 1980): Jeffrey pine, white fir (*Abies concolor* (Gord. & Glend.) Lindl.), sugar pine (*Pinus lambertiana* Dougl.), lodgepole pine (*Pinus contorta* var. *murrayana* Dougl. ex Loud.), and incense-cedar (*Calocedrus decurrens* (Torr.) Floren.). Common understory species on the study sites include mountain snowberry (*Symphoricarpos oreophilus* Gray), greenleaf manzanita (*Arctostaphylos patula*

Greene subsp. *platyphylla* (Gray) P.V. Wells), whitethorn ceanothus (*Ceanothus cordulatus* Kell.), and blue sage (*Salvia pachyphylla* Epling ex Munz). Grasses currently found on the sites include cheatgrass (*Bromus tectorum* L.), squirreltail (*Elymus elymoides* (Raf.) Swezey subsp. *elymoides*), deergrass (*Muhlenbergia rigens* (Benth.) A.S. Hitchc.), New Mexico muhly (*Muhlenbergia pauciflora* Buckl.), and pine dropseed (*Blepharoneuron tricholepis* (Torr.) Nash). Jeffrey pine, Jeffrey pine – mixed conifer, and mixed white fir are the most common forest types (Minnich and Franco-Vizcaino 1998).

The soils of the SSPM are largely unclassified, but those derived from diorite parent materials in forested upland sites near the study area are Typic Xeropsamments (Franco-Vizcaino et al. 2002; Stephens and Gill 2005). Soils are shallow, well to excessively drained, and relatively acidic (pH 5.3). The most common soil texture is loamy sands. Soil chemistry and texture in this study are typical of granite-derived soils in similar forests in California (Potter 1998).

The SSPM is at the southern margin of the North American Mediterranean climate zone (Pyke 1972; Markham 1972; Minnich et al. 2000). Accurate climate data for the plateau is very limited, but the mean precipitation from 1989 to 1992 near our study sites at Vallecitos Meadow was 55 cm (Minnich et al. 1997, 2000). Most precipitation occurs during the winter months, but there is a secondary peak from July to August when the western margin of the North American monsoon system extends to the SSPM (Minnich et al. 1993, 2000).

Our study was conducted on and near the two sites sampled for the fire-history study (Stephens et al. 2003). The sites are separated by ~1.5 km at 2400–2600 m elevation on the upper plateau at 31°02′N, 115°27′W. Site 1, located on granitic parent material, is Jeffrey pine – mixed conifer with patchy manzanita and very little grass in the understory. Site 2, located on metamorphic quartz schist, is almost exclusively Jeffrey pine with patchy manzanita and areas of grass with <5% cover in the understory.

Phytolith sampling

Samples of leaf and woody material from all major plant species present on the two sites were collected to create a phytolith reference collection. Phytoliths were extracted with a standard dry-ashing procedure using a muffle furnace at 550 °C for 4 h, followed by washing in 10% HCl (Piperno 2006; Pearsall 1989; Kondo et al. 1994).

Soil samples were collected from several locations. (*i*) SS-1 grid (SS-1 G): Surface and 5 cm depth samples were collected from 49 plots at the intersection of grid lines laid out at 200 m intervals on site 1 (Stephens and Gill 2005). Soils on most plots were shallow, and horizons were poorly defined. Vegetation on plots was mostly upland Jeffrey pine – mixed conifer with patchy shrubs and very sparse grass cover. (*ii*) SS-1 forest and meadow transect plots (SS-1 F and SS-1 M): Surface and 5 cm depth samples were collected from plots sampled every 10 m along a single, randomly selected 100 m transect spanning the current Jeffrey pine – mixed conifer forest – dry meadow ecotone in Vallecitos Meadow near site 1. The ecotone was very sharply defined, with no obvious gradient; the

Fig. 2. Location of Sierra San Pedro Mártir and study sites.
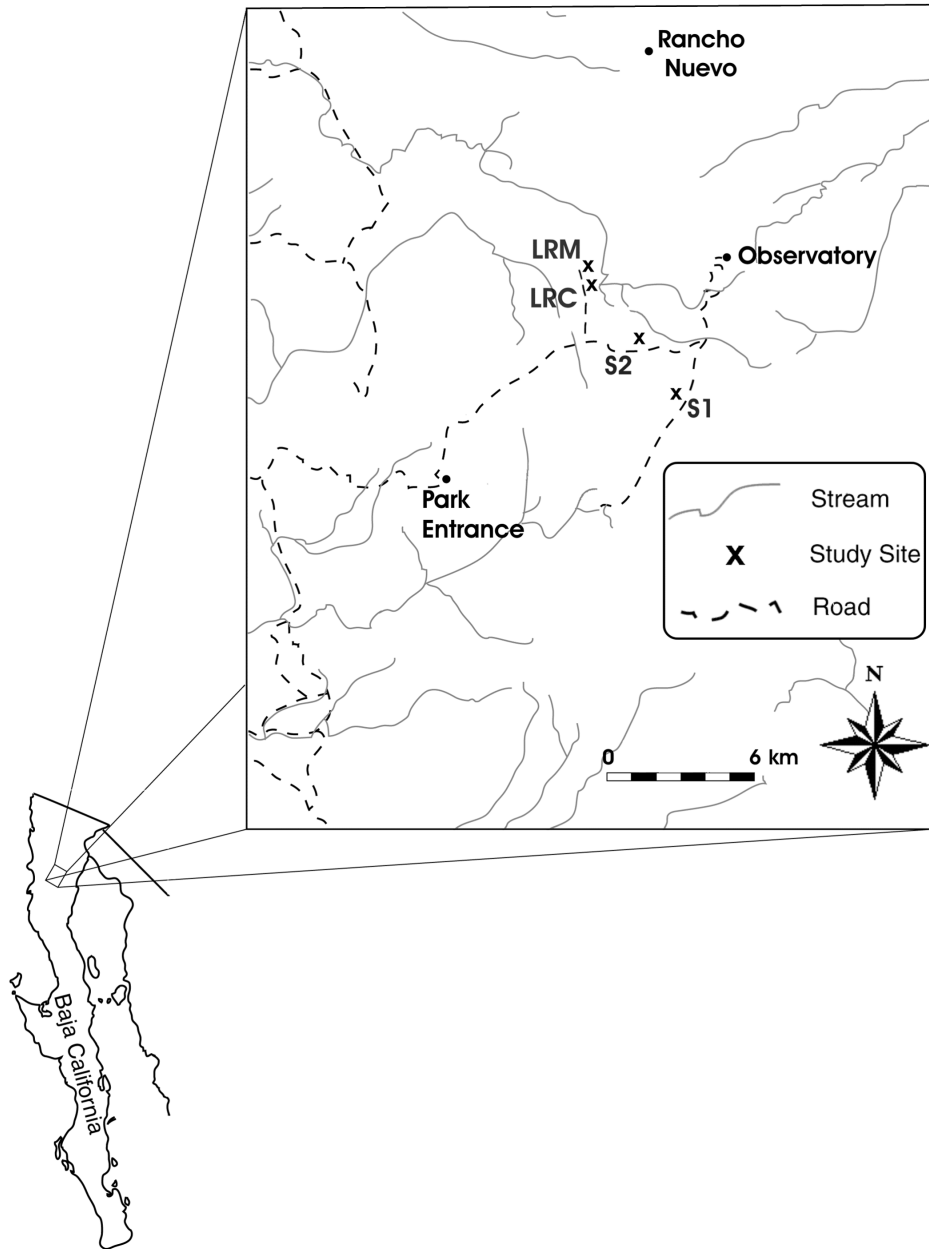
transect produced five forested plots and five meadow plots. Forested plots were similar to SS-1 G plots, with more lodgepole pine. Meadow plots had no tree cover; graminoid and forb cover increased with increasing winter precipitation but was generally <50% during the 4 years observed. (*iii*) SS-2: Surface and 5 cm depth samples were collected from three 10 m^2 dry upland plots on site 2. Each plot was randomly selected within much larger, non-contiguous patches dominated by Jeffrey pine, but where grasses currently make up ~5% understory cover. Each sample was a composite of soil collected from 10 randomly chosen points within each plot. (*iv*) SS-1 profile 1 and profile 2 (SS-1 P1 and SS-1 P2): Samples were collected at 12 cm intervals from base to surface from two exposed soil profiles without stratigraphic layers within the grid on site 1. Profile 2 was from a 1.42 m cutbank on the

edge of an intermittent stream; profile 1 was from a 0.67 m face of exposed colluvium, located 50 m up a gentle slope from profile 2. (*v*) LRM and LRC: Samples were collected from base to surface from two exposed sedimentary soil profiles ~5 km from the fire-history sites. Each clear stratigraphic layer, probably indicating a sediment deposition episode, was sampled. LRM was a 1.39 m cutbank in the channel of a small, dry stringer meadow with no tree cover and graminoid and forb cover >75%. LRC, which was ~1 km from LRM, was a 2.01 m cut bank in alternating alluvial and colluvial sediments in a small channel with some tree and shrub cover. Graminoid and forb cover was <50%.

A trowel was used to collect ~100 g of soil for each sample. Surface soil samples were collected by removing the litter to expose mineral soil. The 5 cm sample was collected

by exposing a vertical face in a shallow pit. Profile samples were collected by inserting the trowel at the desired level in the freshly cleaned face, and represent a composite of sediment in a 1–2 cm band centered on the measured depth.

Phytoliths were extracted from soil samples by standard procedures (Carbone 1977; Kondo et al. 1994): particle dispersion in sodium hexametaphosphate, removal of carbonates in hydrochloric acid, organic matter digestion in 30% hydrogen peroxide, clay removal by gravity sedimentation, followed by three heavy liquid flotations in zinc bromide at specific gravity 2.30 to ensure complete extraction. Samples of discarded reagents and washes were examined under the microscope to ensure phytoliths were not lost during processing.

Because the biogenic silica residue contained diatoms and residual mineral silica particles, phytolith mass for each sample was estimated by examining 10 microscope fields on a slide, estimating the percentage of nonphytolith material, and subtracting this percentage from the measured residue mass (Carnelli et al. 2001). For counting phytoliths, both reference material and soil sample residue was resuspended in immersion oil to allow rotation of phytoliths to observe three-dimensional characteristics and scanned with a phase contrast microscope at 400×. Reference material slides were scanned for phytolith types in nonoverlapping rows, looking particularly for diagnostic forms. Phytolith types were tallied for each soil sample until 400 were counted; the percentage of diagnostic grass phytoliths present in each sample was then calculated. For statistical analysis, an arcsine transformation of percentage data was performed to normalize distributions. Differences in mean percent soil phytolith mass and grass phytolith percentage between sites SS-1 G, SS-1 F, SS-1 M, and SS-2 were tested in SPSS using one-way analysis of variance (SPSS Inc. 2001). Because sample sizes and variances were unequal, Dunnett's T3 multiple comparison test was used to determine which means were significantly different (Norusis 2000). The difference between surface and 5 cm depth samples was tested separately at each site using a two-tailed, paired t test. No statistical analysis was attempted for SS-1 P1, SS-1 P2, LRM, and LRC because only one sample was collected from each level in the soil profile.

Results

Scans of phytoliths from plant reference material revealed low phytolith content (almost all <0.2% dry mass) and no diagnostic phytolith shapes for common trees or shrubs found on the sampled SSPM sites. As expected, all grass species sampled contained large quantities, between 2% and 5% dry mass, of phytoliths. Short cells (saddles, trapezoids and rondels, bilobates, and crenates), trichomes, bulliform cells, and several forms of elongated phytoliths were not found in other sampled plants and were considered diagnostic for grasses. Diagnostic forms comprised >50% of total phytoliths observed in all sampled grasses.

The paired t test revealed no significant differences in phytolith concentration between surface and 5 cm depth samples on any of the sites ($p > 0.15$ for all), so only surface sample data were analyzed further. The SS-1 grid samples ($N = 49$) averaged 0.04% phytolith mass/soil dry mass

(Fig. 3). Only 3% of phytoliths present were grass diagnostic forms. Soil samples taken under forest cover ($N = 5$) in the forest–meadow transect also contained few total phytoliths and few grass phytoliths (Fig. 3). Soil samples taken within Vallecitos Meadow ($N = 5$) as part of the forest–meadow transect contained 0.12% phytoliths, with 39% grass phytoliths. Samples from SS-2 ($N = 3$) showed phytolith mass and grass phytolith percentage intermediate between SS-1 and meadow soil samples (Fig. 3). One-way analysis of variance showed values from these sites were significantly different for both percent phytolith mass ($p < 0.001$) and grass phytolith percentage ($p < 0.001$). Dunnett's T3 multiple comparison test showed significant differences (Fig. 3) in percent phytolith mass between SS-1 meadow transect plots and SS-1 forest transect plots ($p = 0.003$) as well as SS-1 grid plots ($p < 0.001$). Grass phytolith percentage was significantly different (Fig. 3) between SS-1 meadow plots and all other plots ($p < 0.001$ for all).

Samples from exposed soil profiles within SS-1 revealed consistently low phytolith masses throughout the profiles (Figs. 4 and 5). SS-1 P2, on the edge of the intermittent stream channel, showed higher total phytolith content and grass phytolith percentages than SS-1 P1, several metres above the channel.

Samples from the profiles of the stratified sites, LRM and LRC, contained many strata with much higher phytolith mass (two of which exceeded 1%) and grass phytolith percentage (approaching 40%) than any of the other sites (Figs. 6 and 7). There was considerable variation of phytolith mass between strata within the profiles; the trend was toward less mass with increasing depth.

Many of the phytolith morphotypes observed in samples from plots with low diagnostic grass phytolith concentrations were irregular fragments and nondiagnostic elongate phytoliths that probably came from grasses. Also commonly observed were nondescript plates and blocky morphotypes found in low concentrations in specimens from several tree and shrub species.

Discussion

Soil phytolith concentration

Numerous researchers have found that grassland soils contain 5–10 times more phytoliths by mass than forest soils, which generally have phytolith content between 0.1 and 0.5% by mass (Witty and Knox 1964; Jones and Beavers 1964; Wilding and Drees 1968; Norgren 1973; Miles and Singleton 1975). The ponderosa pine–bunchgrass type in northern Arizona, which (despite differences in species composition) is the closest investigated modern phytolith analog for the postulated prehistoric Jeffrey pine–bunchgrass type in the SSPM, showed total phytolith content of 1%–2.5% (Kerns 2001; Kerns et al. 2001, 2003), with grass phytoliths making up approximately half of the total (B. Kerns, USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, personal communication, 2004). SSPM forest soils contain at least an order of magnitude fewer total phytoliths and grass phytoliths than found in ponderosa pine–bunchgrass forest soils and are at the low end of phytolith content commonly found in forest soils without a grass understory (Fig. 3). Although caution is re-

Fig. 3. Mean total phytolith content as a percentage of soil dry mass and mean proportion of grass phytoliths in the phytolith assemblage for surface soils from four sites in the mixed conifer forest in the Sierra San Pedro Mártir, Baja California, Mexico. Error bars are SEs. Bars with different letters are significantly different (Dunnett's T3 multiple comparison test, $p < 0.01$).
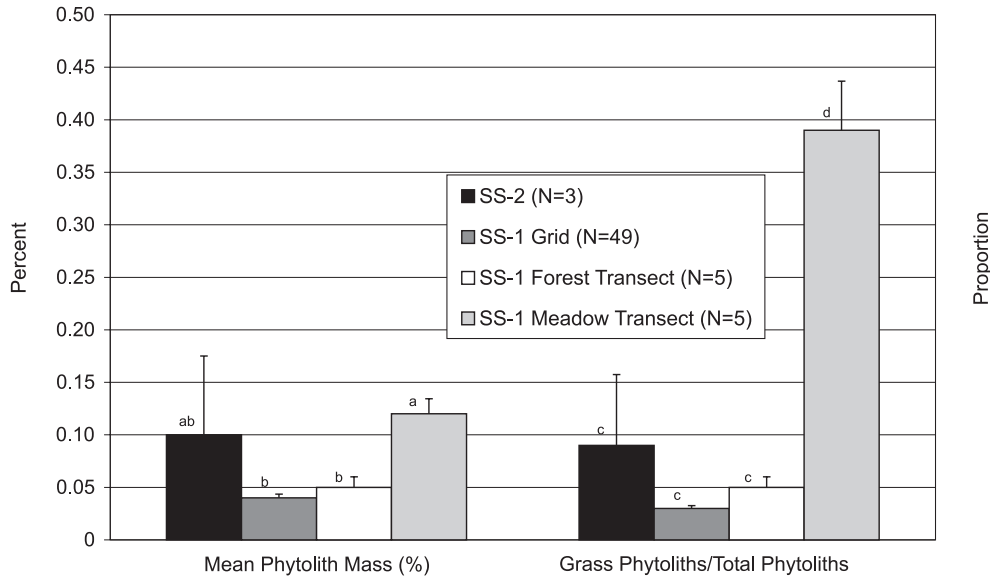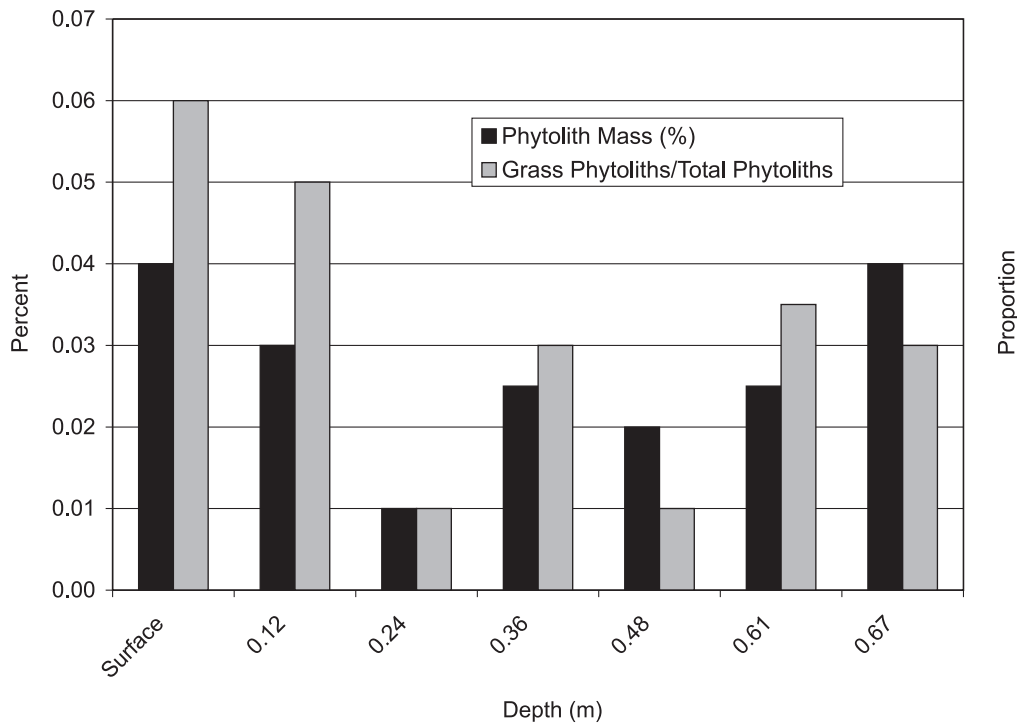

Fig. 4. Total phytolith content as a percentage of soil dry mass and proportion of grass phytoliths in the phytolith assemblage for soils sampled from an exposed profile upslope from an intermittent stream channel, site SS-1 P1 in the Sierra San Pedro Mártir.


quired when comparing phytolith data from different vegetation types in different regions, we interpret the data to indicate long-term sparse phytolith production in both the forest overstory and understory. Grasses or other plants producing significant quantities of phytoliths were probably not present with substantial cover on these sites prior to European contact.

The biomass of the dominant overstory species, Jeffrey pine, contains <0.1% phytoliths by mass. Unlike its close relative, ponderosa pine (reported to produce significant amounts of diagnostic spiny body phytoliths; Kerns 2001), Jeffrey pine sampled in the SSPM has no diagnostic phytoliths, even though Jeffrey pine sampled on volcanic parent material soil in the central Sierra Nevada did contain spiny body phytoliths (R. Evett, unpublished data). Parent material is known to affect phytolith production (Piperno 2006); the

Fig. 5. Total phytolith content as a percentage of soil dry mass and proportion of grass phytoliths in the phytolith assemblage for soils sampled from an exposed profile on the edge of an intermittent stream channel, site SS-1 P2 in the Sierra San Pedro Mártir.
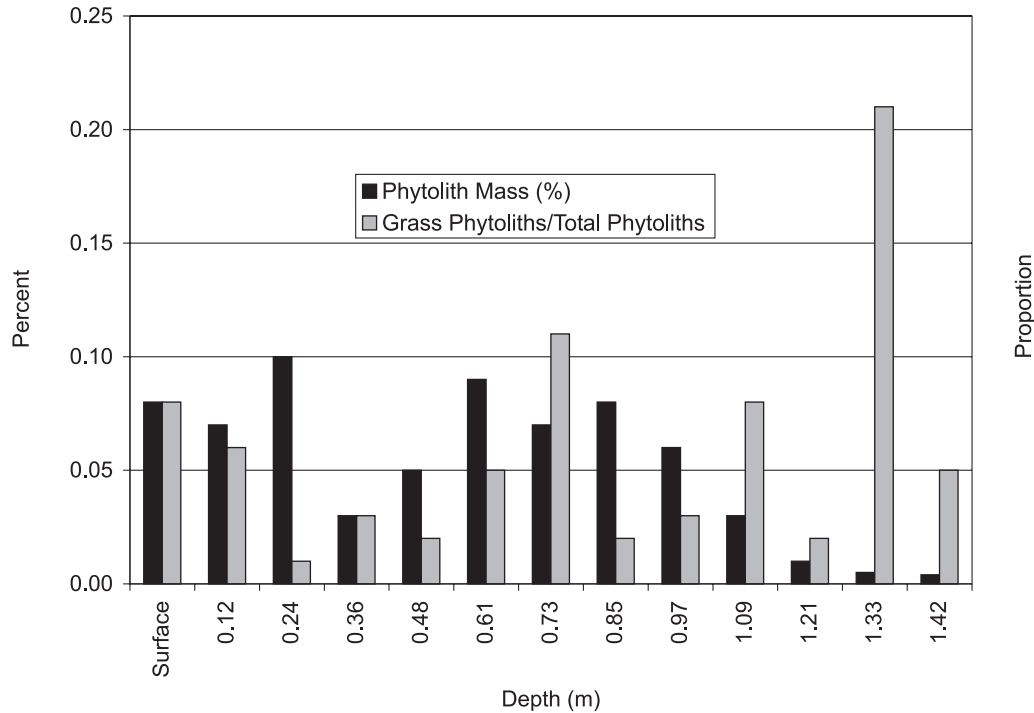
granitic soils prevalent in the SSPM may account for the difference (Norgren 1973). In any case, if substantial grass cover was present in the understory for any meaningful period of time, grasses would contribute 10–50 times more phytoliths per unit of biomass than most other plants, grass phytoliths would build up quickly in the soil, and these phytoliths would dominate the assemblage. The paucity of grass phytoliths in the soil of all sampled sites with substantial tree cover indicates that prior to and following European contact, grasses were very minor components of the forest vegetation.

The phytolith data, while clearly showing there was only sparse grass cover in the understory, do not provide complete answers regarding the nature of the prehistoric forest understory. Currently, there are areas in SSPM forests with substantial shrub cover. Because shrubs sampled for the phytolith reference collection contained very few phytoliths of any kind and none were diagnostic, it was not possible to determine with phytolith evidence whether shrubs were more or less extensive in the past.

Phytolith dissolution and migration

Two alternative explanations for low soil phytolith content must also be considered: phytolith dissolution and phytolith migration. Phytoliths are known to dissolve when soils are very basic, with pH approaching 8, but are well preserved in all but the most acidic soils (Piperno 2006). SSPM diorite-derived soils are moderately acidic, with mean pH 5.3 (Stephens and Gill 2005) and no visible evidence of alkaline conditions at any site or within any sampled profile. Because most diagnostic grass phytoliths are solid pieces of silica, they are not quickly dissolved except under extreme conditions (Bartoli and Wilding 1980).

Most phytoliths extracted from the soil surface and 5 cm depth plots were well preserved; a small percentage showed evidence of corrosion, probably older, weathered phytoliths remaining in the surface layers through soil mixing processes. Phytolith preservation in sampled soil profiles deteriorated with depth, but most phytoliths were clearly identifiable even at the base of the profiles. SS-1 profile 2 showed a decline in phytolith content near the base of the profile, probably the result of weathering and gradual dissolution of phytoliths in older sediments. All evidence suggests rapid phytolith dissolution is unlikely in the SSPM.

Because they are mostly silt-sized particles, phytoliths can migrate downward in the soil profile (Starna and Kane 1983), particularly in the sandy loam soils common in SSPM forests. Recent experimental work with phytoliths in sandy sediments suggests the percolation rate can approach 0.30 cm/year (Fishkis et al. 2004). This process is counterbalanced by soil mixing through bioturbation (Grave and Kealhofer 1999), which can return phytoliths to the soil surface (Alexandre et al. 1999). If phytolith migration is a problem in SSPM forests, there should be evidence in the distribution of phytoliths in the soil profile data. If percolation were a dominant process (Grave and Kealhofer 1999), phytoliths would be sorted by size, with larger phytoliths present higher in the profile. Conversely, phytoliths evenly distributed throughout the profile may be an indication of bioturbation. There is no evidence of phytolith percolation in any of the four soil profiles sampled (Figs. 4–7). The largely colluvial soils in SS-1 profiles 1 and 2 show relatively even distribution of total phytoliths and grass phytoliths throughout the profiles; there are no peaks in phytolith content with depth indicative of zones of phytolith deposition (Figs. 4 and 5). Grass short cells, the smallest phytoliths counted, do not increase with depth. The relatively even dis-

Fig. 6. Total phytolith content as a percentage of soil dry mass and proportion of grass phytoliths in the phytolith assemblage for soils sampled from an exposed profile in a dry meadow, site LRM in the Sierra San Pedro Mártir.
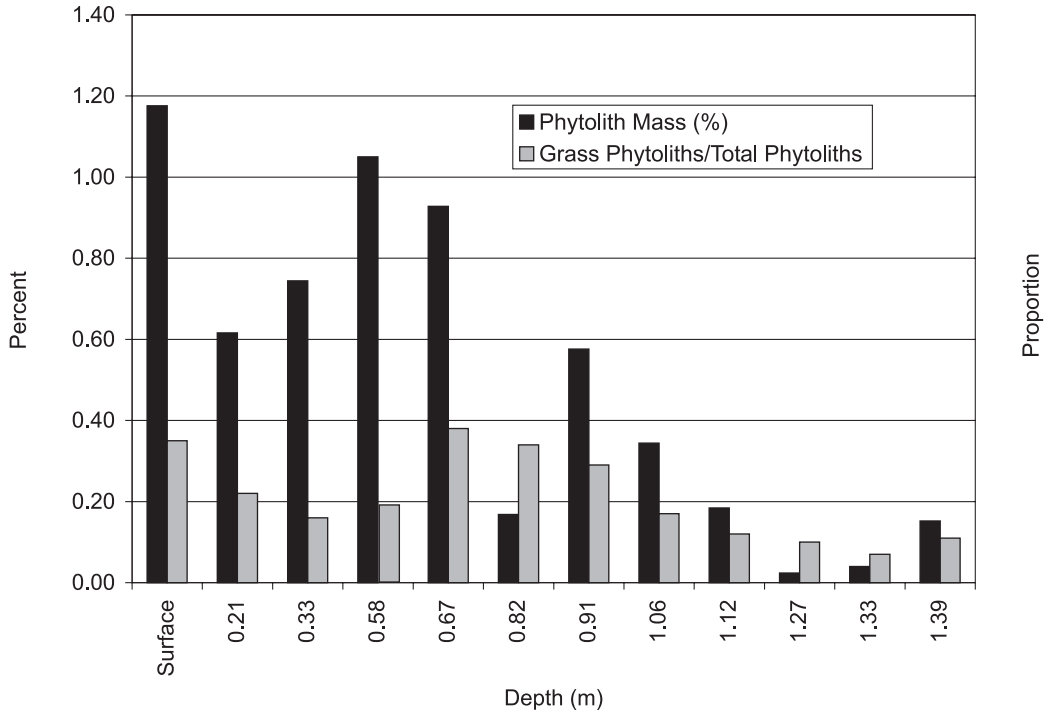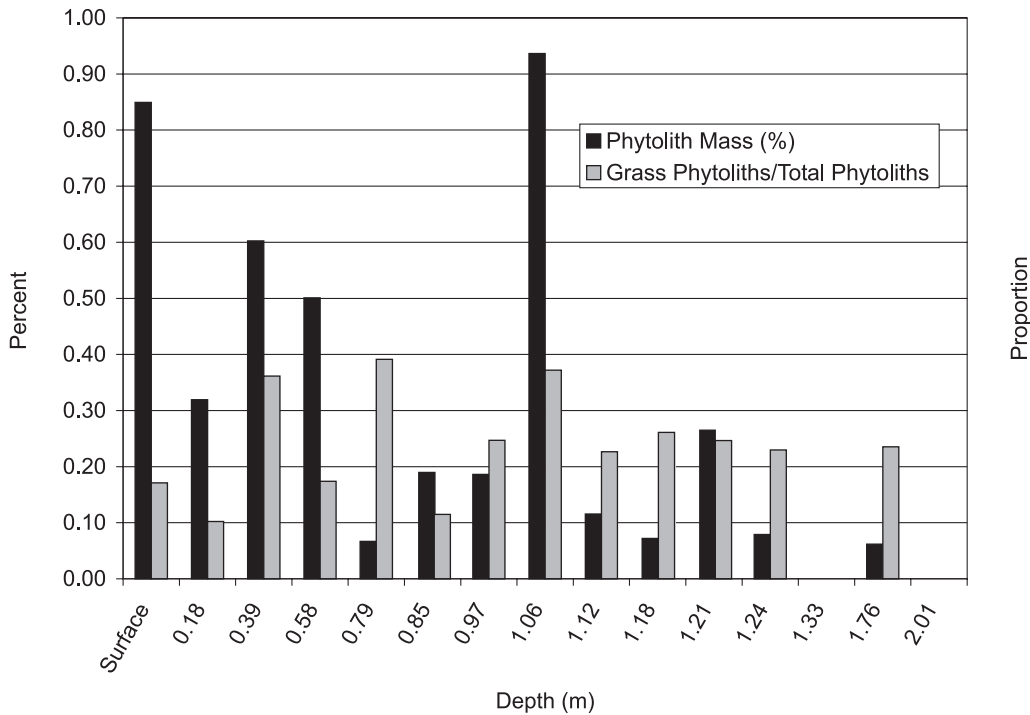

Fig. 7. Total phytolith content as a percentage of soil dry mass and proportion of grass phytoliths in the phytolith assemblage for soils sampled from an exposed profile in moist colluvium, site LRC in the Sierra San Pedro Mártir.

tribution of soil phytoliths suggests bioturbation is an important process in these soils. An alternative explanation is that there was steady deposition in the soil of phytoliths from a stable vegetation type that did not change much over time. There is no indication that soil processes removed phytolith evidence for a prehistoric grass understory from sampled sites.

The LRM and LRC profiles have strata with much more variable phytolith contents (Figs. 6 and 7). The strata were probably deposited under alternating alluvial and colluvial

periods of varying length, so this variability is expected even if the phytolith deposition rate did not change much over time. Grass phytolith content fluctuated from 10% to 40% throughout the profile with no obvious trends. There is no evidence that the strata have broken down over time, which would be expected if soil particle migration was extensive (Grave and Kealhofer 1999).

Phytolith assemblage age

The age of sediments in sampled profiles is unknown, because no radiocarbon dating was attempted. The decrease in phytolith content and increased corrosion of phytoliths with depth suggest that the basal sediments in all sampled profiles are considerably older than 200 years B.P., the postulated time when grasses began disappearing from the forest understory.

To assess the likely age of the soil phytolith assemblage in the SSPM, an understanding of geomorphic processes is required. All of the profile sites have little slope and the sediment source area is limited; rapid aggradation or erosion of sediment is unlikely. However, soils are shallow and poorly developed throughout the sampled area, suggesting there is considerable long-term transport of sediment from upland areas to large meadow deposition areas. Because the slope of most of the soil sampling sites is <5%, with no obvious indication of instability, the most likely process of sediment transport on these sites is soil creep into colluvial hollows. Hollows probably experience episodic downcutting, perhaps following the conjunction of a recent fire and a rare extreme precipitation event, periodically providing large amounts of sediment for transport to alluvial fans in meadows during extreme flood events. This model suggests that upland soils are quite stable and considerable time is required before a phytolith leaves an upland site and is deposited in a meadow. Analysis of a large, stratified downcut in an alluvial fan in La Encantada meadow ($\sim$15 km from the study sites, radiocarbon basal date $\sim$1000 years B.P.) revealed the mean time between large deposition events (from various sources in an area of several square kilometres throughout the watershed, where slopes are commonly much greater than 5%) was approximately 50 years (R. Evett, unpublished data). Most pieces of radiocarbon-dated charcoal in La Encantada sediments were at least several hundred years older than the time since deposition in the meadow, indicating a long time lag between an upland fire event and meadow deposition.

Fredlund and Tieszen (1994) proposed a model of inheritance and dispersal to understand the composition of a soil phytolith assemblage. Inheritance is the process where the phytolith assemblage of a relatively stable site with slow phytolith dissolution rate builds up gradually over time as phytoliths from the long-term average vegetation are incorporated into the soil. Five dispersal processes (gravity, eolian, fire, herbivory, and fluvial–colluvial) act to translocate phytoliths to and from a site. In SSPM forests, the highly local gravity (decay-in-place) process probably dominates, with colluvial or fluvial processes providing modest phytolith translocation and smaller contributions from extralocal fire and eolian processes. The effect of the frequent surface fire regime on phytolith dispersal is difficult to quantify, but is probably not substantial. Phytoliths on the soil surface

may be entrained in the atmosphere during low-intensity fire events, but in the absence of high winds, settle within (at most) a few kilometres of their origin, leading to a relatively minor overall effect of soil phytolith assemblage homogenization but little loss of phytoliths from the ecosystem. Soil phytolith concentration remained high in the ponderosa pine – bunchgrass type in northern Arizona, another ecosystem with prehistorically frequent surface fires, supporting this interpretation (Kerns et al. 2001, 2003).

In conclusion, for an upland site with <5% slope, the evidence indicates the soil contains at least several hundred years (probably considerably longer) of phytolith accumulation and that most phytoliths were deposited in the soil by vegetation growing on the site.

Moisture availability

The soil phytolith data suggest a moisture availability hypothesis to explain the lack of substantial grass cover in the SSPM forest understory. There appears to be a correlation between moisture availability and total phytolith and grass phytolith content in the soil (Fig. 8). When arrayed on a moist to dry summer moisture availability gradient, the most mesic sites (LRM and LRC), which currently have the highest cover of grasses and forbs, also have the highest phytolith contents. The driest sites, in the forest understory of SS-1, have the lowest. SS-1 profile 2, nearer to moisture in the intermittent stream channel, has more phytolith content than SS-1 profile 1, which is located nearby but at a few metres higher elevation. The SS-2 site, although appearing equally as dry as SS-1, has slightly finer textured soil that probably retains more moisture, which may explain why there are currently more grasses and the soil phytolith content is somewhat higher.

The granitic, sandy forest soils in the SSPM have excessive drainage with extreme water deficits (Franco-Vizcaino et al. 2002), apparently not retaining sufficient moisture to support much shallow-rooted perennial plant cover. Because there is less summer precipitation in the SSPM than in the monsoonal region of Arizona and New Mexico (Stephens et al. 2003) where forests with grass understories are common, there may be a summer moisture deficit insurmountable for grasses in the SSPM. In areas where soil moisture is not limited in the SSPM, such as portions of the large meadow at La Grulla, there is abundant graminoid cover.

Recent phytolith research at the South Grove Natural Preserve, a giant sequoia (*Sequoiadendron giganteum* (D. Don) Endl.) grove in Calaveras Big Trees State Park in the central Sierra Nevada in California, another mixed conifer site with minimal grass cover in the Mediterranean climate region where a prehistoric grass understory has been proposed to explain a frequent, low-intensity fire regime (Swetnam et al. 1992), also showed there was no extensive grass cover prior to European settlement (Evett et al. 2006). Although additional phytolith evidence from many other sites in California is required, results from these two studies suggest that grasses may have been less important for fire regimes in the Mediterranean climate region than previously thought.

Fire-history implications

Soil phytolith data from our study sites suggests that grass cover in the forest understory was probably not extensive.

Fig. 8. Total phytolith content as a percentage of soil dry mass and proportion of grass phytoliths in the phytolith assemblage for surface soils sampled in coniferous forests of the Sierra San Pedro Mártir arrayed along a moist to dry summer moisture gradient.
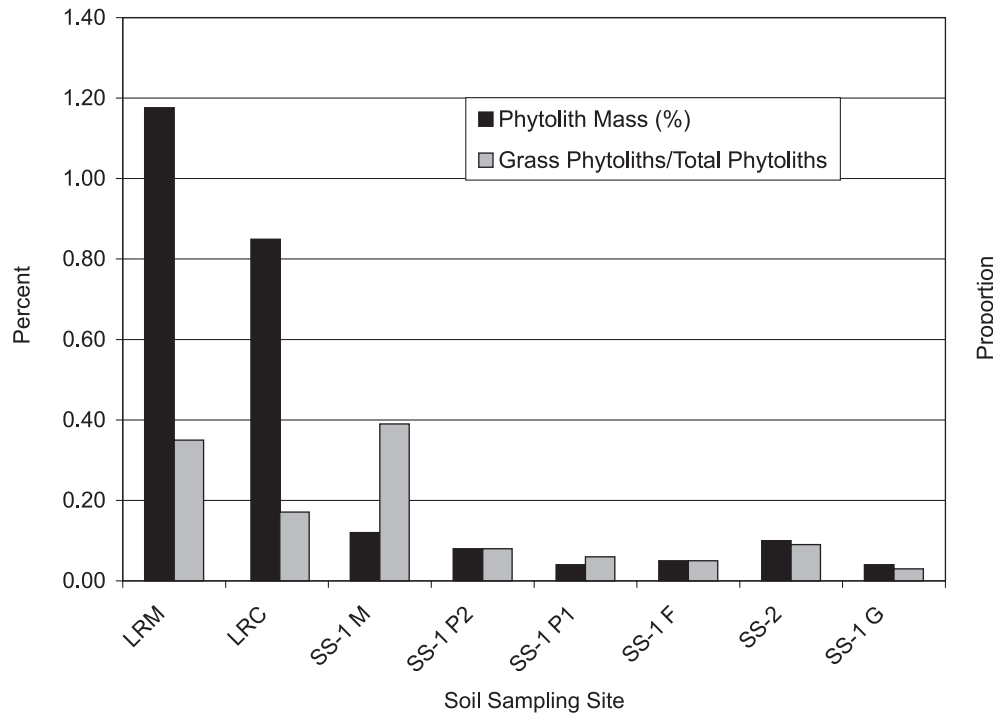
Because so many variables are involved, quantitative assessment of the extent of past grass cover through phytolith analysis is not possible. Grass cover may have been somewhat higher in the past but probably never dominant. From personal observation, it is clear that the currently very sparse grass cover has little effect on the fire regime, but the threshold of grass cover required to substantially affect the fire-return interval through increased fuel continuity is unknown. A simulation model of fire in mixed conifer forests in the Sierra Nevada showed that short fire-return intervals (in the range of prehistoric SSPM intervals) may be possible without grasses or shrubs in the understory (Miller and Urban 2000).

The dramatic changes in the fire regime coinciding with the introduction of livestock in SSPM forests may have been partially due to indirect effects of the presence of livestock, such as trail formation and trampling, rather than direct forage consumption. Livestock trails, which are currently common in some areas of SSPM forests connecting meadows and water sources, are known to disrupt fuel continuity in forests with low-intensity surface fire regimes (Swetnam et al. 2001). Although livestock trails may have limited fire spread and lengthened fire intervals in local areas, most of the forest has few trails; it is unlikely these were a major cause of the 1790–1831 fire hiatus.

Conclusion

The phytolith record indicates that grass has not been a major component of the forest understory in the SSPM for at least the past several hundred years. Phytolith evidence suggests that because there was minimal grass available in SSPM forests, livestock introduced into the SSPM in the late 18th century probably did not drive observed changes in the tree-ring fire-scar record, although there may have

been minor indirect effects. Changes in the fire regime coincident with the introduction of livestock were most likely due to changes in climate and (or) human factors, not overgrazing of grass in the forest understory.

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