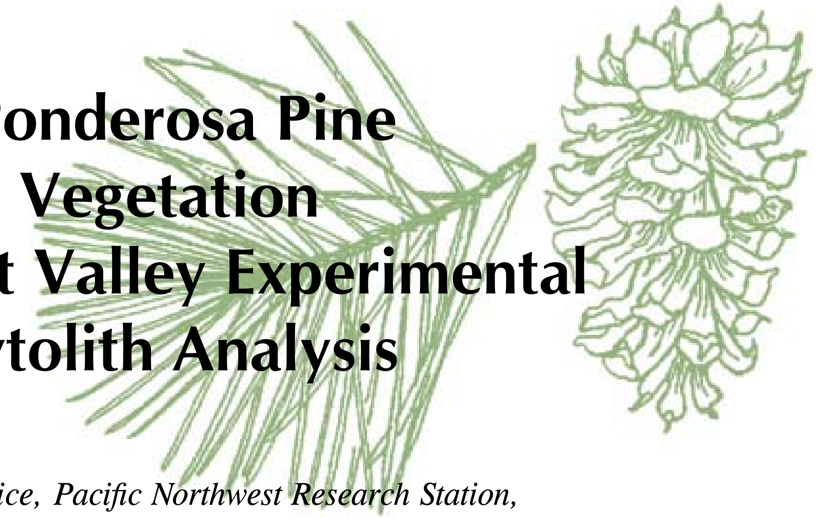

# Understanding Ponderosa Pine Forest-Grassland Vegetation Dynamics at Fort Valley Experimental Forest Using Phytolith Analysis

**Becky K. Kerns,** *U.S. Forest Service, Pacific Northwest Research Station, OR*; **Margaret M. Moore** *and* **Stephen C. Hart,** *School of Forestry, Northern Arizona University, Flagstaff, AZ*

**Abstract—***In the last century, ponderosa pine forests in the Southwest have changed from more open park-like stands of older trees to denser stands of younger, small-diameter trees. Considerable information exists regarding ponderosa pine forest fire history and recent shifts in stand structure and composition, yet quantitative studies investigating understory reference conditions are lacking. We developed and applied an approach using phytoliths to understand forest-grassland vegetation dynamics and historical conditions. Phytoliths are particles of hydrated silica that form in the cells of living plants that are often morphologically distinct. Upon plant death and decay, the stable silica remains in the soil. Soil phytoliths are a useful tool to examine the vegetation history of an area. We created and published a phytolith reference collection, including a previously undescribed diagnostic phytolith for ponderosa pine, examined relationships between contemporary vegetation and surface soil phytolith assemblages using a phytolith classification system, and used phytoliths to explore forest-grassland vegetation dynamics. Results indicate that soil phytolith assemblages reflect long-term accumulation of organic matter in soils, and do not mirror contemporary vegetation at the scale of several meters, but rather several kilometers. Our data suggest that in the past, some* $C_4$ *(warm-season) grasses were more widely distributed but less abundant, grasses were more spatially continuous, total grass production was greater, and some species (*Koeleria *sp. and* Bromus *sp.) were more common in the study area. These results provide important information on historical understory conditions useful to ecologists and land managers for developing and implementing strategies promoting desired future conditions in the region.*

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# Introduction

There is considerable evidence that in the southwestern United States, present day ponderosa pine stand structure and composition, accumulation of wildfire fuel, and frequency and severity of wildfire, are historically uncharacteristic (Covington et al. 1997, Covington and Moore 1994, Fule et al. 1997, Savage et al. 1996, Swetnam et al. 1996). Decades of exclusion and suppression of frequent, low intensity surface fires has been implicated as the main cause, although timber harvesting and replanting, historical periods of overgrazing, and climate shifts were also likely important. Substantial information exists regarding forest fire history and recent shifts in tree stand structure and composition, but quantitative studies investigating understory reference conditions are lacking.

Phytolith analysis is a promising tool for understanding vegetation dynamics in these ecosystems. Phytoliths are morphologically distinct particles of hydrated silica that form in the cells of living plants (Figure 1). Upon plant death and decay, many silica phytoliths resist dissolution and remain in the soil for centuries to millennia as evidence of the vegetation history of an area. Because grasses generally produce an order of magnitude more phytoliths than trees, many soils beneath grassland vegetation contain significantly more phytoliths by mass than soils beneath forest vegetation (Jones and Beavers 1964, Norgen 1973, Wilding and Drees 1971). Examination of phytolith concentration in soils can be used to decipher changes in grassland and forest ecotones through time. Analysis of individual phytolith morphology and phytolith assemblages can provide more detailed taxonomic information regarding vegetation change, particularly for species in the grass family (Fredlund and Tieszen 1994, Kerns et al. 2001, Mulholland 1989).

The goal of our work was to provide data regarding phytolith assemblage formation, herbaceous understory reference conditions, and provide additional insights into the vegetation dynamics in a ponderosa pine–bunchgrass community within the Fort Valley Experimental Forest.

# Methods

The study site was located in northern Arizona, U.S.A., within the Fort Valley Experimental Forest, 10 km northwest of Flagstaff. Present-day forest structure is characterized by small patches (0.02-0.29 ha) of larger old-growth ponderosa pine trees in clumps of three or more (White 1985) interspersed with dense thickets of younger, smaller ponderosa pine trees, and relatively open canopy areas (<0.01 ha) with bunchgrasses and other herbaceous plants. Understory species composition is dominated by native bunchgrasses, including *Muhlenbergia montana*, *Festuca arizonica*, *Poa fendleriana*, *Blepharoneuron tricholepis* and *Elymus elymoides* (Kerns et al. 2001). Common forbs include *Cirsium wheeleri*, *Solidago sparsiflora*, and *Lotus wrightii*. The only understory shrub found was *Ceanothus fendleri*.

Fifteen 40-$m^2$ circular plots were established within the three forest canopy types found on the site (5 plots per canopy type): 1) old-growth pine (OG); 2) dense young pine thicket (DYP); and 3) open canopy (OC). Above-ground herbaceous plant biomass was determined by harvesting all plants within a 1.5 m x 0.5 m rectangular subplot. The forest floor layer was then removed from the subplot and two composite mineral soil samples were collected: 0-2 cm depth and 2-7 cm depth. Soils were air-dried and visible organic matter removed prior to passing soil through a 2-mm sieve. Phytoliths were extracted using a modified heavy liquid flotation technique (Pearsall 1986). Phytolith forms were viewed three dimensionally in a medium of Canada Balsam and classified into eight diagnostic types based on a system developed for the local flora (Kerns 2001). Only grass short-cells were considered; because they are fairly equal in size and silicification, they were assumed equally resistant to post-depositional degradation. The only non-graminoid phytolith form described and used in this study was the spiny body diagnostic for ponderosa pine (Figure 1, Kerns 2001). Photographs of diagnostic phytoliths from dry ash plant material were made using a LEO 435VP Scanning Electron Microscope located at the Northern Arizona University Electron Microscope Facility.

Analysis of variance was used to test for differences among the three canopy types in total above-ground herbaceous biomass, graminoid functional group (e.g., $C_3$ and $C_4$ grasses), phytolith morphotypes and phytolith concentration. If differences were significant ($p < 0.10$), pairwise tests were conducted using Tukey's procedure for multiple comparisons. Variables were transformed as appropriate. Non-metric multidimensional scaling was used to assess similarities in species and phytolith composition among the plot canopy types (Minchin 1987). Vector fitting was used to examine relationships between different forest structure variables and vegetation and phytolith assemblages (Kantivilas and Minchin 1989).

# Results and Discussion

## Current Vegetation

Open canopy plots had significantly more herbaceous plant biomass (20.3 ± 2.7 g/$m^2$) compared to OG (5.1 ± 2.4 g/$m^2$) and DYP (2.5 ± 1.2 g/$m^2$). Warm-season grasses ($C_4$) were only found on OC plots; these plots also had significantly more species present compared to plots of other canopy types. The most common grass was *Elymus elymoides*, a $C_3$ species found in all plots. *Festuca arizonica* and *Poa fendleriana* were only found in OG plots. *Ceanothus fendleri*, an important browse species and possible N-fixing plant, was not found on any of the DYP plots. Non-metric multidimensional scaling (NMDS) indicated that species composition corresponds to canopy type. Stand age, light availability, and O horizon thickness were significant vectors associated with the ordination (Kerns et al. 2001). These results suggest that the recently documented increase in tree density, decrease in light availability, and accumulation of forest floor material have probably resulted in loss of understory production and diversity, as well as potentially important functional species.

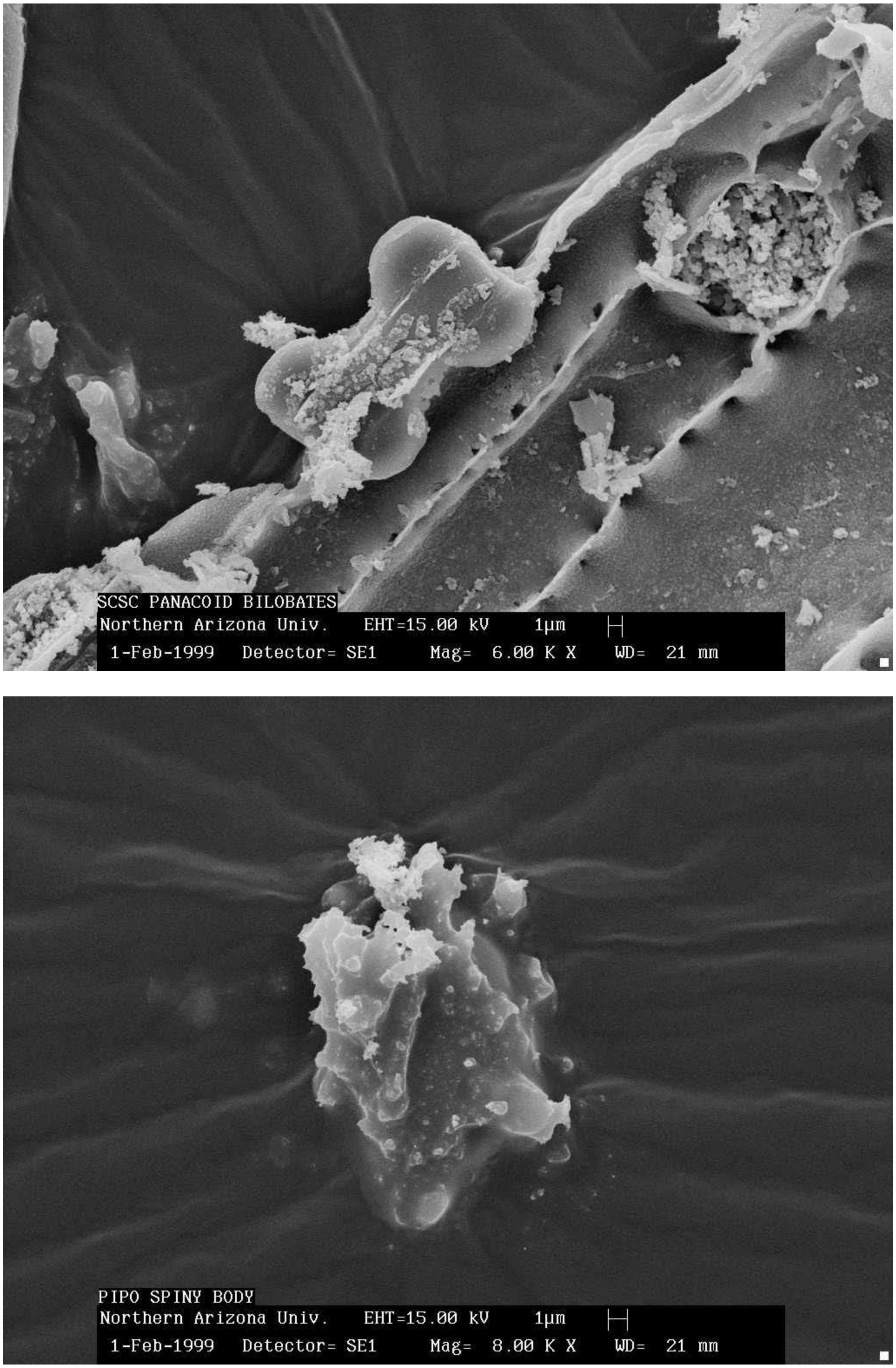

**Figure 1.** Scanning electron microscope photos of two diagnostic phytoliths. Above: panicoid lobate in situ from the grass *Schizachyrium scoparium*. Below: spiny body from *Pinus ponderosa*.

## *Soil Phytolith Assemblages*

We created and published a phytolith reference collection including a previously unknown diagnostic phytolith for ponderosa pine (Kerns 2001). We then used a phytolith classification system to examine relationships between contemporary vegetation and surface soil phytolith assemblages as well as forest-grassland vegetation dynamics (Kerns et al. 2001, 2003). Our results indicated that local or plot-scale vegetation patterns associated with overstory canopy types were only weakly detected. Surface phytolith assemblage ordination revealed some correspondence to contemporary vegetation; however, even on open canopy plots dominated by warm season grasses with few to no trees, the percentage of warm season grass and ponderosa pine type phytoliths were not statistically different from heavily forested plots where warm-season grasses were absent (Kerns et al. 2001). Past research has shown inconsistent results in terms of local *in-situ* phytolith formation (Fredlund and Tieszen 1994, Fisher et al. 1995), possibly due to differing methodologies or factors that influence phytolith assemblage formation. Fire, herbivory and erosion may cause phytolith mixing and assemblage homogenization, leading to the lack of local sensitivity in our phytoliths assemblages. It is also likely that understory species were not spatially stable through time and that many phytoliths have remained preserved in the soil. Our results suggest that phytolith assemblages should be viewed as a long-term average of vegetation composition, not an instantaneous snapshot of vegetation.

Our results also indicated that vegetation composition has shifted through time. Results are summarized in Table 1. Grasses were more spatially continuous in the past (several hundred years ago; Kerns et al. 2001), lending additional support to the idea that grass productivity was greater in the past. In the past some $C_4$ grasses (species in the Chloridoideae, e.g. *Blepharoneuron tricholepis*, *Muhlenbergia* spp.) were more widely distributed but relatively less abundant compared to $C_3$ grasses. Several mechanisms that could explain this shift (e.g. increased temperatures, over grazing and preferential selection of $C_3$ grasses), are reviewed in Kerns et al. (2001). It is important to reiterate that surface phytolith assemblages representing the present are long-term averages of vegetation composition. The assemblages do not reflect a snapshot of the present-day vegetation. Thus the increase in some $C_4$ type phytoliths seen in surface soils could be explained by extensive grazing of domestic ungulates that favored $C_3$ grasses from late 1800's to approximately the mid-1900's. Because tree cover has increased over the past 50 years, it is generally thought that $C_4$ grasses have decreased substantially due to shading.

**Table 1.** Summary of results for relative changes in vegetation in the study area as determined from surface and subsurface soil phytolith assemblages.

| Vegetation | Present[a] | Diagnostic Phytolith Evidence |
|---|---|---|
| Ponderosa pine | Increased | More spiny bodies in surface soils |
| All grasses | Decreased and spatially restricted | Phytolith concentration |
| $C_3$ grasses | Decreased, particularly *Koeleria macrantha* and *Bromus* spp. | More rondels & crenates in subsurface soils |
| $C_4$ grasses (Chloridoideae) | Increased but spatially restricted | More saddles in surface soils |

[a] The present is determined from surface phytolith assemblages which represent long-term averages of vegetation composition and do not represent a snapshot of present-day vegetation.

Another important finding that emerged from our study was that phytolith forms diagnostic of *Koeleria cristata* and native species in the genus *Bromus* (i.e., *Bromus ciliatus* and *Bromus anomalus*) were more abundant in subsurface compared to surface soil horizons. Although these species are presently uncommon in the study area, they may have been more abundant in the past (Table 1).

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