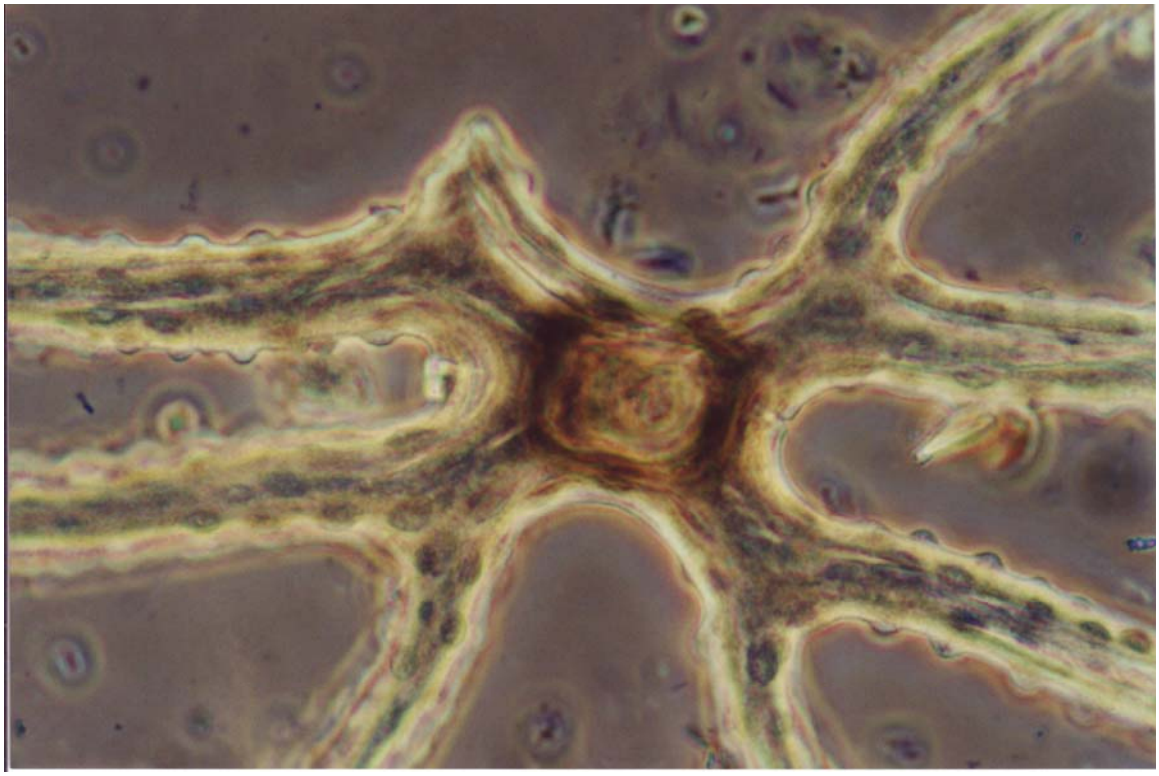
The Ecological History of the City of Rocks National Reserve Part II: The Biological Archive

Prepared by Lesley Argo Morris
Utah State University

May 2008



Stellate dendriform granulate hair phytolith from *Alyssum desertorum*
Photo by Lesley Argo Morris, 2007

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EXECUTIVE SUMMARY

Historical ecology is an emerging and interdisciplinary field that seeks to explain the changes in ecosystems over time through a synthesis of information derived from human records and biological data. The methods in historical ecology cover a wide range of temporal and spatial scales. However, methods for the more recent past (about 200 years) are largely limited to the human archive and dendrochronological evidence which can be subject to human bias, limited in spatial extent or not appropriate for non-forested systems. There is a need to explore new methods by which biological data can be used to understand historic vegetation and disturbance regimes over the recent past especially in arid ecosystem types. Soil phytolith analysis has the potential to provide much needed information regarding historical conditions in both areas. Phytoliths are structures formed in plants through deposition and accumulation of silica within and around cell walls that are released from plants and preserved in sediments long after death and decay of plant material. The City of Rocks National Reserve in southern Idaho was an excellent place to develop new methods in historical ecology because the human records of historic environmental conditions were so rich.

There were two overarching and interconnected objectives for this research. The first was to reconstruct an ecological history of the City of Rocks National Reserve from the period of overland emigration to present. The second objective was to explore the utility of soil phytolith analysis for inferring vegetation and disturbance regime change over the recent past by testing its sensitivity to record known changes. We employed modern analogue studies, a multi-core approach and detailed core analysis to test for known changes through analysis of extraction weights, relative abundance of phytolith assemblages, microscopic charcoal and burned (darkened) phytoliths. Our results showed that this combination of history and soil phytolith analysis can be useful for inferring vegetation changes (e.g. increases in introduced grasses) and disturbances (e.g. fire) in ecological histories.

INTRODUCTION

Historical ecology seeks to explain the changes and the processes that have created current landscapes through a synthesis of information derived from human records and biological data (Russel, 1997). The human archive is the record of historic conditions contained within written, oral and photographic sources. The biological archive is the record of historic conditions contained within the natural environment and is discovered through dendrochronology, packrat middens, palynology, and soil phytolith analysis. The methods in historical ecology cover a wide range of temporal and spatial scales (Egan and Howell, 2001). However, methods for the more recent past (less than 200 years) are largely limited to the human archive and some dendrochronology evidence (Egan and Howell, 2001) which can be subject to human bias, limited in spatial extent and not appropriate in some forest types and non-forested systems (Swetnam et al., 1999).

Phytolith analysis is quickly becoming a popular method for determining historic vegetation (Piperno, 2006). Phytoliths are structures formed in plants through deposition and accumulation of silica within and around cell walls (Rovner, 1971; Fredlund, 2001). These phytoliths are released from plants into the soil through death and decay of plant material (Rovner, 1971). Phytoliths preserve well in terrestrial sediments while pollen grains are more stable in anaerobic lacustrine (lake) sediments (Golyeva, 2001). This is particularly important for arid and semi-arid environments where lacustrine evidence is not as common (Fredlund, 2001). These microfossils can remain stable in sediments from as early as the Eocene (Stromberg, 2004). There is a need to explore new methods by which biological data can be used to determine historic vegetation and disturbance regimes over the past 200 years in arid and non-forested ecosystem types. Soil phytolith analysis has the potential to provide much needed information regarding historical conditions in both areas.

The City of Rocks National Reserve in southern Idaho was an excellent place to explore some unique combinations of the human and biological archive because the human records were rich with information regarding historical environmental conditions and it contained representative ecosystem types of the Great Basin Desert region. In return, an ecological history for the Reserve provides much needed historical information that assists in interpretation, management, planning and preservation of its unique cultural and natural resources. Deliverables from this project to the City of Rocks National Reserve have included a written

summary of the ecological history contained in the human archive (Morris, 2006a), a mapped fire history from 1926 to present (Morris, 2006b), 42 hours of oral history, a digital library of all archival documents used in the study, digital copies of 100 emigrant diaries and recollections from the period of overland emigration, 100 historical photos, a set of over 60 repeated historical photos, and a replica of a Holmes stereoscope with three stereographs of the Reserve taken in 1868. This rich human archive, in turn, allowed for the exploration of new methods using soil phytolith analysis by providing useful information on vegetation that was tested as modern analogues. This report provides the results derived from the biological archive using soil phytolith analysis.

Research Objectives and Questions

There were two overarching and interconnected objectives for this project. The first was to reconstruct an ecological history of the City of Rocks National Reserve from the period of overland emigration to present, approximately the last 200 years. The second objective was to explore the utility of soil phytolith analysis for inferring vegetation and disturbance regime change over the past 200 years by testing its sensitivity to record known changes. These objectives were met by examining the following broad questions:

1) What does the human archive reveal about how the vegetation has changed at the City of Rocks since the period of overland emigration?
2) What are the characteristic phytolith types for dominant Great Basin native and introduced flora?
3) Is the phytolith record useful for investigating historical fire events?
4) Does the stratigraphy of the terrestrial soil phytolith assemblage record changes in vegetation and disturbance regimes over the more recent past?

Research Design and Methodology

This project required two phases of research. The first phase involved gathering information from the human archive by collecting and examining written and oral documentation of historic conditions at the study site. The second phase involved gleaning information from the biological archive through soil phytolith analysis. In this two-phase design, the first step necessarily

informed the second. Results from the human archive provided information about change and disturbance that were then used to develop and test hypotheses about the sensitivity of the soil phytolith stratigraphy to record these events. Therefore, formulation of hypotheses, sampling strategy and sampling location depended heavily upon what was found in the human archive. The first broad question was addressed in Part I: The Human Archive (Morris, 2006a). The following chapters addressed each of the remaining broad questions and are summarized below.

Chapter 1 – Phytoliths: "jewels of the plant world"

Even with the growing popularity and utility of phytolith analysis in historical fields of science, the topic is still fairly new and obscure to most researchers. Therefore, this chapter offers a brief overview of phytolith production, classification and identification, as well as the issues and theories behind phytolith analysis.

Chapter 2 – Phytolith types and type-frequencies in native and introduced species of the sagebrush steppe and pinyon-juniper woodlands of the Great Basin, USA.

This chapter catalogued phytolith morphotypes and production from common native and introduced flora from two primary plant community types in the Great Basin Desert region of the USA – sagebrush steppe and pinyon-juniper woodlands. The reference collection included 143 species over 40 families including 68 introduced and 75 native plants. We examined 96 forbs, 33 grasses, sedges and rushes as well as 14 trees and shrubs. Over 100 of these species have not had their phytolith morphotypes or production described previously. We found that about 51% of the plants produced none or only trace amounts of phytoliths while the remaining 49% were common to abundant producers. All the grass species were abundant producers and our analysis revealed important differences in both morphotype and frequency production between native and introduced grass species as groups. At least half of the forbs were also common phytolith producers and mostly generated the common dicotyledon morphotypes such as silicified epidermal cells and hairs. Our findings showed that several of the morphotypes in native and introduced forbs are unique for the genus and species within the reference collection. Finally, we found very little phytolith production in the woody species and no phytoliths for pinyon (*Pinus monophylla*) or juniper (*Juniperus osteosperma*). Therefore, there was no identifiable phytolith assemblage for pinyon-juniper woodlands in the Great Basin.

Chapter 3 - Can soil phytolith analysis and charcoal be used as indicators of historic fire in the pinyon-juniper and sagebrush steppe ecosystem types of the Great Basin Desert Region, USA?

Soil charcoal and phytolith analysis have been successfully employed in other regions to garner information about fire regimes through the Holocene. The modern analogue study by Morris et al. (in press) showed the potential utility of phytoliths for understanding historic fires at the study site. The purpose of this study was to further explore the utility of soil phytolith analysis in terrestrial soils from the study area. We tested if soil charcoal and burned phytoliths could be found in historic terrestrial sediments in these ecosystem types, quantified how their frequencies varied with distance and depth from a known fire, and assessed if a known historic fire could be detected within the soil stratigraphy. The results illustrated the difficulty of interpreting phytoliths and charcoal in terrestrial sediments after a fire. However, the soils in these ecosystem types seem to be well stratified and contain both burned phytoliths and microscopic charcoal for examination. This research demonstrated that soil charcoal and phytolith analysis could be used to examine questions about historical fires in these two ecosystems of the Great Basin Desert region.

Chapter 4 - Testing soil phytolith analysis as a tool to understand vegetation change in the sagebrush steppe and pinyon-juniper woodlands of the Great Basin Desert region

The objective in this chapter was to examine the utility of soil phytolith analysis to reflect vegetation changes over the period of about 200 years in two common ecosystem types of the Great Basin – sagebrush steppe and pinyon-juniper woodlands. Its sensitivity as a record for the more recent past was tested by sampling in locations where vegetation changes were known to have occurred based on human records. Results from previous human archive research (Morris, 2006a) showed that over the past two centuries, the vegetation has changed in two major ways in the study area. First, there are more woody species including denser sagebrush and increased cover and density of pinyon and juniper as these woodlands have encroached down slope and into the valleys. Second, there has been a marked loss of native grasses and an increase in introduced grasses, particularly cheat grass (*Bromus tectorum)* and crested wheatgrass (*Agropyron desertorum)*. These known changes were used to test the sensitivity of the soil phytolith stratigraphy to record such events. We employed both a multi-core approach and

detailed core analysis to test for these and other known changes through analysis of extraction weights, relative abundance of groups of phytoliths and detailed analysis of phytolith assemblages in the soils at a fine scale (one centimeter depth increments).

This is the first study to examine the use of soil phytoliths in a continuous core sampling method in these ecosystem types. We found that these soils can be stable and well stratified enough to record changes in the vegetation if the sampling is done with care to find sites that have not burned recently, have low slopes, and are outside of cultivated areas. The utility of soil phytolith analysis was tested by looking for known vegetation changes in the soil stratigraphy such as increased cover of woody species like sagebrush and pinyon-juniper woodlands. Our results show that extraction weights will track increases in pinyon-juniper woodland cover and density. Phytolith assemblages in the soil stratigraphy also reflect increasing dominance of invasive grass species like *Bromus tectorum*. Finally, detailed analysis at a fine scale of extraction in one centimeter depth increments revealed shifts in soil phytolith assemblages that suggest connection to known changes in climate, vegetation and land uses from the Little Ice Age to present. Soil phytolith analysis appears to hold promise as a biological proxy for understanding historic and prehistoric environmental conditions and deserves further exploration and research.

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CHAPTER 1 - PHYTOLITHS: "JEWELS OF THE PLANT WORLD"

Introduction

Phytoliths have been called the "jewels of the plant world" (Fredlund, 2001 pp. 335). They were first discovered in living plants during the rise of microscopy in 1835 by a German scientist named Struve (Piperno, 1988). Christian Ehrenberg, another German scientist in the mid 1800s, was the first to recognize that siliceous formations in wind blown dust and soil samples were from plants (Fredlund, 2001). He called these silica bodies "phytolitharia" from the Greek meaning "plant stone" (Piperno, 1988; Fredlund, 2001). The name is fitting because these structures are formed within plants through the deposition and accumulation of silica within, around and between cell walls (Fredlund, 2001). Piperno (1988) divided the history of phytolith research into four periods: discovery and exploration from 1835 to about 1900, a botanical phase from 1900 to 1936, an ecological era with applications in soil science and vegetation history from 1955 to about 1975, and the modern period with new focus upon archaeological research, production, morphology and frequency in sediments.

Now, phytoliths are studied in nearly every major biome and from samples ranging from atmospheric dust to oceanic sediment cores (Fredlund, 2001). They are popular with the historical fields of archeology, palaeoecology, geology, and soil genesis. Even with their growing popularity in historical fields of research, phytoliths remain a relatively obscure topic for most people. Therefore, this chapter offers a brief overview of some of the basics in phytolith analysis that are not covered in the following chapters. More complete reviews on the subject can be found in Piperno (1988, 2006), Pearsall (1989), Rapp and Mulholland (1992), or Fredlund (2001). The following sections will review the production and function of silica in plants, how phytoliths are identified and classified, and the use, issues and underlying theories of phytolith research in vegetation history.

Physiology, Production and Function

The precise mechanisms responsible for silica structures in plants are not well understood (Piperno, 1988). In general, however, phytoliths are produced by the concentration of silicon dioxide (SiO_2) within leaves and other plant tissues (Fredlund, 2001). Dissolved silica in the

form of monosilicic acid ($Si(OH)_4$) is absorbed through the roots and carried through the transpiration stream by the xylem (Piperno, 1988). With the reduction of water during transpiration, the dissolved silica is precipitated and deposited as a weakly hydrated silicon dioxide (SiO_2 with 5-15% H_2O) (Rovner, 1971; Bartoli and Wilding, 1980). The silicon dioxide found in plants is identical to the well known opal gemstone (Rovner, 1971). Therefore, they are also often referred to as "opal phytoliths", "plant opal", "biogenic opal", "opaline silica" or "grass opal" (Rovner, 1971; Piperno, 1988). These small incrustations range in size from 2 to 1000 microns with most believed to range around 20 to 200 microns (Rovner, 1971). They are found mostly within the leaf epidermal tissues, however, they also exist in woody tissues, seeds (Rovner, 1971; Fredlund, 2001) and even in roots (Sangster and Hodson, 1992). The silicon dioxide is deposited in several different ways: 1) by filling in cells forming solid casts, 2) cell linings 3) cell wall replacement, 4) plant hairs, spines and other structures, 5) miscellaneous structures (Rovner, 1971). These different types of silicification are used in identification and classification systems that will be discussed later.

Silica accumulation is variable between species, genus, family and even environmental conditions (Piperno, 1988; Fredlund, 2001). Monocots generally accumulate the most silica and produce the most phytoliths (Rovner, 1971). For comparison, needles from the family Pinaceae contain 0.08 to 1.37 percent silica (Klein and Geis, 1978) while shoots in the grasses contain from 5 to 20 percent silica by dry weight (Kaufman et al., 1985). Some families with high percent by dry weight include: Equisetaceae (horsetail), Poaceae (grasses), Palmae (palm) and Cyperaceae (sedges) (Fredlund, 2001). Piperno (2006) offers a review of known patterns, production, and percent of silica phytoliths generated by plant families. Phytolith production is variable but it is also patterned. Replication of certain shapes and types of phytoliths within family, subfamily and tribe may indicate some genetic control over silicification (Piperno, 1988). However, the proportion of silica in plants can also be influenced by the level of dissolved silica in the soil. Availability of dissolved silica is affected by soil pH, temperature and moisture (Piperno, 1988).

It is also not clearly understood why plants produce phytoliths or accumulate silica in their cells (Rovner, 1971; Kaufman et al., 1985; Massey et al., 2006). The processes can be either active (expending energy to absorb) or passive (no expending of energy) depending upon the taxon of plant (Piperno, 1988). Plants can exclude dissolved silica with cutin and/or suberin on

their root surfaces (Parry and Winslow, 1977). Although silica is recognized as important to the normal development of grass shoots, it is not directly related to metabolism and, therefore, cannot be considered an "essential element" (Kaufman et al., 1985 pp. 487). However, silica accumulation may provide several benefits for the plant including: structural support for withstanding transpiration pressure (Rovner, 1971; Piperno, 1988), resistance to herbivory (Massey et al., 2006) and fungi, increasing incident solar radiation, and possibly temperature regulation (Rovner, 1971; Kaufman et al., 1985).

Extraction, Identification and Classification

In order for phytoliths to be useful for research in vegetation history, there must be some means of both identification and classification. Identification can take place from both the extant plant tissues (*in situ*) and as disaggregated particles in sediments or other materials. Methods for extraction in both instances have been developed and refined over time. Complete descriptions and comparisons of the methods for extraction from plants are provided by Parr et al. (2001a; 2001b) and from soils by Pearsall (1989) and Piperno (2006).

Extraction from live plant tissue can be completed in one of two ways – chemical digestion or dry-ashing (Rovner, 1971; Piperno, 1988). Chemical digestive techniques require the use of strong acids to digest (or dissolve) organic material (Rovner, 1971; Pearsall, 2000). Dry-ashing involves heating plant material in a muffle furnace at temperatures from 400 ˚C to 500 ˚C (Fredlund, 2001). Although the melting of point of silica is high (950 ˚C) (Piperno, 1988), this method is discouraged by some researchers because of its potential to disfigure the silica (Rovner, 1971). However, it is still very commonly and successfully employed (Piperno, 1988; Parr et al., 2001b). A recent development for extraction from live plants, digestion via microwave oven, is reportedly even faster and better than dry-ashing techniques (Parr et al., 2001a).

Extraction of phytoliths from soils (or sediments) is accomplished through variations on several standardized steps: sieving sediments, dispersion of clays, removing organic material, and separating the phytoliths using density fractionation (Piperno, 2006). Some researchers prefer to separate sand, silt and clay sediments for analysis, others prefer to combine them, and most just analyze the silt fraction 5 to 50 µm (Piperno, 2006). There are also variations upon the type of heavy liquid used for floatation (e.g. zinc bromide or sodium polytungstate) but

whichever material is used, the silica is separated from the sediments using a specific gravity of 2.3 g m^{-3}. The phytoliths and extractant are rinsed, dried and stored either dry or in ethyl alcohol (Blinnikov, 2005; Piperno, 2006). The extracted phytoliths are mounted in a fluid to assist with three dimensional viewing (such as Canada Balsam or other oil) with a biological light microscope with magnification from 400x to1000x (Fredlund, 2001; Piperno, 2006). The phytoliths can be documented with photomicroscopy and/or the use of SEM (scanning electron microscopes) (Wilding and Drees, 1971).

Once separated from the plant tissues or sediments, a system of classification is necessary to discuss the observed phytoliths. Mulholland and Rapp Jr. (1992a) describe three approaches used in classifying phytoliths – parataxonomic, botanical and morphological. The following is a summary from their discussion. The parataxonomic approach treats the phytoliths as separate objects to which the Linnean system of binomial naming is applied. Ehrenberg's ground breaking work in the mid 1800s was based upon this type of classification. Parataxonomic classification is acceptable under the International Code of Botanical Nomenclature and is also used in palynology (the study of pollen fossils). This approach is used when identification of the original plant may not be possible. The botanical approach, on the other hand, organizes phytoliths with information regarding their orientation and location within plant tissues. This system is only useful, however, if the phytoliths are observed *in situ* and is not as reliable or informative with disaggregated phytoliths in the sediments. The morphological approach applies a three dimensional descriptive system to phytoliths that are disaggregated from plant tissues. Within the morphological approach there are two methods. One describes and classifies the phytoliths purely upon their geometric characteristics. The other applies both geometric shape and an anatomical component (e.g. hair or hair base) (Mulholland and Rapp Jr., 1992b).

There has been very recent work to standardize the nomenclature among phytolith scientists by a group appointed by the Society for Phytolith Research (Piperno, 2006). Their efforts include formal protocols for describing and naming new types of phytoliths as well as redefining some and conserving other former nicknames (Madella et al., 2005). This new system, referred to as the International Code for Phytolith Nomenclature 1.0 uses three descriptors: shape, texture or ornamentation, and anatomical origin, if known. Former nicknames such as "dumbbell" are now known as bilobates. Some of the conserved names include "rondels", "papillae" and "dendritic" (See Plates in Chapter 2 for examples of these forms) (Madella et al., 2005). The

lack of a formal naming system has made comparison across studies difficult at times unless good photographic evidence is provided (Blinnikov, 2005).

Herbaceous and woody species are now being examined more comprehensively after being ignored for sometime (Bozarth, 1992; Wallis, 2003). Therefore, differentiation between dicotyledons and monocotyledons, woody and herbaceous, grass and forbs, family, genus and even to species is beginning to open new windows for viewing historical vegetation. It has long been recognized that dicotyledons and monocotyledons consistently produce different types of phytoliths (Rovner, 1971; Piperno, 1988; Bozarth, 1992) (See Plates in Chapter 2 for examples). Grasses consistently form a variety of opal phytoliths (Mulholland and Rapp Jr., 1992a) and there are nine phytolith forms found only in dicotyledons (Bozarth, 1992). Relatively few plant taxa provide diagnostic phytoliths (Ollendorf, 1992). Cyperaceae (sedges) can be identified at least to the family level (Ollendorf, 1992). Some researchers have been able to establish diagnostic phytoliths at the genus (Klein and Geis, 1978) and even species level (Kerns, 2001) within the Pinaceae.

Issues, Theory and Use

Palynology had already been well developed by the time researchers began using phytoliths to infer past vegetation (Piperno, 1988; Fredlund, 2001). Rovner (1971) is credited with bringing the utility of phytoliths to the forefront for archaeology and palaeoenvironmental study (Piperno, 1988; Wallis, 2003). Others credit Wilding (1967) for the first use of radiocarbon dating and opening the door to evidence from phytoliths in soils for vegetational history (Fredlund, 2001). Other major contributors have included Twiss (1969) for his pivotal study that paralleled phytoliths analysis with that of palynology (Fredlund, 2001). Indeed, phytolith research shares a great deal in common with palynology although it has advantages and disadvantages in comparison (Fredlund, 2001).

Phytoliths are touted as being particularly useful in paleoecological studies of grasslands because, in contrast to pollen, monocotyledons produce more and systematic forms (Rovner, 1971). Phytoliths preserve better in terrestrial sediments than pollen which persist better in anaerobic lacustrine (lake) sediments (Golyeva, 2001). This is particularly important for arid and semi-arid environments where lacustrine evidence is not as common (Fredlund, 2001). Phytoliths are also durable fossils that have been shown to date back to the late Pleistocene

(Wilding, 1967) and even as early as the Eocene (Stromberg, 2004). Finally, many believe that phytoliths have the potential to provide a more localized record of plant community changes while pollen analysis tends to be regional (Blinnikov et al., 2002). On the other hand, phytolith analysis is also subject to many problems that are unique to this discipline including: classification, deposition and transportation and preservation (Fredlund, 2001).

Classification

As discussed previously, classification of phytoliths can be very complex and problematic. Classification is further confounded by issues of "redundancy" and "multiplicity". While a single type of pollen may be produced by a plant taxon, this is not always the case with phytoliths (Fredlund and Tieszen, 1994). Redundancy occurs when the same phytolith type is produced by many taxa while multiplicity occurs when one plant generates many different types of phytoliths (Rovner, 1971). Redundancy and multiplicity clearly create problems for interpretation of past vegetation. Two methods proposed for dealing with these issues are the "black box" and the "gray box" approaches (Powers, 1992; Fredlund and Tieszen, 1994). Under the black box method, phytoliths are assessed as entire "assemblages" or "suites" rather than attempting to identify the family or species of origin (Powers, 1992). Then, ancient suites can be compared with modern analogs of possible source vegetational assemblages (Powers, 1992). The gray box method is very similar in its emphasis upon vegetational rather than floristic reconstruction (Fredlund and Tieszen, 1994) but it attempts to link phytolith morphotypes to some "element" within its source (e.g. culm, leaf or physiological function) (Powers, 1992). For example, morphotypes from grass leaves have been used as indicators for predicting the distribution of C_3 and C_4 grasses (Twiss, 1992).

Deposition, Release and Transportation

Even beyond the issues with classification, there are questions and problems that arise with understanding the fossil record left behind by deposition of phytoliths into various sediments. Phytoliths are released from plants through death and decay of plant material (Rovner, 1971). Release can come in the form of litter fall as well as death of the organism in total. Therefore, the rate of deposition can vary for a single plant as well as between plants. For example, annually deposited phytoliths from leaves may be more concentrated in the soil record than those

from woody tissues. These variations can lead to overrepresentation, underrepresentation or the complete absence of phytoliths in the fossil record (Piperno, 1988). This is particularly a problem when comparing grasslands and forests. Grasses not only produce more phytoliths but also release more of them annually. As a result, they may be over represented within the soil fossil record (Fredlund, 2001). There are also other factors that influence the deposition rates of phytoliths such as fire and herbivory that can further complicate interpretation.

Transportation of released phytoliths is also a concern for interpretation. In early studies involving phytoliths, many researchers assumed a "decay in place" model of phytolith deposition and ignored issues of "taphonomy" (Fredlund, 2001). Taphonomy is the study of processes that intervene between the death of an organism and its inclusion into the fossil record (Shipman, 1981; Fredlund, 2001). Phytoliths are very small plant fossils that are easily transported by wind erosion, water erosion, fire and herbivory. In grasslands, for example, these processes are believed to horizontally transport 40 to 50% of the plant biomass (Fredlund, 2001). Very recently, researchers have worked to develop a conceptual model of taphonomy of phytoliths using modern analogues in similar soil types to archeological sediments in Tanzania (Albert et al., 2006). They recognized two primary filters that would bias phytolith preservation at two stages of incorporation into the sediments. The first was between death of plant and addition to the soils (e.g. herbivory) and the second was post depositional (e.g. pH of the sediments) (Albert et al., 2006). However, in areas where fire is a primary factor in the ecosystem processes, both of the filters Albert et al. (2006) proposed could be driven largely by this force. More work is needed to understand how fire relates to the taphonomy of phytoliths (Piperno, 2006).

Another issue regarding transportation of phytoliths is their potential for vertical movement within sediments, sometimes referred to as "illuviation" or "translocation" (Piperno, 2006). Given their size, some researchers argue that phytoliths are just as susceptible to vertical movement in the soil profile as silt (Fredlund, 2001). Others argue that concentrations of phytoliths in the A horizons of soils indicates that the vertical movement is nominal (Piperno, 1988). Over the past 40 years, researchers have "made it clear, however, that vertical phytolith movement does not cause unique or distinctive problems in phytolith study" (Piperno, 2006 pp. 111). Phytoliths are known to be concentrated in the A horizons in soils and to decrease dramatically in the B horizons (Jones and Beavers, 1964; Piperno, 2006). Where accumulation was substantial in the lower sediments, the cause was more likely to have been development of

soils on loess (Jones and Beavers, 1964) or soils with a high degree of shrinking and swelling (Hart and Humphreys, 2003). As further evidence, phytolith concentrations are typically used as an "index" for identifying buried A horizons (e.g. Hart and Humphreys, 2003; Piperno, 2006). Furthermore, vertical translocation would arguably cause homogenization across the profile as opposed to distinctive zonations of different assemblages as is observed most frequently (Fredlund et al., 1998). Soil phytoliths can also move up or down in the soil column through bioturbation (e.g. animal burrowing) (Piperno, 2006). In addition, post depositional erosion could remove whole portions of the soil profile and, therefore, truncate the vertical sedimentary record. Both of these issues make chronological understanding of the soil phytolith record important and difficult in terrestrial sediments (Piperno, 2006).

It is also important to understand that phytolith assemblages within soil sediments do not represent discrete "snapshots" in time (Kerns et al., 2001). Rather, the assemblages within the stratigraphy represent the sum of accumulation and losses over time and represent more of a long term average (Kerns et al., 2001). This notion of the incorporation of phytoliths into assemblages over hundreds of years was termed "inheritance" by Fredlund and Tieszen (1994). The inheritance at a site is affected by both the rate of soil accumulation as well as the mean residence time of the phytoliths due to preservation (Fredlund and Tieszen, 1994). Therefore, interpretations of phytolith assemblages must include consideration of deposition and transportation in the inheritance at a site as well as preservation of those phytoliths.

Preservation

Finally, there are issues that arise with phytoliths due to their variable preservation across plant type and environmental conditions. The degree of phytolith preservation is linked to several factors including: 1) soil pH (> pH 9 will lead to rapid dissolution); 2) type of silicification (entire or just cell walls); 3) iron and aluminum absorbed to the surface that protects it; 4) characteristic of the sediment (e.g. slow decomposition rates); and 5) phytolith surface area (Piperno, 2006). For example, the silicified epidermal sheets formed commonly by herbaceous and in leaves of woody taxa are often thin and weakly preserved in comparison to the short cell phytoliths of grasses that almost completely fill in cells (Fredlund, 2001; Piperno, 2006). Again, this has the potential to bias the fossil record with more representation by certain types of plants. However, some researchers have been quite successful in recovering phytoliths thought to be

poorly preserved such as hairs and silicified epidermal sheets from a variety of sediments (e.g. Albert and Weiner, 2000; Blinnikov, 2005). Modern analogs can also help determine the differences in preservation of different phytoliths (Fredlund, 2001). The combination of variable preservation and environment means that this problem may have to be addressed on a site-by site basis (Piperno, 2006).

Counting Procedures and Presentation

The number of phytoliths counted per slide for analysis is a balance between the number needed to carry out either statistical or abundance analysis and a level of practicality (Piperno, 2006). However, typically between 200-250 particle counts per slide are adequate even within studies with highly diverse flora (Piperno, 2006). As with pollen counts, there can be little variation in percentages beyond counts of 200 (Colinvaux et al., 1999). When statistical analysis is applied to the data to create transfer functions, minimum counts of 300-400 particles may be employed (Piperno, 2006). Counting is carried out in a systematic linear fashion on the slide to the predetermined count. Sometimes, additional scans of the slide are carried out to note the presence of rare taxa morphotypes (Piperno, 2006). Conversely, the overrepresented taxa can be tallied to a predetermined amount and then excluded in the remainder of the count (Piperno, 2006).

The results are usually presented in phytolith diagrams that plot the percent of each type in the assemblage against the depth and/or age of the stratigraphy (Piperno, 2006). The percents, in this case, represent a relative abundance of the sum counted and are not an absolute abundance of total particles on the slide. As with palynological results, there are some researchers who apply any number of statistical analyses to the relative abundance counts (e.g. (Kerns et al., 2001; Blinnikov, 2005) and there are just as many who interpret the information based upon knowledge of the site, radiocarbon dating, history, and other information contained in the geologic record (e.g. Blinnikov, 1994; Piperno and Becker, 1996). Radiocarbon dating for phytolith analysis can be accomplished through bulk sediment dates or from the occluded carbon contained within the phytoliths (Wilding, 1967; Iriarte, 2006).

Analysis and Interpretation

While diagnostic forms can be of great use in inferring past vegetation, there need not be an identification of specific taxon for phytolith analysis to be useful (Piperno, 1988; Powers, 1992; Fredlund and Tieszen, 1994; Blinnikov et al., 2002). For example, if the phytolith form is known to be from a woody species as opposed to a grass, this information is useful in identifying past community types (Piperno, 1988). Phytolith researchers have used the differences between the morphotypes of the two growth forms to follow the cyclical changes from arboreal to grass taxa in archeological sediments (Grave and Kealhofer, 1999) and with ratios (or indexes) to compare changes the woody component density to grasslands (e.g. Alexandre *et al*., 1997). Another method involves using overall phytolith assemblages discovered in modern analogue studies of sediments under current vegetation as a way of interpreting phytolith assemblages recovered in historic sediments (e.g. Blinnikov et al., 2002; Delhon et al., 2003). More and more, researchers are discovering the importance of comparing the phytolith record to modern day analogs for better inference to the past (Piperno, 1988; Fredlund and Tieszen, 1994; Fredlund, 2001; Blinnikov et al., 2002).

Also, frequency analysis of morphotypes within extant vegetation are used to help interpret historic phytolith assemblages (Blinnikov, 1994; Kerns et al., 2001; Carnelli et al., 2004). Finally, some have used known production differences between grasses and woody species to test the overall weight of the extracted phytoliths or some count of total grass phytoliths expressed as percent by volume in soils to examine the stability of forests and grasslands (e.g. Witty and Knox, 1964; Miles and Singleton, 1975; Fisher et al., 1987).

Conclusion

Interest in phytoliths and their potential uses in many fields of science has gone through several historical phases and a great deal of development in the past 20 years (Piperno, 1988) (Piperno, 2006). The potential for phytolith analysis in historic vegetation studies has been recognized for some thirty years already. Yet, there is still a great deal of work to be done to better understand all aspects of phytolith research including production, function, identification, classification, transportation, deposition and preservation (Fredlund and Tieszen, 1994). Historically, the emphasis upon phytoliths in grasses and grassland research in its earliest stages created the impression that dicots do not form as many phytoliths or useful diagnostic forms

(Fisher et al., 1995; Piperno, 2006). In fact, quite often the fossil record will hold distinctive forms of phytoliths that cannot be identified because they have not been catalogued yet (Fredlund, 2001). Therefore, the most recent push in this field is in the examination, identification and cataloguing of herbaceous and woody species across a number of plant communities. For example, Wallis (2003) has just recently systematically examined phytoliths in the Australian flora. However, even with its limitations and remaining questions, phytolith analysis has demonstrated its potential in inferring past vegetation across a broad range of environments and time scales. As more research is done with these "jewels of the plant world", perhaps they will exhibit an even greater value than expected.

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CHAPTER 2 - PHYTOLITH TYPES AND TYPE-FREQUENCIES IN NATIVE AND INTRODUCED SPECIES OF THE SAGEBRUSH STEPPE AND PINYON-JUNIPER WOODLANDS OF THE GREAT BASIN, USA

Introduction

Phytolith analysis is an increasingly popular tool for revealing historic vegetation patterns and human uses across the fields of historical ecology, palaeoecology, palaeoethnobotany and archaeology (Meunier and Colin, 2001). Phytoliths are silica casts of plant cells created within living vegetation that can remain in sediments long after the living tissue has decayed (Rovner, 1971). Phytolith analysis is limited by a lack of catalogued phytoliths and a need to relate historic soil phytolith assemblages to modern day analogs (Fredlund, 2001; Piperno, 2006) particularly in North America (Blinnikov, 2005). Researchers often have to assemble a reference collection for an area prior to defining research questions. Previous research in the US has described phytoliths at the community level in ponderosa pine forests (Kerns, 2001) and at the regional level in the Pacific Northwest (Blinnikov, 2005). However, there are no described reference collections from two of the Great Basin region's most dominant community types – sagebrush steppe and pinyon-juniper woodlands. Soil phytolith research in these more arid areas is very important because few lakes are available for sedimentary analysis. Investigations into the potential for soil phytolith analysis to inform historic ecology and palaeoecology are currently underway in the Great Basin (Morris et al., in press).

While some species described in previous studies overlap with the flora of the Great Basin, no one has systematically examined and catalogued phytoliths of this region's forbs and introduced species. Phytolith morphotypes from introduced species may provide a key to interpreting the stratigraphy in the soil because the timeframe of their introduction is known. For instance, phytolith morphotypes common in the invasive cheatgrass (*Bromus tectorum)* were

noted as possible evidence of "the arrival of the Euro-American settlers" (Blinnikov et al., 2002; Blinnikov, 2005). Blinnikov (2005) analyzed and described 38 species (12 trees, 6 shrubs 17 grasses and 3 forbs). Forbs have been particularly overlooked in most cataloguing efforts. Furthermore, most of the regional studies and reports on dicotyledons have focused solely on the leaf material and have not explored the phytolith production in wood (Bozarth, 1992; Kerns, 2001; Blinnikov, 2005). Notable exceptions to this have come from studies involving the Pinaceae family and other coniferous trees (Klein and Geis, 1978; Kerns, 2001). Here we report upon the phytolith production and morphotypes of common Great Basin native and introduced species found in two wide spread ecosystem types – pinyon juniper woodlands and sagebrush-steppe.

Study Area

There are several ways in which the Great Basin boundary can be defined including hydrographically, physiographically, and even culturally (Grayson, 1993). However, since this paper focuses on plant communities, it is most appropriately defined by the floristic boundary (Figure 1). Most of the Great Basin ecosystems are within the rain shadow of the Sierra Nevada Mountains in western Nevada and eastern California which depletes the moisture from Pacific storms (Beatley, 1975). The Great Basin is known as a "cold" desert because the majority of its precipitation comes in the form of winter snow (MacMahon, 1988). Two major ecosystem types within the floristic Great Basin are the sagebrush steppe and pinyon-juniper woodlands.

The sagebrush steppe is the largest of the North American temperate semi-desert types (West, 1983). The ecosystem gets its name from the historically equal dominance of shrubs from the genus *Artemisia* and various species of bunchgrasses (West, 1983). Sagebrush steppe

Figure 1 Map of the western portion of the United States showing the Great Basin Floristic Region.

occurs in areas with precipitation varying from 150-400 mm (Flaschka et al., 1987). Around 60% of this precipitation arrives as snow from winter storms generated in the Pacific Oceans (Miller et al., 1994). European settlement into this portion of the interior western US did not begin until the 1860s (Miller et al., 1994). This period of European settlement introduced livestock grazing, agriculture development and many exotic plant species to the region (Miller et al., 1994).

There are estimates of between 43 and 100 million acres of pinyon-juniper woodland in the southwestern United States (Tueller et al., 1979). Nearly 17.6 million acres of this ecosystem

type occur in the Great Basin alone (West et al., 1998). In general, these woodlands are found in areas with 203-508 mm of annual precipitation (West et al., 1975). The major tree species in the Great Basin pinyon-juniper woodlands are *Pinus monophylla* (single leaf pinyon) and *Juniperus osteosperma* (Utah juniper). The understory species are highly variable across the region and can be found in adjacent forests, shrub steppes or grasslands (West et al., 1975).

Methods

We created a reference collection of 143 plant species representing native and introduced Great Basin flora from southern Idaho and northern Utah. Of the 143 plants, 68 introduced species and 75 native species were processed. We catalogued: 96 forbs, 33 grasses, sedges and rushes, and 14 tree and shrub species. The collection spans 40 families. There were 46 native forbs, 16 native grasses, 2 native rushes, 1 native sedge and 10 native tree and shrub species. There were 50 introduced forbs, 14 introduced grasses and 4 introduced tree species.

Phytoliths from the reference plants were extracted using dry-ashing techniques (Pearsall, 2000; Kerns, 2001). The plant material was divided into leaf, stem and seed/flower portions for analysis unless impractical. All forb and grass material was washed using deionized water and dried overnight. It was then weighed and placed into crucibles for dry-ashing. Forb and grass material was ashed in a muffle furnace at 450° C for 4-5 hours. Woody material from trees and shrubs was separated into leaf (needle), stem and seed/flowering parts. In addition, some tree bark material was examined separately. The stems and bark were washed in a sonic bath for ½ hour, air-dried overnight, weighed, placed in crucibles and then ashed in the muffle furnace for 5-6 hours at 450° C.

Phytolith morphotypes are redundant across many taxa within the Poaceae (Rovner, 1971). Therefore, procedures to identify phytolith types and their type frequencies within grasses are often used (Kerns, 2001; Carnelli et al., 2004; Blinnikov, 2005). These frequencies are usually expressed as a percentage of the total number of phytoliths counted on a slide. Following the methods of Blinnikov (2005) and Kerns (2001) we conducted cell counts of at least 100 morphotypes in the native and introduced grasses. We counted only disarticulated cells that were intact and recognizable with the exception of broken hair bases. We did not include the distal portions of a broken hair. Since the most common morphotypes in our species assemblage were different than either Blinnikov (2005) or Kerns (2001), the morphotypes we included were somewhat different than in either previous study. However, we attempted to use common types and the modified classification system as much as possible for comparison with Blinnikov (2005) because that study has the most species overlap with ours. Finally, our type frequency analysis was conducted on the leaf and culm material only and, in most cases, inflorescences were examined separately. At least one photo for each morphotype counted is included in Plates II and V.

We employed the descriptive index developed by Wallis (2003) to estimate and rank phytolith production among the species in our reference collection. Slides of the material were viewed under 100-400x magnification and rated under the following four categories:

1) Non-producer (NP) – no phytoliths observed in any field of view
2) Trace (T) – a small number of phytoliths observed on the entire slide, with none in most fields
3) Common (C) – a small number of phytoliths observed in the majority of fields
4) Abundant (A) – a large number of phytoliths observed in the majority of fields

We only described the phytoliths in detail here that were from common or abundant producing species (Wallis, 2003). When possible, we described phytolith morphotypes using the International Code for Phytolith Nomenclature (Madella et al., 2005). Identification of plant species in the reference collection was confirmed by the Intermountain Herbarium at Utah State University where the plant specimens and ashed material are housed. Photographs of all the phytolith morphotypes from the complete reference collection may also be viewed on line (Morris, 2008).

Results and Discussion

Out of the 143 species examined in this collection, only 6 had different abundance classes for leaf and stem material. All of these species were trees and shrubs. Of the 137 remaining species, 51% were non-producers or only trace producers of phytoliths, 24% were common and 25% were abundant producers. The production indexes for all species are summarized in Tables I and II.

Dicotyledons are known to produce at least nine morphotypes (Bozarth, 1992). Most of these types were observed in the collection of both native and introduced forbs. They include silicification of the epidermal cells known as polyhedral epidermal (Plate I, o) and jigsaw or anticlinal epidermal (Plate I, p), mesophyll (Plate IV, a), vascular tissues (e.g. tracheids) (Plate III, c), various hairs and hair bases (Bozarth, 1992; Plates I and IV). All of these dicotyledonous morphotypes are considered less useful than other types of phytoliths because they are redundant across taxonomic groups and tend to not preserve well in sediments (Piperno, 2006). However, dicotyledonous species are often neglected and many forbs have not been catalogued (Carnelli et al., 2004). Furthermore, groups of epidermal cells (called silica skeletons) have been extracted

Table I Complete list of all native species examined in this study grouped by family. For Production Index (P.I.), NP = nonproducer, T = trace, C = common, and A = abundant.

Family	Common Name	Scientific Name	P. I.
	Grasses, Rushes and Sedges		
Cyperaceae	Nebraska sedge	*Carex nebrascensis*	A
Equisetaceae	Scouring rush	*Equisetum laevigatum*	A
Juncaceae	Northern rush	*Juncus balticus*	NP
Poaceae	Indian ricegrass	*Achnatherum hymenoides*	A
	Nevada needlegrass	*Achnatherum nevadense*	A
	Saltgrass	*Distichlis stricta*	A
	Rough barnyardgrass	*Echinochloa muricata*	A
	Squirreltail	*Elymus elymoides*	A
	Thickspike wheatgrass	*Elymus lanceolatus*	A
	Idaho fescue	*Festuca idahoensis*	A
	Needle and thread grass	*Hesperostipa comata*	A
	Meadow barley	*Hordeum brachyantherum*	A
	Great Basin wildrye	*Leymus cinereus*	A
	Mat muhly	*Muhlenbergia richardsonis*	A
	Sandberg bluegrass2	*Poa secunda* ssp. *juncifolia*	A
	Sandberg bluegrass	*Poa secunda* ssp. *secunda*	A
	Bluebunch wheatgrass	*Pseudoroegneria spicata*	A
	Sand dropseed	*Sporobolus cryptandrus*	A
	Alkalai sacaton	*Sporobolus airoides*	A
	Forbs		
Amaranthaceae	Prostrate pigweed	*Amaranthus blitoides*	T
Apiaceae	Narrowleaf lomatium	*Lomatium triternatum*	T
Asteraceae	Yarrow	*Achillea millefolium*	C
	Mountain dandelion	*Agoseris glauca*	T
	Pussy toes	*Antennaria microphylla*	NP
	Western mugwort	*Artemisia ludoviciana*	C
	Arrowleaf balsamroot	*Balsamorhiza sagittata*	C
	Dusty maiden	*Chaenactis douglasii*	T
	Spreading fleabane	*Erigeron divergens*	C
	Low Fleabane	*Erigeron pumilus*	C
	Sawtooth gumweed	*Grindelia squarrosa*	C
	Broom snakeweed	*Gutierrezia sarothrae*	T
	Stemless goldenweed	*Haplopappus acaulis*	C
	Annual sunflower	*Helianthus annuus*	C
	Poverty sumpweed	*Iva axillaris*	C
	Marshelder	*Iva xanthifolia*	C
	Hoary aster	*Machaeranthera canescens*	T
	Cockleburr	*Xanthium strumarium*	C
Brassicaceae	Wall flower	*Erysimum asperum*	C

Table I Continued

Family	Common Name	Scientific Name	P.I.
	Forbs Continued		
Boraginaceae	Spotted forget-me-not	*Hackelia patens*	C
	Stoneseed	*Lithospermum ruderale*	C
	Sagebrush bluebell	*Mertensia oblongifolia*	C
Euphorbiaceae	Prostrate spurge	*Chamaesyce maculata*	C
Fabaceae	Beckwith milkvetch	*Astragalus beckwithii*	T
	Wild licorice	*Glycyrrhiza lepidota*	T
	Silver lupine	*Lupinus argenteus*	T
Lilliaceae	Wild onion	*Allium brandegei*	T
	Sego lily	*Calochortus nuttallii*	T
	Death camus	*Zigadenus paniculatus*	NP
Linaceae	Flax	*Linum lewisii*	T
Malvaceae	Gooseberry-leaf mallow	*Sphaeralcea grossulariifolia*	T
Onagraceae	Willowweed	*Epilobium brachycarpum*	NP
Plantaginaceae	Broadleaf plantain	*Plantago major*	T
Polemoniaceae	Carpet phlox	*Phlox hoodii*	C
	Longleaf phlox	*Phlox longifolia*	C
Polygonaceae	Whorled buckwheat	*Eriogonum heracleoides*	T
	Slender buckwheat	*Eriogonum microthecum*	T
	Cushion buckwheat	*Eriogonum ovalifolium*	T
Ranunculaceae	Larkspur	*Delphinium nuttallianum*	C
Rubiaceae	Bedstraw catchweed	*Galium aparine*	C
Santalaceae	Bastard toadflax	*Comandra umbellata* T	
Scrophulariaceae	Desert paintbrush	*Castilleja angustifolia*	C
	Yellow paintbrush	*Castilleja flava*	C
	Blue-eyed Mary	*Collinsia parviflora*	C
	Matroot penstemon	*Penstemon radicosus*	T
Solonaceae	Wright groundcherry	*Physalis longifolia*	C
	Trees/Shrubs		
Asteraceae	Big sagebrush	*Artemisia tridentata*	T/C*
	Rabbit brush	*Chrysothamnus viscidiflorus*	T
Caprifoliaceae	Snowberry	*Symphoricarpos oreophilus*	NP
Cupressaceae	Utah juniper	*Juniperus osteosperma*	NP
Pinaceae	Pinyon pine	*Pinus monophylla*	T
Rosaceae	Mountain mahogany	*Cercocarpus ledifolius*	T
	Chokecherry	*Prunus virginiana*	C/T
	Antelope bitterbrush	*Purshia tridentata*	T/NP
	Wild rose	*Rosa woodsii*	C/NP
Salicaceae	Yellow willow	*Salix lutea*	NP

* Dual abundance classes are expressed as leaf/stem

Table II Complete list of al introduced species examined in this study grouped by family. For Production Index (P.I.), NP = nonproducer, T = trace, C = common, and A = abundant.

Family	Common Name	Scientific Name	P.I.
	Grasses		
Poaceae	Crested wheatgrass	*Agropyron desertorum*	A
	Smooth brome	*Bromus inermis*	A
	Japanese brome	*Bromus japonicus*	A
	Cheatgrass	*Bromus tectorum*	A
	Orchardgrass	*Dactylis glomerata*	A
	Barnyardgrass	*Echinochloa crus-galli*	A
	Quackgrass	*Elytrigia repens*	A
	Timothygrass	*Phleum pratense*	A
	Bulbous bluegrass	*Poa bulbosa*	A
	Kentucky bluegrass	*Poa pratensis*	A
	Bermuda grass	*Cynodon dactylon*	A
	Stinkgrass	*Eragrostis cilianensis*	A
	Feral rye	*Secale cereale*	A
	Green foxtail	*Setaria viridis*	A
	Forbs		
Amaranthaceae	Tumble pigweed	*Amaranthus albus*	T
	Redroot pigweed	*Amaranthus retroflexus*	T
Asteraceae	Russian knapweed	*Acroptilon repens*	T
	Ragweed	*Ambrosia artemisiifolia*	C
	Musk thistle	*Carduus nutans*	T
	Chicory	*Cichorium intybus*	T
	Canada thistle	*Cirsium arvense*	T
	Bull thistle	*Cirsium vulgare*	C
	Prickly lettuce	*Lactuca serriola*	C
	Scotch thistle	*Onopordum acanthium*	T
	Dandelion	*Taraxacum officinale*	T
	Yellow salsify	*Tragopogon dubius*	C
Boraginaceae	Catchweed	*Asperugo procumbens*	C
	Forget-me-not	*Myosotis micrantha*	C
Brassicaceae	Desert Alyssum	*Alyssum desertorum*	A
	Shepard's purse	*Capsella bursa-pastoris*	A
	Hoary cress	*Cardaria draba*	T
	Purple mustard	*Chorispora tenella*	T
	Flixweed tansy mustard	*Descurainia sophia*	C
	Dyers woad	*Isatis tinctoria*	T
	Clasping pepperweed	*Lepidium perfoliatum*	NP
	Tumble mustard	*Sisymbrium altissimum*	T
Chenopodiaceae	Lambsquarter	*Chenopodium album*	NP
	Halogeton	*Halogeton glomeratus*	T

Table II Continued

Family	Common Name	Scientific Name	P.I.
	Forbs Continued		
Chenopodiaceae	Kochia	*Kochia scoparia*	T
	Russian thistle	*Salsola iberica*	NP
Convolvulaceae	Field bindweed	*Convolvulus arvensis*	T
Cucurbitaceae	White bryony	*Bryonia alba*	C
Dipsacaceae	Common teasel	*Dipsacus sylvestris*	NP
Euphorbiaceae	Blue spurge	*Euphorbia myrsinites*	T
Fabaceae	Goats rue	*Galega officinalis*	NP
	Black medic	*Medicago lupulina*	NP
	White sweetclover	*Melilotus albus*	T
	Sweet clover	*Melilotus officinalis*	T
Geraniaceae	Redstem fillaree	*Erodium cicutarium*	T
Lamiaceae	White horehound	*Marrubium vulgare*	NP
	Catnip	*Nepeta cataria*	T
Malvaceae	Common mallow	*Malva neglecta*	T
Oxalidaceae	Yellow woodsorrel	*Oxalis corniculata*	NP
Plantaginaceae	Narrowleaf plantain	*Plantago lanceolata*	NP
Polygonaceae	Prostrate knotweed	*Polygonum aviculare*	NP
	Curly dock	*Rumex crispus*	T
Portulaceae	Common purselane	*Portulaca oleracea*	NP
Ranunculaceae	Bur buttercup	*Ceratocephala testiculata*	C
Scrophulariaceae	Common mullein	*Verbascum thapsus*	T
	Speedwell	*Veronica biloba*	T
Solonaceae	Black henbane	*Hyoscyamus niger*	NP
	Bitter nightshade	*Solanum dulcamara*	T
	Hairy nightshade	*Solanum sarrachoides*	T
Zygophylaceae	Puncturevine	*Tribulus terrestris*	T
	Trees and shrubs		
Eleaegnaceae	Russian olive	*Elaeagnus angustifolia*	NP
Salicaceae	White poplar	*Populus alba*	T/C*
Tamaricaceae	Saltcedar	*Tamarix chinensis*	NP
Ulmaceae	Siberian elm	*Ulmus pumila*	NP/C

* Dual abundance classes expressed as leaf/stem

from modern soil sediments (Blinnikov, 2005) and in some archeological contexts (Albert and Weiner, 2000). We found a number of silica skeletons and hairs that we believe have unique characteristics which may further aid researchers in understanding which taxa these morphotypes represent.

Woody species have received a little more attention than forbs in phytoliths studies. Several studies have examined the common families of trees and shrubs in the Great Basin including the Pinaceae, Cupressaceae, Asteraceae and Rosaceae (Klein and Geis, 1978; Kerns, 2001; Blinnikov, 2005). Bozarth (1992) looked at 20 woody species, however, he only examined their leaves. In these, he found silicified epidermal cells similar to those in herbaceous dicotyledons. Others have looked specifically at the woody stems of several plant families (Scurfield et al., 1974; Kondo et al., 1994; Albert and Weiner, 2001). The Pinaceae, in particular, has received quite a bit of attention in the literature because several species produce unique morphotypes (Klein and Geis, 1978; Kerns, 2001; Blinnikov, 2005). Several of our woody tree and shrub species have not been previously examined and we also looked at the seeds, cones and flowering parts. We did not find a abundant silicification in our woody reference collection. However, many of the trees and shrubs produced calcium oxalate crystals. These calcium phytoliths are less likely to be recovered from natural and archaeological sediments because they are susceptible to dissolution in acids used in extractions (Coil et al., 2003). Therefore, we only describe them briefly for the woody species.

Native Forbs

Of the 46 native forbs, 48% were only trace or non-producers of phytoliths while 52% of them were common producers (Table I). There were no native forbs rated as abundant. The 24

species rated as common producers came from 9 different families: Asteraceae, Boraginaceae, Brassicaceae, Euphorbiaceae, Polemoniaceae, Ranunculaceae, Rubiaceae, Scrophulariaceae and Solonaceae.

Asteraceae

Eleven of the 15 native species of Asteraceae examined were common producers of phytoliths: *Achillea millefolium, Artemisia ludoviciana, Balsamorhiza sagittata, Erigeron divergens, Erigeron pumilus, Grindelia squarrosa, Haplopappus acaulis, Helianthus annuus, Iva axillaris, Iva xanthifolia* and *Xanthium strumarium*. They commonly produced many hairs, polyhedral epidermal sheets and tracheids. All of these species formed segmented hairs that are characteristic of the family (Bozarth, 1992) except *Achillea millefolium* and *Grindelia squarrosa.*

Achillea millefolium is a perennial forb found on both dry and mesic sites (Shaw, 1989). It is an important and resistant forage species for cattle and game species and recovers well on highly disturbed sites (Monsen et al., 2004). *Achillea millefolium* made the majority of its phytoliths in the leaves while the stem was not highly silicified. Leaf phytoliths included acicular psilate unsegmented hairs (Plate I, a) and anticlinal epidermal sheets. We also observed striations on some of these anticlinal epidermal cells (Plate I, b).

Artemisia ludoviciana is an herbaceous aromatic perennial reaching up to 69 cm near riparian areas or in dry and rocky sites in the sagebrush steppe (USDA, 2007). It is considered an important ethnobotanical herb (USDA, 2007). *Artemisia ludoviciana* was reported to produce anticlinal epidermal sheets (Bozarth, 1992) and we observed striations on them as well (Plate I, c). This species also produced tracheids.

Balsamorhiza sagittata is a broadleaf perennial with a woody taproot. It is an important forage species for native grazers like deer and elk as well as cattle and sheep (Monsen et al.,

2004). *Balsamorhiza sagittata* was previously described by Bozarth (1992) and Blinnikov (2005). We observed the same segmented hairs they described and found them mostly present in the leaf and flowering head portions of the plant. They appeared thinly silicified and tended to break and disfigure somewhat during processing (Plate I, i). It also produced many tracheids.

Two species in the *Erigeron* genus were both common producers of phytoliths. They are both low growing biennial herbs that favor moist places and partial shade (USDA, 2007). *Erigeron divergens* and *Erigeron pumilus* both generate very long (over 500 microns) acicular psilate segmented hairs (up to 4 smooth segments) in the leaf and stem (Plate I, d). The flower/seed portion contained several trachiary elements.

Although *Grindelia squarrosa* is a native species, it spreads along roadsides and disturbed areas and is sometimes considered an invasive weed (Young and Clements, 2005). *Grindelia squarrosa* had some very weakly silicified epidermal sheets and some acute acicular psilate unicellular hairs on the leaves (Plate I, f). In addition, we observed some weak silicification around cells in the stem that made half moon to circular shapes (Plate I, e). The seed head produced mostly charcoal but also had some trachiary elements.

Haplopappus acaulis is a perennial herbaceous species (sometimes considered a subshrub) that grows in dry open habitats (USDA, 2007). *Haplopappus acaulis* had some thinly silicified acicular psilate segmented hairs with very rounded or inflated looking segments (Plate I, g). It also made a quite unique bifid hair base with striations along the sides (Plate I, h).

Helianthus annuus is a common sunflower that is widely distributed and can be found on disturbed sites (Shaw, 1989). The leaves and flowering head of *Helianthus annuus* were dominated by short segmented hairs that were heavily darkened by the processing and are covered with granulate processes. The stem produced a few hairs and some tracheids. Bozarth

(1992) reported that this species also produced silicified polyhedral epidermal sheets and irregularly perforated opaque platelets in the achenes. Our flowering head may not have contained any developed seeds because we did not observe this type in our specimen.

Two species within the genus *Iva* were common producers. While *Iva axillaris* is perennial and *Iva xanthifolia* is an annual, both species are considered weedy as they are common along roadsides and disturbed areas (Shaw, 1989). Both *Iva axillaris* and *Iva xanthifolia* are dominated by acicular psilate segmented hairs with and without bases still attached. They also both contained a few weakly silicified epidermal sheets.

Xanthium strumarium is considered to be of "questionable origin" (Shaw, 1989) by some botanists because there is debate over whether it is a native to North America or not. It is now commonly considered a noxious weed because its seedlings are poisonous to livestock and its seeds (cockleburs) infest wool and hair of animals (USDA, 2007). *Xanthium strumarium* leaves formed conical psilate segmented hairs with 3 rounded portions that occurred with and with out bases attached (Plate I, q) and polyhedral epidermal cells. The hairs on the stems were also segmented with 3-4 sections but were longer and had no bases attached. The seed had extremely weakly silicified epidermal portions and some hairs similar to the stem. Bozarth (1992) described silicified polyhedral epidermal cells and regularly perforated opaque cells in this species. He also described the hairs as having a rounded or oval shaped bases and a short apex (Bozarth, 1992).

Boraginaceae

All three native species of Boraginaceae (*Hackelia patens, Lithospermum ruderale* and *Mertensia oblongifolia*) in the collection were common producers of phytoliths. The phytolith production was mostly of unsegmented (or unicellular) hairs. This family only rarely produces

segmented hairs (Bozarth, 1992). The hairs varied in length and ornamentation but were always unicellular and produced round hair bases that often remained attached. *Hackelia patens* produced conical psilate hairs varying in length from 196 to almost 1000 microns with and with bases attached (Plate I, k and l). In *Lithospermum ruderale*, on the other hand, there were long (from 150 to over 700 microns) conical granulated hairs. These species are both common perennial forbs in sagebrush on dry open sites (Shaw, 1989). *Mertensia oblongifolia* was also dominated by conical psilate hairs (from 100 to 500 microns) with and without the hair bases attached. This perennial species is commonly found in sagebrush and pinyon juniper woodlands (Shaw, 1989).

Brassicaceae

There was only one native Brassicaceae, *Erysimum asperum*, in the collection. This species is a perennial forb common on open rocky sites (Shaw, 1989). It was a common producer of phytoliths due to the dominance of fusiform (Plate 1, j) and bifurcated (y-shaped) hairs. These hairs have been described as medifixed and trifixed depending upon how they attach to the leaf surface (Khalik, 2005). This species produced fusiform tuberculate unicellular hairs that attached to the surface of the plant at the center (medifixed) and bifurcated tuberculate unicellular hairs that also attached at the center point (trifixed).

Euphorbiaceae

The only native Euphorbiaceae in the collection, *Chamaesyce maculata*, was also a common producer of phytoliths. This species is common among disturbed sites and is said to be a native but qualified as "probably a native of eastern North America" by Shaw (p. 152, 1989). We did not observe any hairs in *Chamaesyce maculata*. Instead, the common phytoliths were anticlinal

epidermal sheets (some blackened from the processing) as well as long celled polyhedral epidermal sheets and several tracheids.

Polemoniaceae

Both native species of Polemoniaceae in the collection were common phytolith producers. They were also both in the genus *Phlox*. *Phlox hoodii* is a low growing cushion like plant with very sharp tipped leaves found in open dry sites with sagebrush (Shaw, 1989). The tips of the leaves contained highly silicified cells. This species also has what could be characterized as anticlinal papillate epidermal cells. We observed similar phytoliths in *Phlox longifolia*. This herbaceous perennial forb has an upright growth form and occurs on dry open sites. In *Phlox longifolia*, we observed rectangular papillate striate epidermal cells (Plate I, t). They were somewhat similar to the papillae observed in *Bromus* but could be distinguished by the anticlinal cells or the striations from either *Phlox*. We did not observe any similar phytoliths produced in this collection and these may be unique phytolith morphotypes for this genus.

Ranunculaceae

We sampled one native species in this family, *Delphinium nuttallianum*. *Delphinium nuttallianum* is an important forb in both ecosystem types and gains quite a bit of attention since it is poisonous to livestock (Whitson et al., 2000). It was found to be a common producer of epidermal and tracheid phytoliths. The anticlinal epidermal sheets appeared thinly silicified, however, each cell disarticulated individually (Plate I, n). This was quite different from most epidermal silicified sheets that usually only break as smaller and smaller groups of cells. In addition, the charcoal or burned structures of this species created honeycombed shapes that were not entirely opaque.

Rubiaceae

The one native species of Rubiaceae, *Galium aparine*, was also a common producer of phytoliths. Although a native, this annual species is considered an agricultural pest because it creates difficulty in harvesting hay and because its bristly seeds cling to animal fur and clothes (Whitson et al., 2000). This species generated abrupt conical psilate hairs with hair base cells attached (Plate I, s) as well as anticlinal epidermal sheets.

Scrophulariaceae

We examined four native species of Scrophulariaceae but only three were common producers of phytoliths: *Castilleja angustifolia*, *Castilleja flava* and *Collinsia parviflora*. *Castilleja angustifolia* and *Castilleja flava* are semiparasitic perennials of sagebrush (Shaw, 1989). *Castilleja angustifolia* created long acicular granulate segmented hairs (3 sections) with and without bases still attached (Plate I, m). In addition, its polyhedral epidermal sheets were often darkened from the processing into blackened polyhedral epidermal sheets that were very weakly silicified. *Castilleja flava* also made long segmented hairs that were both psilate and granulate. All these hairs were thinly silicified and curled or bent from the heat of processing. This species also produced extremely weakly silicified epidermal sheets with oblong cells. *Collinsia parviflora* is a diminutive annual herb that is most prolific in an early wet spring in the sagebrush steppe (personal observation). It produced long narrow acicular psilate unicellular hairs with out any hair base cells attached and weakly silicified anticlinal epidermal cells.

Solonaceae

One native Solonaceae, *Physalis longifolia*, was examined and found to be a common producer of phytoliths. This plant is also considered a “native weed” (Shaw, 1989) because it is a native of North America but “naturalized” to its current distribution across the US West

(USDA, 2007). It is a striking plant commonly called "Chinese lantern" because the inflated calyx covering the berry looks like a paper lantern. The leaves of this species produced common epidermal or mesophyll structures. The stem contained an interesting suborbicular phytolith of unknown origin that seemed to be thinly silicified (Plate I, r). In addition, the stem created well silicified polyhedral epidermal sheets that were darkened from the processing and had roughened surfaces.

Native Grasses, Rushes and Sedges

All 16 of the native grasses, one scouring rush and one native sedge (95%) were abundant phytolith producers (Table I). *Juncus balticus* was the only rush examined in this collection and it was a non-producer (5%). The results of our type frequency analysis were quite similar for most of the species that were analyzed in previous studies (Table III). Most of the variability can probably be explained by the type of morphotypes counted and the preparation of plant material. Our morphotype descriptions and frequency results for the abundant producers are discussed below.

Achnatherum hymenoides, *Hesperostipa comata* and *Achnatherum nevadense* are all species from the *Stipeae* Tribe within the Poaceae. As such, they form the recognizable bilobate shape with a trapezoidal bottom known as the "stipa type" (Fredlund and Tieszen, 1994). *Achnatherum hymenoides* produced the most of this morphotype (39%) among these dominant native species (Plate II, a-b). *Achnatherum hymenoides* is one of the most common grasses in the arid and semiarid western US where it is highly palatable to livestock and its seeds are an important food source for wildlife (Monsen et al., 2004). It is generally found on drier sites but can occupy more mesic zones as well (Monsen et al., 2004).

Species Name	Saddle	Bilobate	Stipa Type	Plate wavy short	Plate wavy long	Long cell smooth	Long deeply indented	Long cell indented	Plate rectangular	Square-based hair	Round-based hair	Trichome	Oblong knobby hair	Papillae	Pyramidal rondel	Keeled rondel	Horned rondel	Other	Total
Achnatherum hymenoides	0	0	39	1	0	28	1	1	5	1	8	0	0	0	1	1	10	1	136
Achnatherum nevadense	0	0	15	13	1	4	0	0	1	1	1	0	3	1	0	0	0	47	165
Elymus elymoides	0	0	0	6	14	9	17	2	4	1	14	0	0	1	14	6	0	13	112
Elymus lanceolatus	0	0	0	0	0	6	1	6	1	1	2	0	0	0	13	45	24	3	120
Hesperostipa comata	0	0	8	0	0	3	3	1	0	0	5	1	16	2	11	12	32	2	130
Leymus cinereus	0	0	0	0	0	6	18	21	1	0	8	0	15	0	9	17	0	4	156
Poa secunda ssp. juncifolia	0	0	0	2	6	20	6	13	1	6	1	3	0	0	8	7	4	25	109
Poa secunda ssp. secunda	0	0	0	5	1	14	5	9	1	0	11	0	0	15	4	21	0	14	111
Pseudoroegneria spicata	0	0	0	2	15	22	1	11	0	18	4	1	0	0	10	9	0	8	123
Festuca idahoensis	0	0	0	0	50	10	15	3	1	0	0	0	1	0	0	18	3	0	120
Hordeum brachyantherum	0	0	0	0	5	7	33	0	2	0	11	0	2	0	4	31	5	0	132
Distichlis stricta	91	0	0	0	0	0	0	6	1	0	0	0	1	0	0	0	0	0	109
Muhlenbergia richardsonis	37	0	0	0	0	4	5	4	0	0	0	0	0	0	4	4	0	21	112
Sporobolus cryptandrus	84	9	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	118
Sporobolus airoides	12	1	0	0	0	1	0	12	0	0	1	6	0	0	0	14	5	33	138
Echinochloa muricata	0	39	0	10	0	8	5	5	0	0	0	0	0	0	1	0	0	12	117

Table III Percentages of phytolith morphotypes found in common native Great Basin grasses.

Hesperostipa comata generated fewer stipa types (8%) and more of the short cells known as rondels. As with Blinnikov (2005), we found frequencies over 30% for production of horned rondels (32%) by *Hesperostipa comata* (Plate II, f). *Hesperostipa comata* is a widely distributed cool season bunchgrass in the western US that is highly sensitive to overgrazing and is said to be the "first species to disappear from native pastures and range sites" under such conditions (Monsen et al., 2004 p. 418).

The common stipa type form was rather thin in cross sectional view in *Achnatherum nevadense* (Plate II, d) and it produced more thin, weakly lobed pieces (47% other) than true stipa types (15%) (Plate II, e). *Achnatherum nevadense* is found in seven western states in the US in sagebrush and open woodlands (USDA, 2007).

Phytolith morphologies in the *Carex* genus have a wide variation even among the sedge cones that characterize the family Cyperaceae (Ollendorf, 1992). *Carex nebrascensis* produced many of the well known sedge cone morphotypes including rounded psilate and rounded apex with satellites as individuals and in platelets, and angular psilate and pointed apex without satellites in platelets and as individuals (Ollendorf, 1992). Some of the platelets take on a bilobate appearance in top view but are easily distinguished from any grass morphotype by rotation to the cross sectional profile (Plate II, aa). Although not the diagnostic form for this family or genus, this species also produced elongated and rectangular forms similar to *Carex* that were described by Blinnikov (2005). In *Carex nebrascensis*, these elongated rectangular forms have many processes along the longest edge and are irregular at the ends (Plate II, bb). There were also unicellular hairs without bases that are similar to the ones found in the Poaceae.

The morphotypes in *Distichlis stricta* were heavily dominated by saddles (91%) and just a few long indented cells (6%). It did not appear to produce any of the bilobate morphotypes.

Distichlis stricta is a dominant grass species in lower-elevation desert shrub communities where it can form pure stands in saline soils. It is not a preferred forage species for cattle (Monsen et al., 2004). This species is one of the five native C_4 grasses we examined in this collection.

The morphotypes in the genus *Elymus* did not group together. The morphotypes of *Elymus elymoides* were made up of almost equal proportions of long wavy types (14%) (Plate II, g), deeply indented long cells (17%) round hair bases (14%) (e.g. Plate II, c) and other shapes consisting of round bottomed rondels (13%) (Plate II, h). We noted a large number of hairs in our sample, however, since they were broken, only the hair bases were counted. Blinnikov (2005) also remarked upon the high percentage of hairs in this species and believed they may be a good indicator of the species presence in sediments. The waves were very shallow in this species compared to others such as *Festuca idahoensis* (Plate II, n). This loosely caespitose perennial species is often an early successional species on overgrazed and disturbed sites and is a common understory grass in sagebrush steppe (Monsen et al., 2004).

Elymus lanceolatus, on the other hand, was quite distinguishable by its high percentage of rondels including keeled (45%) (Plate II, i), horned (24%) and pyramidal (13%) (Plate II, j). *Elymus lanceolatus* is a cool season perennial bunchgrass that is often regarded as a disturbance tolerant species because it recovers quickly and flourishes in sagebrush and pinyon-juniper woodland communities after fire (Monsen et al., 2004).

Echinochloa muricata was dominated by the bilobate (39%) and cross forms (20%) commonly found in the C_4 grasses. These bilobates are easily distinguished from the native stipa type by their well defined shaft and the difference in their in cross sectional profile (Plate II, u-x). This species, along with the taxonomically very similar *Echinochloa crus-galli*, have been controversial species for the genus (Gould et al., 1972). They are difficult to distinguish and

there are both native and "adventive populations" in North America (Gould et al., 1972). *Echinochloa muricata var. microstachya* is the most common of its genus found in the American West (Gould et al., 1972) and it could either be a native relict or possibly introduced with Europeans where it is found today (Barkworth, 2007; Piep, 2007); personal communications). Today, *Echinochloa muricata* is a widely distributed C_4 grass throughout the lower 48 states and is generally found in wet areas (USDA, 2007).

Equisetum laevigatum was the only species of rush examined in the Equisetaceae family. This species produced the stomata and epidermal cells with granulate surfaces and "elevated projections along the edges" that are considered to diagnostic of the genus (Plate II, cc) (Piperno, 2006). In addition, there were many cylindrical bilobate and polylobate verrucate epidermal morphotypes that were distinguishable from those in the grasses by the verrucate surface (Plate II, dd).

Half of the morphotypes in *Festuca idahoensis* were long wavy plates (50%) (Plate II, n). Although it produced a fair amount of keeled rondels (18%) as well, the long wavy plates appeared to be the most important indicator morphotype for this species in our dataset. Our results differed from Blinnikov's (2005) assessment of morphotypes in this species. He found a much higher frequency of horned rondels and believed they distinguished this species from its codominant in sagebrush steppe, *Pseudoroegnaria spicata*. *Festuca idahoensis* is an important perennial bunchgrass in the both ecosystems, particularly as a forage species for wildlife and livestock. In lower elevations, it can be restricted to more mesic sites (Monsen et al., 2004).

Hordeum brachyantherum was dominated by long deeply indented cells (33%) (Plate II, o) and keeled rondels (31%). This cool season perennial bunchgrass is best adapted to moist sites (USDA, 2007).

Leymus cinereus was dominated by the long deeply indented (18%) and long indented cells (21%) (Plate II, k). We also found it generated a fair amount of oblong knobby hair bases (15%) (Plate II, l) and keeled rondels (17%). Blinnikov (2005) considered *Leymus cinereus* to be difficult to distinguish from other closely related *Agropyron* grasses. This is the largest of the native cool season bunchgrasses. It can be found mixed in with other species, in pure stands and areas that receive runoff water such as roadsides and washes (Monsen et al. 2004).

Muhlenbergia richardsonis also produced mostly saddle morphotypes (37%) and few long cells. Other morphotypes made up 21% of the count. These shapes included cells that looked very similar to those found in *Carex* species (Plate II, aa). In *Muhlenbergia richardsonis* these cells were rounded to sinuous platelets with processes and multiple (usually two) psilate apices (Plate II, s). *Muhlenbergia richardsonis* is a C_4 grass commonly found in wet areas in the western US (USDA, 2007).

There were two *Poa secunda* subspecies examined in this study, *Poa secunda* ssp. *juncifolia* and *Poa secunda* ssp. *secunda*. Both *Poa secunda* are small, densely tufted cool season perennials that are highly resistant to grazing and trampling (Monsen et al., 2004). Both of these species contained a high percentage of long smooth cells (14-22%) (e.g. Plate V, k). Keeled rondels dominated in the subspecies *secunda*. We observed that the rondels in the subspecies *juncifolia* were not well formed and were difficult to identify. Many of them ended up in the category "other" and could have also been included as short wavy types that Blinnikov (2005) found to dominate the *Poa* species in his study. *Poa secunda* ssp. *secunda* "other" shapes also included several irregularly shaped short cells and several (11 total) prickles (Plate II, q). The relatively high percentage of papillae cells (Plate II, r) is probably due to the fact that this sub species was processed as a whole rather than separated into leaf and culm material.

Pseudoroegnaria spicata is one of the most important, productive and palatable grasses in sagebrush and pinyon-juniper communities. It is very sensitive to the overgrazing and has been lost from many sites due to poor grazing management (Monsen et al., 2004). We found *Pseudoroegnaria spicata* generated mostly long wavy plates (15%), long smooth cells (22%) and square based hairs (18%). We observed nearly equal proportions of pyramidal (10%) and keeled (9%) rondels. Our results differed from Blinnikov's (2005) frequencies for this species. He observed more pyramidal rondels and less long wavy and smooth cells. Again, we were counting similar but not exactly the same set of morphotypes in our frequency analysis and this may explain some of the differences.

The morphotypes in *Sporobolus airoides* contained nearly even frequencies of saddles (12%), long indented cells (12%) and pyramidal rondels (14%). The majority of its shapes were considered in the other category (33%). These were bilobates without a long shaft that appeared very square and were thick in cross section (Plate II, t). *Sporobolus airoides* is a C_4 grass that can be found in higher elevations but develops pure stands in lower elevation, moist and alkaline sites (Monsen et al., 2004).

Sporobolus cryptandrus, on the other hand, was dominated by saddle types (84%) (Plate II, y) and produced more typical bilobates (9%) (Plate II, z) and very few rondels at all (2%). This species is a component of many communities, including sagebrush steppe and pinyon-juniper woodlands. This C_4 grass often invades disturbed sites and is grazing tolerant due to low desirability by livestock, late development and a protected root crown (Monsen et al., 2004).

Native Trees and Shrubs

There were 10 native trees and shrubs examined. The plant material was divided into leaves, stem, seed/flowering portion and bark (when available). None of these species were considered abundant producers of phytoliths. None of the bark, seeds, cones or flowering parts examined for these 10 species produced any phytoliths other than calcium phytoliths. In several cases, the leaf and stem material had different abundance classes. The vast majority of the woody species' material (79%) could be considered trace to non-producers of phytoliths. The common producers made up 21% of the material. The only families with common phytolith producing plant material were Asteraceae and Rosaceae. The common producers, *Prunus virginiana* and *Rosa woodsii,* were from leaf material (Table I). There was only one, *Artemisia tridentata*, where stem material could be ranked as common. Most of the native trees and shrubs produced calcium oxalate (CaOx) crystals that we have not seen described previously for these species. Calcium oxalate crystals were not present in any of the *Juniperus* plant material, however, *Pinus monophylla* and *Cercocarpus ledifolius* both produced abundant blocky, prismatic and elongate rectangular styloid forms (Plate III) (Franceschi and Nakata, 2005).

Asteraceae

We examined two shrub species in the Asteraceae and only the stem of *Artemisia tridentata* can be considered a common producer of phytoliths. While the leaf material produced a few blocky shapes as well, the stem of this species created a common small blocky form usually <20 microns in length (Plate III, a). Blinnikov (2005) first described this blocky form in *Artemisia tridentata* and found it was a good indicator of sagebrush steppe in modern soils from the Columbia Basin. *Artemisia tridentata* is the dominant shrub species in the sagebrush steppe ecosystem type.

Rosaceae

Of the four species of native trees and shrubs examined in this family, only two, *Prunus virginiana* (tree) and *Rosa woodsii* (shrub) had material that commonly produced phytoliths. Both of these species are commonly found in the moist sites, canyons and along streams (Shaw, 1989). *Prunus virginiana* leaves produced a silicified anticlinal epidermal cells (Plate III, f) and tracheids (e.g. Plate III, c). In addition, it produced rhombohedral calcium oxalate crystals (Plate III, g-h) that were unique among the species considered in this collection (Franceschi and Nakata, 2005).

Introduced Forbs

Of the 50 introduced forbs, 78% were either non-producers or produced only trace amounts of phytoliths and 22% were common to abundant producers (Table II). The trace producers formed mostly very weak epidermal silica and some tracheids. The only two species rated as abundant were both from the Brassicaceae family. The nine common producers were from five families: Asteraceae, Boraginaceae, Brassicaceae, Cucurbitaceae and Ranunculaceae.

Asteraceae

Acroptilon repens formed what Bozarth (1992) described as honeycomb assemblages from clusters of the mesophyll cells (Plate IV, a), tracheids, and silicified polyhedral epidermal shapes (Plate IV, b). *Acroptilon repens* was first introduced from Turkestan into Canada in the early 1900's in contaminated alfalfa seed (Watson, 1980). By 1985 it was reported in 21 out of the lower 48 states, prevalent in Canada and could be found on every other continent, except Antarctica (Maddox et al., 1985). It is currently found in 27 states in the US excluding some in

the eastern and southern regions of the country (USDA, 2007). It is known to have been collected within the Great Basin state of Idaho as early as 1926 (Rice, 2007).

Cirsium vulgare formed several interesting phytoliths within the leaf and stem while the seed contained mostly blackened hairs. The tips of the leaf contained highly silicified polyhedral epidermal sheets (Plate IV, f) that disarticulated into separate cells (Plate IV, g) rather than only breaking together as smaller and smaller groups. It also produced cylindric psilate phytoliths of unknown origin, some with lanceolate tips. In the Pacific Northwest, *Cirsium vulgare* was first collected in the state of Washington in 1883 and was in Idaho by 1911 (Rice, 2007). It can now be found in all 50 US states (USDA, 2007).

Lactuca serriola formed polyhedral epidermal cells with some processes particularly at the tips of the leaves. The stems produced a number of conical psilate prickles that seemed to be particular to this species in the collection (Plate IV, d). They disarticulated well and had a rounded apex and concave base (Plate IV, e). There were no other phytolith morphotypes like this one in the collection and, therefore, could represent a unique morphotype for this introduced species in the region. *Lactuca serriola* is a native of the Mediterranean and Central Asia and was first collected in North America in Massachusetts in 1863 (Weaver and Downs, 2003). It was in the western state of Montana by 1881 and collected in Idaho by 1897 (Rice, 2007). Its current distribution includes all 49 US states excluding only Alaska (USDA, 2007).

The leaf of the *Tragopogon dubius* was one of the few that contained silicified stomate cells. In addition, the leaves produced rather unique epidermal cells with irregular sinuated processes (Plate IV, j-k), polyhedral epidermal sheets and what appeared to be silicified mesophyll cells. *Tragopogon dubius* was used as food by early European settlers and is believed to have escaped from cultivation (Clements et al., 1999). It is a common weed on roadsides and waste sites

(Whitson et al., 2000). It was collected in Wyoming in 1900 and in Idaho in 1941 (Rice, 2007). It is currently found in 46 US states excluding the South (USDA, 2007).

Boraginaceae

Two species of Boraginaceae were common producers of phytoliths: *Asperugo procumbens* and *Myosotis micrantha*. *Asperugo procumbens* produced conical psilate unicellular hairs that separated easily from the hair bases (Plate IV, o). Some were curved, however, that could be from the heat of the muffle furnace in processing. They also produced tracheids and some weakly silicified anticlinal epidermal cells (Bozarth, 1992). *Asperugo procumbens* was first collected on the ballast grounds of Philadelphia, Pennsylvania in 1877 (Martindale, 1877). In 1878 it was observed on newly constructed wharves in New York Harbor (Brown, 1878) where it also was believed to have been introduced from ballast water (Britton and Hollick, 1885). It was first collected in the western coastal state of Washington in 1897 and found in Idaho by 1938 (Rice, 2007). It is now found in 24 mostly western and northern states in the union (USDA, 2007).

Myosotis micrantha formed long conical granulate hairs with and without bases still attached (Plate IV, l-m). It produced polyhedral as well as anticlinal epidermal cells with very squared edges (Plate IV, n). In the Pacific Northwest, it was first collected in Washington in 1880 and was found in Idaho by 1926 (Rice, 2007). *Myosotis micrantha* is also currently found in 24 northern and western states (USDA, 2007).

Brassicaceae

Two species of Brassicaceae, *Alyssum desertorum* and *Capsella bursa-pastoris*, produced abundant silica phytoliths. *Alyssum desertorum* produced an abundant amount of very large stellate granulate hairs (Morris et al., in press). *Capsella bursa-pastoris* produced an abundant

amount of hairs including some similar to the stellate granulate hairs found in *Alyssum desertorum*. However, the stellate granulate hairs found in *Alyssum desertorum* commonly had more than four arms and most were dendriform (Plate IV, s). *Capsella bursa-pastoris* also generated a number of hairs that have been described as branched hairs, medifixed and simple hairs (Khalik, 2005). The branched hairs rise from a base and split into three or four arms while the medifixed hairs are affixed to the plant in the center, lay flat with the surface of the leaf, and have two (fusiform granulate hair) or three arms (bifurcated granulate hair) (Khalik, 2005). The hairs on both of these species were granulate to tuberculate. All of these hairs were relatively large ranging from 100-500 microns in length.

The fusiform and bifurcated granulate hairs of the *Capsella bursa-pastoris* (Plate IV, p-r) were similar to the native Brassica, *Erysimum asperum*. However, the stellate granulate hairs from both introduced Brassicas were not observed in the native Brassica from this family. This stellate granulate hair could be a unique indicator for these introduced mustards. Furthermore, *Alyssum desertorum* is a more widespread wildland invasive while *Capsella bursa-pastoris* tends to be more metropolitan and agricultural. Therefore, the stellate dendriform granulate hair morphotypes in a wildland setting could be even further indication of the species *Alyssum desertorum*. Finally, care should be used to interpret the usefulness of these morphotypes to indicate the introduced species based upon potential of other *Brassica* species to produce similar hairs and what can be expected in the flora of a particular study area. For example, several species such as *Draba argyraea* and *Draba aurea* generate some stellate like hairs but the plants are usually found in alpine and subalpine areas (Hitchcock et al., 1969). *Draba densifolia*, on the other hand, contains some stellate hairs and can be found in middle elevations (Hitchcock et al., 1969).

There is little known about the introduction and spread of *Alyssum desertorum* (Young and Clements, 2005) except that in the Pacific Northwest it was first collected in Montana 1933 and first collected in Idaho in 1940 (Rice, 2007). Its current distribution spreads across 12 mostly western states (USDA, 2007). *Capsella bursa-pastoris*, however, has a more rich history. There is genetic evidence for multiple introductions into North America. Populations from central California resemble populations from Spain, while populations from the rest of the United States are more similar to those from temperate regions in Europe (Neuffer and Hurka, 1999). The earliest report was from New England in 1663 (Crosby, 2000). It was then reported as a contaminant in agricultural seed in Delaware by 1889 (Mack and Erneberg, 2002). In the northwestern US, it was first collected in 1880 in Oregon and found in Idaho by 1895 (Rice, 2007). It is now found in all 50 states in the union (USDA, 2007).

Cucurbitaceae

Only one species in the Cucurbitaceae was examined in this study. *Bryonia alba* produced acicular psilate segmented hairs with 3-4 sections that were found with and without hair base cells still attached. The hairs appeared to be deformed by the high temperatures during processing (Plate IV, h). This species also generated an interesting charcoal or blackened structure (Plate IV, i). There is genetic evidence for multiple introductions of *Bryonia alba* because of its use as a medicinal and ornamental plant (Novak and Mack, 1995). It is known to have been sold as an ornamental in Massachusetts (1860-1867), New York (1870-1899) and Illinois (1899) (Mack, 1991). It was not collected in the Pacific Northwest until it was found in Montana in 1953; much later than many of the other introduced species (Rice, 2007). However, this invasive herbaceous vine made up for its late introduction with a rapid growth rate that

gained it the moniker, "kudzu of the Pacific Northwest" (Stannard, 2002). Its current distribution now includes the states of Oregon, Washington, Idaho and Utah (USDA, 2007).

Ranunculaceae

Ceratocephala testiculata formed cylindrical granulated hairs (Plate IV, c) with no hair base cells and extremely weakly silicified polyhedron epidermal cells. *Ceratocephala testiculata* was first collected in US near Salt Lake City, Utah in 1932 (Buchanan et al., 1978). It was collected in Oregon in 1935 and in Idaho as early as 1940 (Rice, 2007). It is now found in 14 northern and western states in the union (USDA, 2007).

Introduced Grasses

As would be expected from the literature and from the results of the native grasses, all 14 introduced Poaceae species were abundant phytolith producers (Table II). Many of the introduced grass species produced morphotypes that were not redundant with the native Poaceae in this region. Blinnikov et al. (2002) noted that the appearance of typical *Bromus tectorum* phytoliths near the surface of his sediments could be an indication of the era of European settlement. He also used this widespread invasive species in his study of sagebrush steppe (Blinnikov, 2005). We found similar frequency types for *Bromus tectorum* in our analysis (Table IV). In addition, several of the introduced species to this region are C_4 grasses. The morphotype differences between C_4 and C_3 grasses have been known for some time and used for understanding shifts in dominance of these grasses worldwide (Kaufman et al., 1985; Twiss, 1992; Fredlund and Tieszen, 1994). Northern portions of the Great Basin floristic region which includes the sagebrush steppe, have a relatively low percentage of C_4 grasses (Teeri and Stowe, 1976). In his study of phytoliths in the Pacific Northwest, Blinnikov (2005) noted that the only

Species Name	Bulliform	Saddle	Bilobate	Cross	Stipa type	Plate wavy	Plate wavy long	Long cell smooth	Long deeply indented	Long cell indented	Plate rectangular	Square-based hair	Round-based hair	Trichome	Oblong knobby hair	Quadrilateral (blocky)	Papillae	Pyramdial rondel	Keeled rondel	Horned rondel	Other	Total
Agropyron desertorum	0	0	0	0	0	0	0	0	22	22	0	12	2	0	2	0	0	10	11	1	11	139
Bromus inermis	0	0	0	0	0	0	0	6	1	0	0	1	3	0	0	0	71	2	2	1	14	126
Bromus japonicus	0	0	0	0	0	1	47	26	0	2	1	0	3	2	2	0	0	1	2	0	7	124
Bromus tectorum	0	0	0	0	0	0	18	18	9	1	1	1	19	0	0	0	19	1	2	0	10	136
Dactylis glomerata	0	0	0	0	4	7	45	18	2	2	0	0	0	1	0	0	0	2	5	0	15	130
Echinochloa crus-galli	0	0	59	18	0	11	0	3	0	8	0	0	0	0	0	0	0	2	0	0	0	111
Elytrigia repens	0	0	0	0	0	0	0	7	23	10	3	0	8	4	6	0	0	13	25	0	0	126
Phleum pratense	0	0	0	0	0	0	0	1	26	14	1	0	0	0	0	0	32	3	16	0	7	107
Poa bulbosa	0	0	1	0	0	3	23	34	17	4	2	0	1	4	0	0	0	8	4	0	0	113
Poa pratensis	0	0	0	0	0	1	7	16	13	0	1	0	6	2	0	0	0	2	19	23	8	119
Cynodon dactylon	4	57	10	0	0	0	0	1	6	10	2	0	0	0	0	8	0	1	2	0	1	104
Eragrostis cilianensis	1	41	23	2	0	0	0	0	16	11	0	0	0	2	0	4	0	0	0	0	0	105
Secale cereale	0	0	0	0	0	0	3	11	7	8	4	1	6	1	0	0	0	8	46	5	2	119
Setaria viridis	0	0	50	2	0	0	0	5	15	13	2	2	4	5	0	0	2	1	0	0	0	112

Table IV Percentages of phytolith morphotypes found in common introduced grasses in the Great Basin floristic region.

bilobate morphotypes in his collection were from the stipa-type and the rare occurrence of a C_4 *Aristida longiseta*. Similarly, the sagebrush steppe region in our study is composed mostly of native C_3 grasses. We believe the distinctive C_4 morphotypes and the differences in frequency types of the introduced grasses may be useful indicators of climatic and vegetation changes, historical land uses and as time markers in the soil profile since their timeframe of introduction is known. The results of our frequency analysis are summarized in Table 4 and are discussed below.

Agropyron desertorum contained equal percentages of long indented cells (22%) (Plate V, b) and long deeply indented cells (22%) (Plate V, a). Its rondels were also equally pyramidal as well as keeled (11%). It produced the most square based hairs (12%) (Plate V, e) of the introduced species but only 2% of the oblong knobby hair base form (Plate V, c). The "other" morphotypes (11%) were mostly blocky forms with tuberculate processes (Plate V, d). *Agropyron desertorum* was widely planted in the Great Basin to increase forage production beginning after World War II (West, 1983). It is well adapted to the cold desert sagebrush steppe and can establish well in plantings and in disturbed sites (Monsen et al., 2004).

Three species of introduced *Bromus* were examined in study, *Bromus inermis*, *Bromus japonicus* and *Bromus tectorum*. None of these species produced very many rondels of any kind (0-2%). *Bromus inermis* was processed whole and, therefore, was dominated (71%) by the papillae cells (e.g. Plate V, g) from the inflorescence this genus is known for producing (Blinnikov, 2005). *Bromus inermis* was introduced from Europe and extensively seeded to restore overgrazed rangelands (Monsen et al., 2004). It was recommended and used for planting in Southern Idaho (Hull, 1973). It now occurs throughout North America in 47 states (USDA, 2007).

Bromus japonicus produced mostly long wavy cells (47%) although their waves were shallow and had mostly squared ends (Plate V, f) and long smooth cells (26%) (Plate V, k). *Bromus japonicus* is a weed on rangelands and in hayfields (Whitson et al., 2000). It was first collected in Pacific Northwest in Washington state in 1903 and was collected in Idaho in 1913 (Rice, 2007). It now occurs throughout the lower 48 states (USDA, 2007).

Bromus tectorum phytoliths were made up of long wavy cells with variable ends (Plate V, j), long smooth cells, round based hairs (Plate V, h) and papillae (Plate V, g) in almost equal proportions (18-19%). The papillae percentage was high even though the inflorescences were processed separately. Blinnikov (2005) found very similar production in his study with the exception that he reported a higher percentage of pyramidal rondels. *Bromus tectorum* was first collected in North America in Pennsylvania in 1790 (Vallient et al., 2007) and was found in Provo, Utah in 1894 (Knapp, 1996). It is considered a problem plant in both degraded rangelands and in winter wheat (Morrow and Stahlman, 1984). It is currently distributed throughout all 50 states (USDA, 2007).

Cynodon dactylon stands out from the other introduced (and native) species due to its production of bulliform cells (4%) (Plate V, l) and the predominance of the saddles (57%) (Plate V, m). The bilobate in this C_4 grass was distinguishable because of its well defined shaft in comparison to the native stipa type counterpart. This species is a common crop and turf weed that is believed to be introduced from Africa (Whitson et al., 2000). It was first collected in the state of Washington in 1897 and in Idaho 1937 (Rice, 2007). It is currently found in 41 US states (USDA, 2007).

Dactylis glomerata was recognizable by its high percentage of long wavy plate cells (45%). Although described similarly to those in the *Bromus* and even some native species, they were, in

fact, recognizably different. The long wavy cells in this species had extremely rounded, deeply formed multiple waves (Plate V, p) and were trapezoidal in cross sectional view (Plate V, q). Some were unevenly lobed on both sides. *Dactylis glomerata* was first collected in the Pacific Northwestern state of Washington in 1882 and in Idaho by 1890 (Rice, 2007). Introduced as a hay and pasture grass, multiple varieties have been bred (Monsen et al., 2004). It was highly recommended and useful for planting in southern Idaho (Hull, 1973) and is now distributed in all 50 US states (USDA, 2007).

Echinochloa crus-galli was dominated by bilobate (59%) (Plate V, n) and cross like (18%) morphotypes (Plate V, o). As mentioned above, the identity and nativity of this species has often been confused with *Echinochloa muricata* (Gould et al., 1972). Today, *Echinochloa crus-galli* is considered a common weed of irrigated and cultivated areas (Whitson et al., 2001) and is now found in every state in the US except Alaska (USDA, 2007).

Elytrigia repens generated mostly long deeply indented cells (23%), keeled rondels (25%) and pyramidal rondels (13%). Some of these long deeply indented types had one straight edge. This species is a common crop, pasture and rangeland weed in moist soils (Whitson et al., 2000). It was first collected in the Pacific Northwest state of Washington in 1882 and was in Idaho by 1901 (Rice, 2007). It is now distributed throughout 44 states excluding the South (USDA, 2007).

Eragrostis cilianensis was also recognizable from its production of saddles (41%), bilobates (23%) and bulliform cells (1%). Even though bulliforms were a small percentage in the overall production in *Eragrostis cilianensis* and *Cynodon dactylon*, there were no other cells like them observed in any of the native C_3 grasses in this collection. This C_4 grass species is a common crop weed (Whitson et al., 2000). It was first collected in Pacific Northwest in Montana in 1887

and was collected in Idaho in 1911 (Rice, 2007). It is now widely distributed in every US state except Alaska (USDA, 2007).

Phleum pratense also produced predominantly long deeply indented types (26%), papillae (32%) (Plate V, s) and keeled rondels (16%). We observed that this species was weakly silicified overall with the exception of the rondels and papillae. The long deeply indented types were very thin with squared-off waves that tended to stay together as sheets or break at the squared-off top of the waves together. In addition, this species formed a number of opaque pieces of variable form. The most recognizable of this opaque form was a rounded piece with a hole in the center (Plate V, r). This species was recommended for planting in southern Idaho (Hull, 1973) and was introduced for hay and forage production on ranges with wet sites (Monsen et al., 2004). It now occurs in all 50 US states (USDA, 2007).

Poa bulbosa produced mostly long wavy cells (23%), long smooth cells (34%) and long deeply indented types (17%). There were very few rondels (4-8%). We observed that the long smooth cells in this species were relatively large and long with pitted edges (Plate V, t). *Poa bulbosa* was first collected in the Pacific Northwest state of Oregon in 1901 and was in Idaho by 1928 (Rice, 2007). It was also one of the many species recommended for planting to increase forage in southern Idaho (Hull, 1973). It is now in 42 states in the US (USDA, 2007).

Poa pratensis stood out from the other introduced grasses by it high production of both horned (23%) (Plate V, u) and keeled (19%) rondel types. We noted that the long wavy types in this species had many waves (9-10) with mostly squared ends. As with the other native *Poa* examined in this study, they created quite a few long smooth cells (16%). *Poa pratensis* was one of the earliest (1685) grass species deliberately introduced to the US but it is restricted to wet, cool areas (Monsen et al., 2004). It is extremely tolerant of grazing and can be used as an

indicator of overgrazing (Monsen et al., 2004). The first collection of *Poa pratensis* in the Pacific Northwest was in the state of Washington in 1876. It was first collected in Idaho in 1892 (Rice, 2007). Its current distribution includes all 50 US states (USDA, 2007).

Secale cereale was the highest producer of rondels in this collection including keeled (46%) (Plate V, v), pyramidal (8%) and horned (5%). Otherwise, there was very little difference in phytolith frequency. This species of ryegrass escaped cultivation to become a serious problem for wheat producers and on rangelands (Whitson et al., 2000). In the Pacific Northwest, in what first collected in Washington in 1897 where it is now listed as a state noxious weed (Rice, 2007; USDA, 2007). It was first collected in Idaho in 1941 (Rice, 2007). *Secale cereale* is now widespread through 48 states (USDA, 2007).

Setaria viridis made the highest amount of bilobates (50%) in this collection of introduced grasses. This shape (Plate V, x) and its frequency are enough to distinguish it from the native grasses in this region. This C_4 grass is a common crop weed (Whitson et al., 2000) and is widely distributed in the lower 48 US states (USDA, 2007). It was first collected in the Pacific Northwest in Montana in 1887 and then in Idaho in 1912 (Rice, 2007).

Introduced Trees

We examined four introduced tree species from four families for this study. None of the species produced abundant phytoliths. In several species, the leaf and stem material were different abundance classes and phytoliths were common only in leaf material. Most of the introduced woody species' plant material (60%) classified as trace to non-producers of phytoliths. The common producers made up 40% of the material and it was all from leaves. The only families with common producing leaf material were Salicaceae and Ulmaceae. Most of the

woody introduced species formed calcium oxalate crystals. One species, *Elaeagnus angustifolia*, formed raphid calcium oxalate crystals worth noting (Plate III) (Franceschi and Nakata, 2005).

Salicaceae

The leaves from the introduced tree species in this family, *Populus alba*, contained silicified polyhedral epidermal sheets (Plate III, b) and tracheids (Plate III, c).

Ulmaceae

We examined one species of introduced Ulmaceae, *Ulmus pumila*. The stems were non-producers and only the leaves generated common phytoliths. The leaf contained polyhedral epidermal sheets and abrupt conical psilate hairs with striations on their bases (Plate III, e).

Conclusion

We found many Great Basin native and introduced species that produce common or abundant phytoliths. In addition, our study has revealed that there are many useful phytoliths produced in the under evaluated group of forbs. The most common forb phytoliths we observed were hairs (and hair base cells) and anticlinal/polyhedral epidermal sheets. Although these phytoliths have been considered less useful due to poor preservation, they have been recovered from a variety of modern sediments (Blinnikov, 2005). Also, hairs and hair bases from plants introduced in the last century may be better preserved over this shorter timeframe. Several silicified epidermal cells were unique in comparison to the other plants in this collection. Again, recognition of these unique types could be useful for a number of questions in the realm of historical ecology, palaeoecology as well as palaeoethnobotany and archeology. For example, the conical psilate prickles generated in *Lactuca serriola* could be a useful indicator of recent sediments and disturbance factors in an ecological context. They could also provide information for

ethnobotanical and archeological studies since *Lactuca serriola* was introduced so early to North America and was used by Native Americans (Vestal, 1952). We believe the description of all of these morphotypes will aid the understanding of vegetation change and plant use if they are found in sediments or archeological contexts.

Our analysis of native and introduced grasses showed important differences in both morphotypes and production frequency. We have described here a number of morphotype differences between native and introduced species of grasses that should be useful indicators of more recent soils (approximately 100 years) and as a way to understand historic land use practices such as agricultural development and grazing. Our morphotype findings are consistent with the literature and lend support to the idea of using differences in morphotypes between C_3 and C_4 grasses as an important way to study vegetation change. In addition, our production frequency analysis demonstrated several differences between native and introduced grasses that may be useful in vegetation histories. For example, introduced grasses produce fewer rondels than most of the native grasses. This is especially pronounced when dominance on the landscape and habitat are considered. Many areas that were once occupied by natives like *Elymus lanceolatus* and *Hesperostipa comata* are now susceptible to invasion by the introduced *Bromus tectorum* and *Agropyron desertorum.* Analysis based on frequency types of rondels between these groups of grasses could reflect this type of grassland conversion.

We did not find a great deal of silicification in our collection of woody and tree species. However, the amorphous silica found in several of the tree species deserves more examination in future research using scanning electron images of the silica *in situ* in the wood as has been done by others (Scurfield et al., 1974; Klein and Geis, 1978; Carnelli et al., 2004). There are, of course, several forbs and grasses with identifiable morphotypes that are associated with pinyon-

juniper woodlands. However, we did not identify any unique silica input from the two dominant tree species in this system. Apparently, there is no clear phytolith assemblage for pinyon-juniper woodlands in the Great Basin. Other plant communities also lack a diverse and recognizable phytolith assemblage. Two common US Mojave Desert plant communities, creosote-bursage scrub and Joshua tree woodlands apparently do not generate a characteristic phytolith assemblage (Lawlor, 1995; Piperno, 2006). It may be, therefore, that the lack of phytolith production demonstrated by comparisons of extraction weights between these woodlands and shrub-steppe or grasslands would be a better way to differentiate these plant communities. This type of analysis by phytolith mass has been used to differentiate between forests and prairie vegetation (Kalisz and Boettcher, 1990).

This study represents a first step in cataloguing phytoliths of the thousands of species found in the Great Basin Desert region. Many plants in this collection produce phytoliths and several species have potentially unique forms. While our study focused upon the aerial portions of herbaceous plants, underground portions of these plants should also be examined in future research. It was previously believed that the underground plant portions did not produce many useful phytolith types but some recent work in rhizomes and tubers has shown otherwise (Piperno, 2006). We sampled one bulb from *Calochortus nuttallii* but found no phytoliths. Both the native and introduced Great Basin flora deserve more study and this cataloguing effort should continue.

Plate I. Light micrographs of native forb morphotypes. Some of these images have been altered using a graphics program to enhance their features and size. (a) *Achillea millefolium* acicular psilate unsegmented hair with hair base cells (b) *Achillea millefolium* anticlinal epidermal with striations (c) *Artemisia ludoviciana* anticlinal epidermal cells with striations (d) *Erigeron pumilus* acicular psilate segmented hairs (e) *Grindelia squarrosa* unknown origin (f) *Grindelia squarrosa* acute acicular psilate unicellular hair with base (g) *Haplopappus acaulis* acicular psilate segmented hair (h) *Haplopappus acaulis* bifid striate hair base (i) *Balsamorhiza sagittata* acicular psilate segmented contorted hair (j) *Erysimum asperum* fusiform tuberculate unicellular hair (k) *Hackelia patens* conical psilate unicellular hair (l) *Hackelia patens* conical psilate unicellular hair (m) *Castilleja angustifolia* long acicular granulate segmented hair with base (n) *Delphinium nuttallianum* disarticulated anticlinal epidermal cell (o) *Physalis longifolia* polyhedral epidermal cells (p) *Artemisia ludoviciana* anticlinal epidermal cells (q) *Xanthium strumarium* conical rounded psilate segmented hair with base (r) *Physalis longifolia* suborbicular form of unknown origin (s) *Galium aparine* abrupt conical psilate unicellular hair with base (t) *Phlox longifolia* rectangular papillate striate epidermal cells.

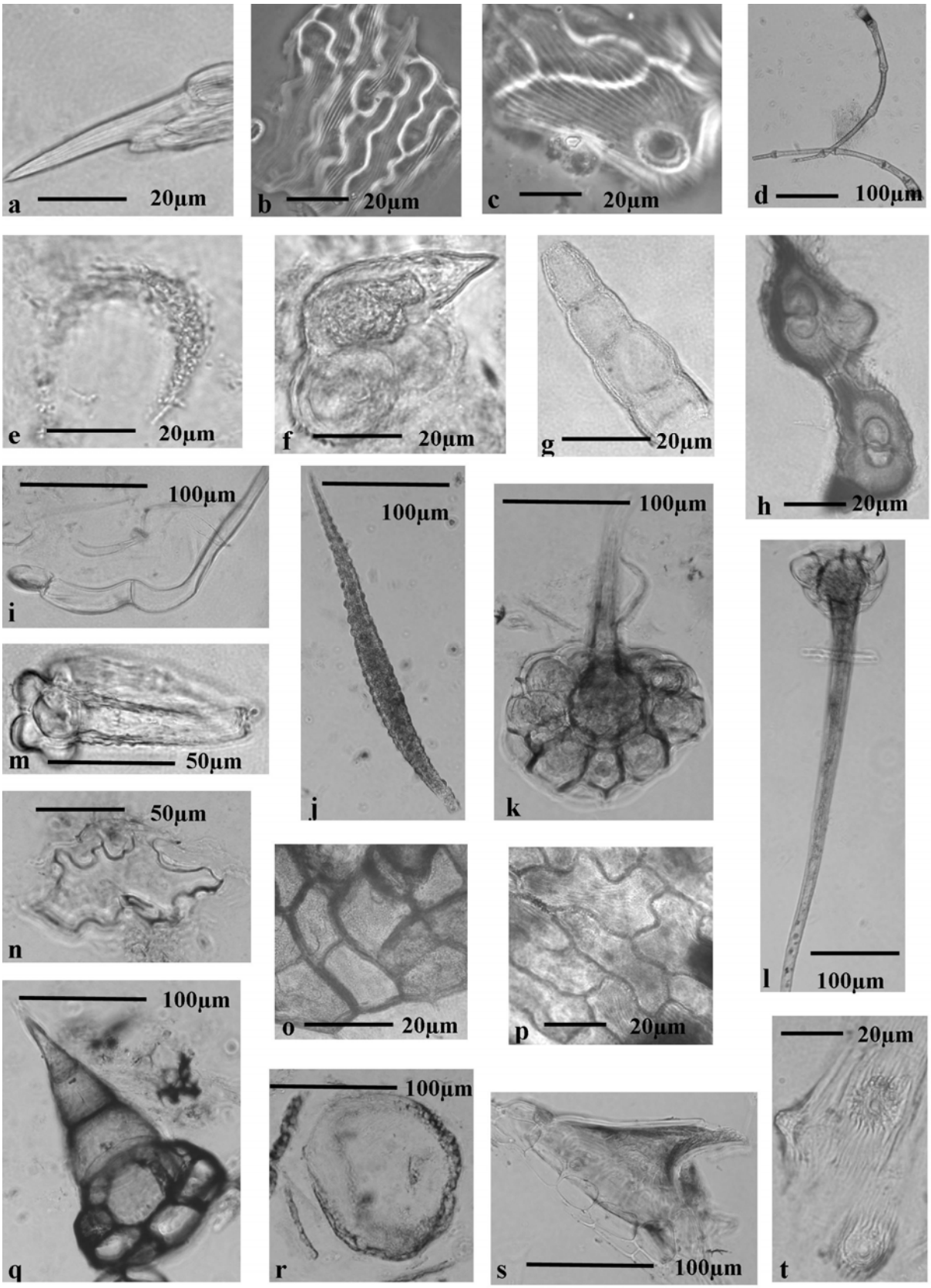
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Plate I

Plate II. Light micrographs of native grass morphotypes. Some of these images have been altered using a graphics program to enhance their features and size. (a) *Achnatherum hymenoides* stipa type in top view (b) *Achnatherum hymenoides* stipa type in cross sectional view (c) *Achnatherum hymenoides* round based hair (d) *Achnatherum nevadense* stipa type in top view (e) *Achnatherum nevadense* thin weakly lobed type in top view (f) *Hesperostipa comata* horned rondel in cross sectional view (g) *Elymus elymoides* long wavy plate (h) *Elymus elymoides* round bottomed rondel (i) *Elymus lanceolatus* keeled rondel (j) *Elymus lanceolatus* pyramidal rondel (k) *Leymus cinereus* long indented (l) *Leymus cinereus* oblong knobby hair (m) *Festuca idahoensis* keeled (n) *Festuca idahoensis* long wavy (o) *Hordeum brachyantherum* long deeply indented (p) *Poa secunda* long wavy plate (q) *Poa secunda* prickle (r) *Poa secunda* papillae (s) *Muhlenbergia richardsonis* sinuous platelets with two psilate apices in cross sectional view (t) *Sporobolus airoides* bilobate in top view (u) *Echinochloa muricata* bilobate in top view (v) *Echinochloa muricata* bilobate cross sectional view (w) *Echinochloa muricata* plate wavy short in top view (x) *Echinochloa muricata* plate wavy short in cross sectional view (y) *Sporobolus cryptandrus* saddle in top view (z) *Sporobolus cryptandrus* bilobate in top view (aa) *Carex nebrascensis* angular psilate pointed apex without satellites in platelets in cross sectional view (bb) *Carex nebrascensis* elongated rectangular with irregular ends (cc) *Equisetum laevigatum* epidermal cells with elevated projections on edges, stomata and cylindrical polylobate verrucate cells *in situ* (dd) *Equisetum laevigatum* disarticulated cylindrical polylobate verrucate in cross sectional view.

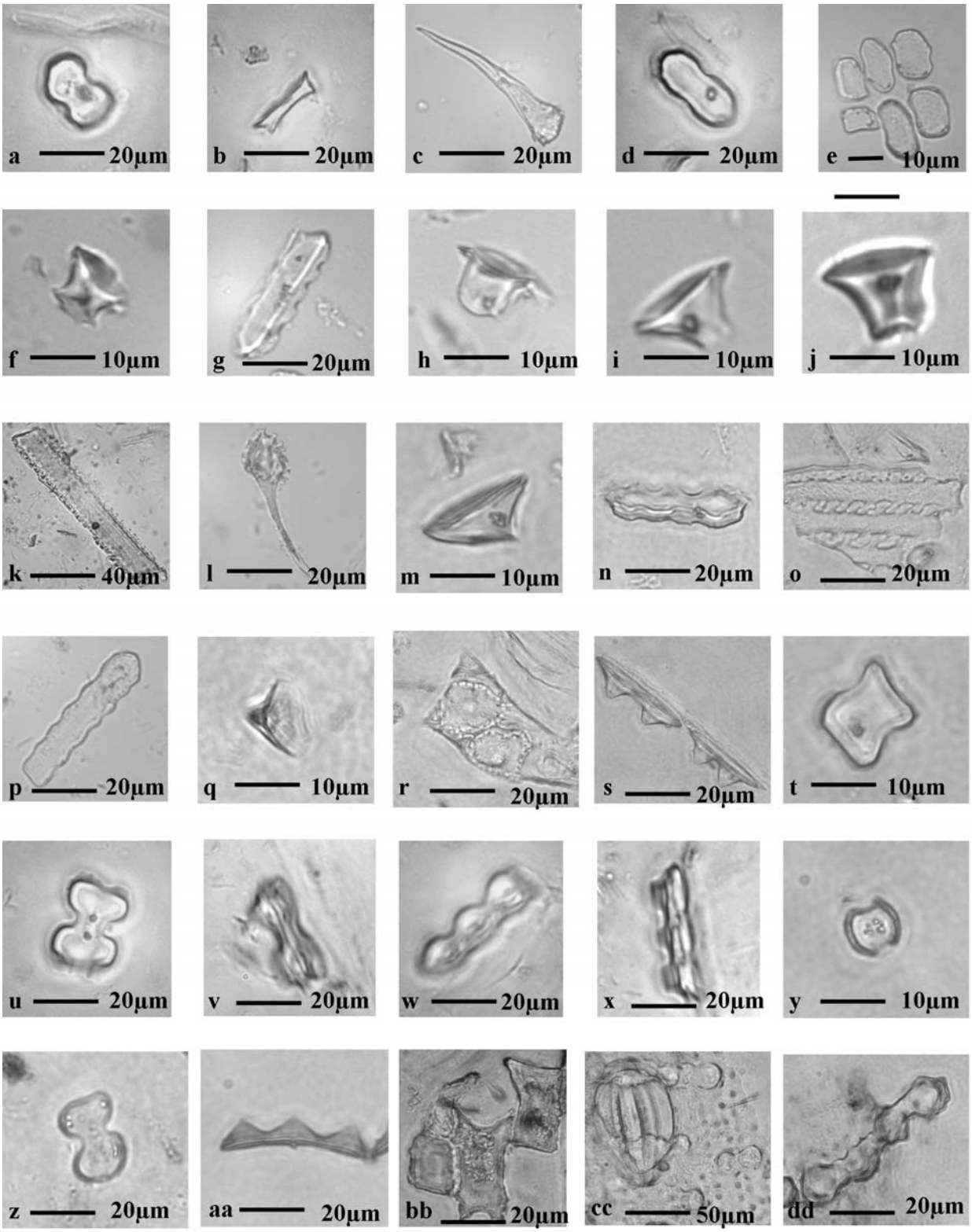
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Plate II

Plate III. Light micrographs of native and introduced tree and shrub morphotypes. Some of these images have been altered using a graphics program to enhance their features and size. (a) *Artemisia tridentata* blocky (b) *Populus alba* polyhedral epidermal (c) *Populus alba* tracheid (d) *Rosa woodsii* polyhedral epidermal (e) *Ulmus pumila* hair base with striations (f) *Prunus virginiana* anticlinal epidermal (g) *Prunus virginiana* rhombohedral CaOx crystals (h) *Prunus virginiana* rhombohedral CaOx crystals (i) *Cercocarpus ledifolius* blocky and rectangular CaOx crystals (j) *Pinus monophylla* blocky CaOx crystals (k) *Elaeagnus angustifolia* raphide CaOx crystals

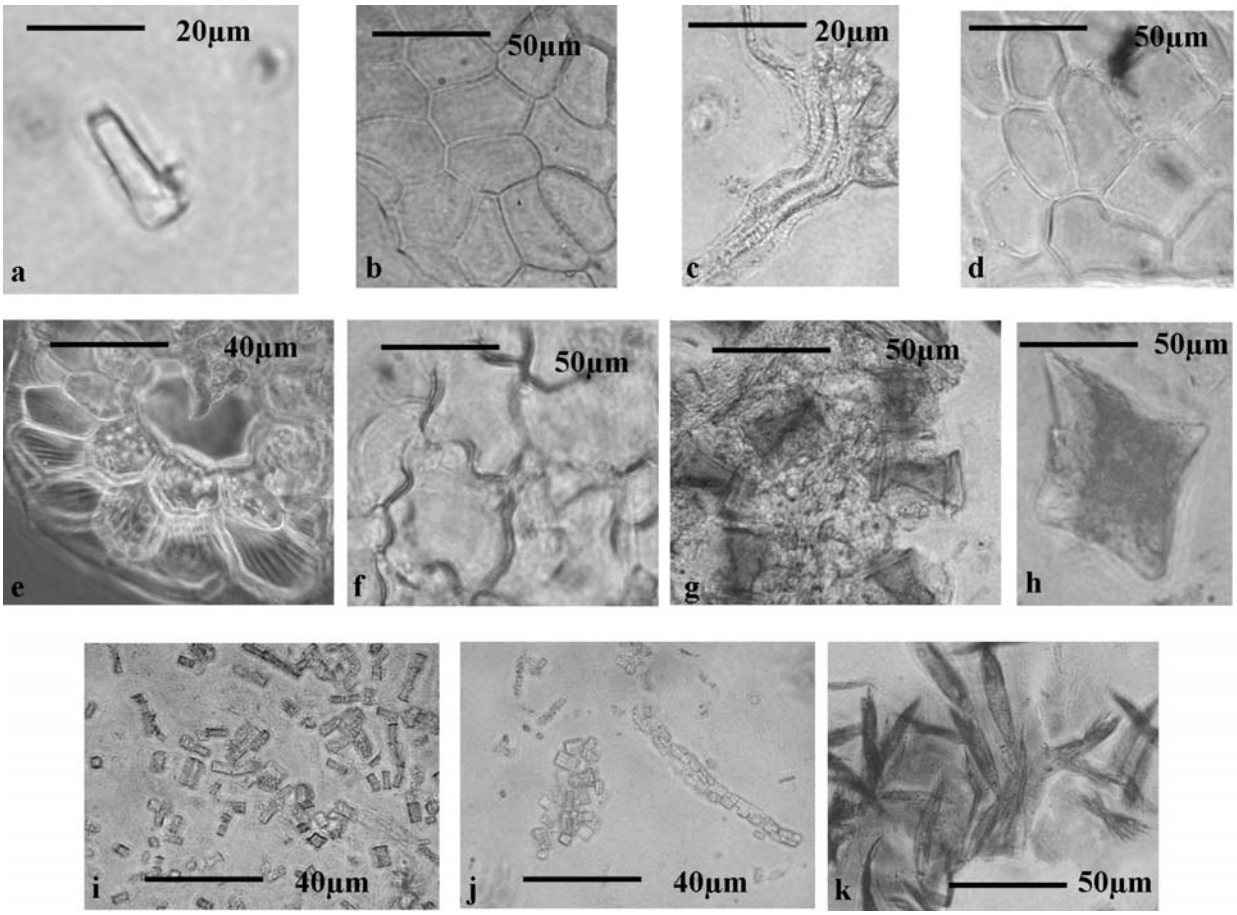
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Plate III

Plate IV. Light micrographs of introduced forb morphotypes. Some of these images have been altered using a graphics program to enhance their features and size. (a) *Acroptilon repens* mesophyll cells (b) *Acroptilon repens* epidermal cells (c) *Ceratocephala testiculata* cylindrical granulate segmented hair with no base (d) *Lactuca serriola* conical psilate prickles (e) *Lactuca serriola* conical psilate prickle (f) *Cirsium vulgare* polyhedral epidermal cells (g) *Cirsium vulgare* disarticulated polyhedral epidermal cell (h) *Bryonia alba* acicular psilate segmented hair without base (i) *Bryonia alba* charcoal (j) *Tragopogon dubius* epidermal cells with irregularly sinuated processes (k) *Tragopogon dubius* epidermal cells with irregular sinuated processes (l) *Myosotis micrantha* long conical granulate unicellular hair with base (m) detail of *Myosotis micrantha* granulated hair surface (n) *Myosotis micrantha* anticlinal epidermal cells with squared edges (o) *Asperugo procumbens* conical psilate unicellular hair detached from base (p) *Capsella bursa-pastoris* stellate tuberculate hair (q) *Capsella bursa-pastoris* bifurcated granulate hairs (r) detail of *Capsella bursa-pastoris* tuberculate hair surface (s) *Alyssum desertorum* stellate dendriform granulate hair.

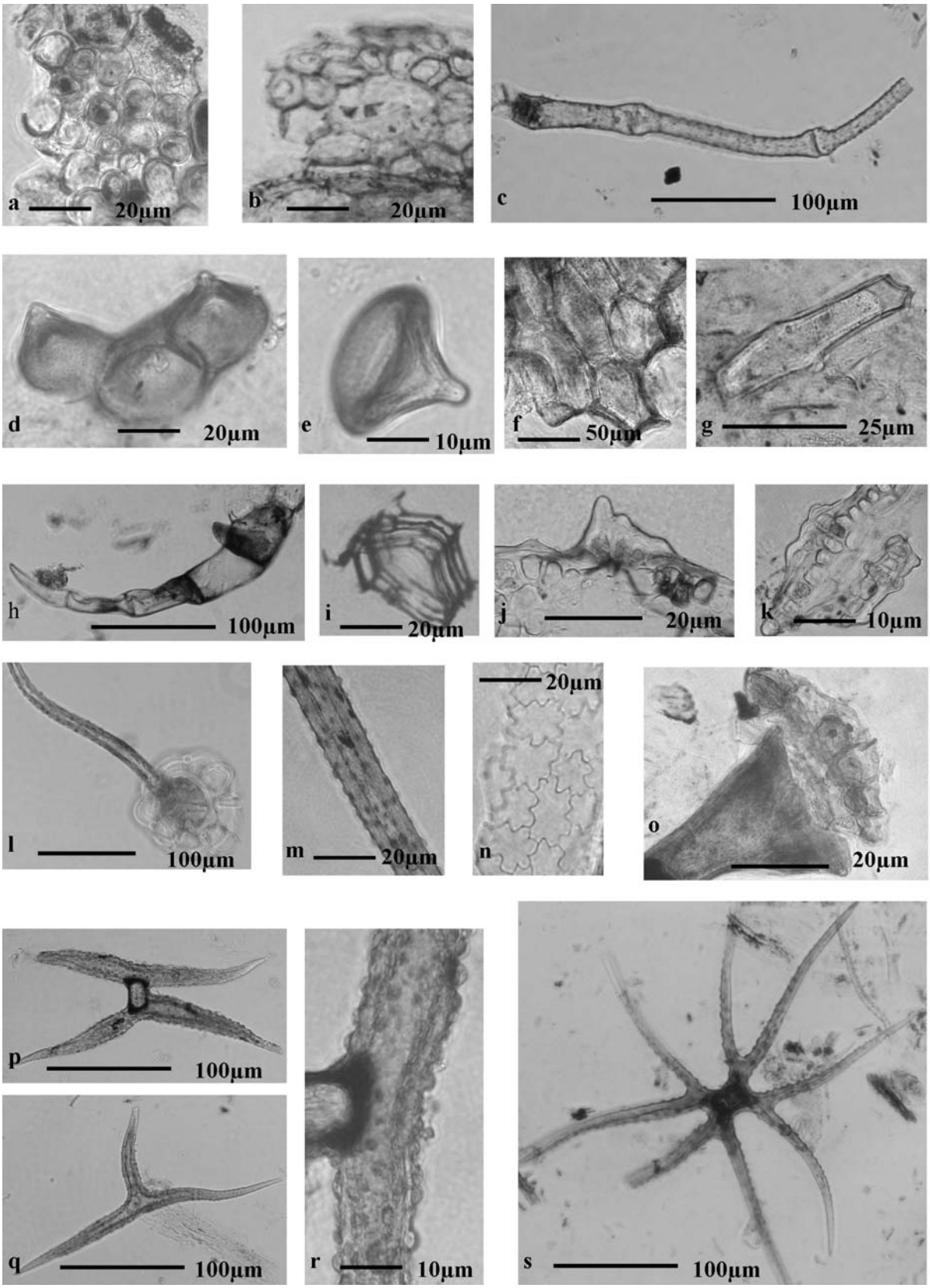
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Plate IV

Plate V. Light micrographs of introduced grass morphotypes. Some of these images have been altered using a graphics program to enhance their features and size. (a) *Agropyron desertorum* long deeply indented morphotype (b) *Agropyron desertorum* long cell indented (c) *Agropyron desertorum* oblong knobby hair (d) *Agropyron desertorum* cubic tuberculate (e) *Agropyron desertorum* square-based hair (f) *Bromus japonicus* plate wavy long (g) *Bromus tectorum* papillae (h) *Bromus tectorum* round-based hair (i) *Bromus tectorum* dendritic (j) *Bromus tectorum* long wavy plate variable ends (k) *Bromus japonicus* long cell smooth (l) *Cynodon dactylon* bulliform cell (m) *Cynodon dactylon* saddle (n) *Echinochloa crus-galli* bilobate (o) *Echinochloa crus-galli* cross (p) *Dactylis glomerata* long wavy plate deeply lobed in top view (q) *Dactylis glomerata* long wavy plate in cross sectional view (r) *Phleum pretense* opaque pieces (s) *Phleum pretense* papillae (t) *Poa bulbosa* long cell smooth with perforated edges (u) *Poa pratensis* horned rondel (v) *Secale cereale* keeled rondel (w) *Setaria viridis* bilobate (x) *Setaria viridis* bilobates and cross types.

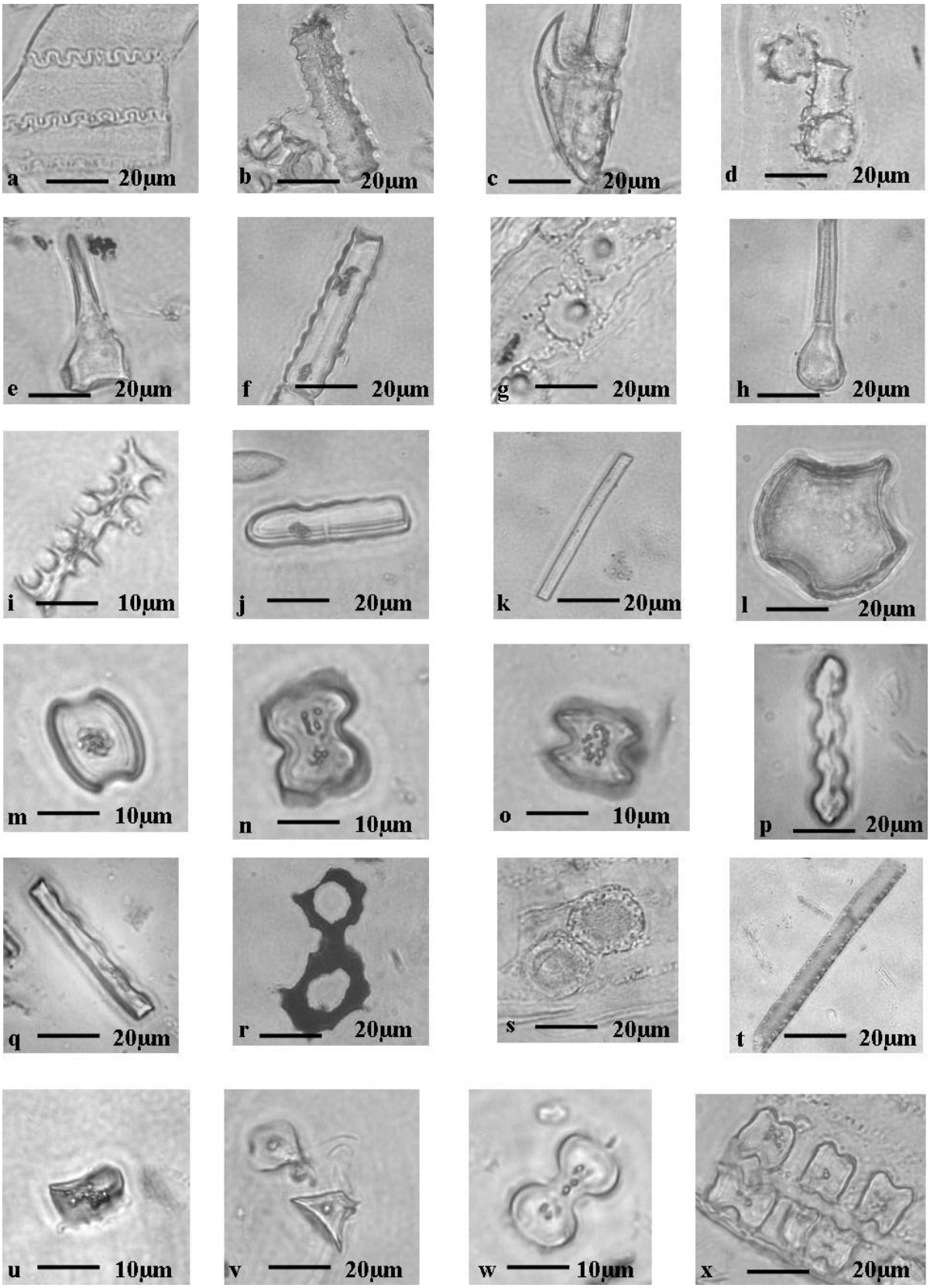
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Plate V

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CHAPTER 3 - CAN SOIL PHYTOLITH ANALYSIS AND CHARCOAL BE USED AS INDICATORS OF HISTORIC FIRE IN THE PINYON-JUNIPER AND SAGEBRUSH STEPPE ECOSYSTEM TYPES OF THE GREAT BASIN, USA?

Introduction

Across the Intermountain West of the United States, wildfires are believed to be increasing in size and intensity, attributed to historic land uses and climate (Westerling et al., 2006). The ecosystem types of the Great Basin Desert region have not escaped this pattern. Both pinyon juniper woodlands and the sagebrush steppe have experienced a great deal of fire in recent decades (Miller and Tausch, 2001; Mensing et al., 2006). It is unclear if these high severity fires were a part of the historic fire regime in this system (Baker and Shinneman, 2004). In addition to the size of these fires, the introduced annual grass *Bromus tectorum* has played a role in increasing the frequencies of fires especially in the sagebrush steppe (Whisenant, 1990). Scientists and land managers need an historical context for fires in order to better understand them and make meaningful policy decisions (Gavin et al., 2007).

Our understanding of the historic fire regimes in these two common ecosystem types of the Great Basin Desert region comes largely from indirect dendrochronological evidence of associated tree species (Miller and Rose, 1999; Miller and Tausch, 2001). Pinyon-juniper woodlands provide variable fire scar records because most of the trees are killed by fire (Miller and Tausch, 2001). This has raised questions about whether low severity fires were really a part of this system, if fire maintained open woodlands, or if stand replacing fires prevented woodlands from encroaching down slope (Baker and Shinneman, 2004). Similarly, fire in sagebrush steppe most often replaces the entire stand (Mensing et al., 2006). Our understanding of fire regimes (Swetnam and Baisan, 1995) and the methods for inferring them in pinyon-juniper and sagebrush steppe need further development due to lack of sufficient fire scars (Baker and Shinneman, 2004; Mensing et al., 2006).

Sedimentary charcoal analysis has been used as a proxy for the study of historic fire regimes in a number of ecosystems where dendrochronological evidence may be limited or to extend the reference conditions beyond the life span of trees (Gavin et al., 2007). Lacustrine sediments are the most common sources for charcoal analysis and soil-charcoal is still a relatively new technique (Berg and Anderson, 2006). Several studies using soil-charcoal have been conducted

in coastal temperate rain forest regions of Canada (Lertzman et al., 2002; Gavin et al., 2003; Sanborn et al., 2006) Alaska (Berg and Anderson, 2006), in the northern ponderosa pine forests of the Western US in Idaho (Meyer and Pierce, 2003; Pierce et al., 2004), the northern French Alps (Carcaillet, 1998) and in the Central Amazon Basin (Piperno and Becker, 1996). For the most part, these soil-charcoal studies have investigated macroscopic charcoal (>400 μm) in charcoal rich layers of the stratum and have used carbon dating of individual pieces of charcoal. This technique has not been examined in terrestrial soils from either the pinyon-juniper woodland or the sagebrush steppe ecosystems.

Phytoliths have been used to infer historic fires in several studies outside of the United States including Thailand (Kealhofer, 1996), Panama (Piperno, 1994), Brazil (Piperno and Becker, 1996) and Canada (Boyd 2002). Phytoliths can be darkened or charred on the surface or darkened by carbon inclusions that fill the cell as a result of fire (Boyd, 2002; Parr, 2006; Piperno, 2006). Phytoliths are often paired with charcoal and analyzed from samples of lacustrine sediments (Piperno, 1994; Piperno, 2006). There are some, however, who have combined these methods in terrestrial soil sediments with success (Piperno and Becker, 1996; Boyd, 2002). Piperno and Becker (1996) found soil phytolith analysis was a useful tool in the humid tropics. Boyd (2002) inferred higher fire frequency in Holocene grasslands by testing surface and buried A horizons. He compared the ratio of clear versus darkened phytoliths, or a Burned Phytolith Index (BPI).

Only one study has examined this BPI methodology using a modern day analogue in a wildland context in the United States (Morris et al., in press). This study indicated that darkened phytoliths could be useful indicators of fire in pinyon-juniper woodlands and sagebrush steppe. While a body of literature addresses the distances and sizes of charcoal fragments for understanding regional versus local fire in lacustrine sediments (Clark and Hussey, 1996; Whitlock and Millspaugh, 1996) and some work has been done in soil sediments (Clark et al., 1998; Ohlson and Tryterud, 2000; Eckmeier et al., 2007), the taphonomy of phytoliths is still largely unknown. Albert et al. (2006) conducted one of the few taphonomic studies of phytoliths by comparing production in extant plants and preservation rates in differing soil types. They did not, however, include fire effects in their examination or model (Albert et al., 2006). More work with microscopic charcoal and phytolith modern analogues is needed to better understand and interpret fire in natural ecosystems in North America (Piperno, 2006).

In this study we explore the utility and taphonomy of these methodologies in terrestrial soils from pinyon-juniper woodlands and sagebrush steppe. We examined three questions: 1) Can soil charcoal and burned phytoliths be found in historic terrestrial sediments in these ecosystems? 2) How do soil charcoal and the darkened phytolith percentages vary with distance and depth from a known fire? 3) Can a known historic fire be detected within the soil stratigraphy on the site?

Study Area

Our study area was located in the City of Rocks National Reserve in southcentral Idaho in the western US. This 5,800 ha Reserve sits at the northern edge of the Great Basin Desert region and contains both pinyon-juniper woodlands and sagebrush steppe. Elevations range from 1,646 m to 2,702 m (Daugherty, 1988). The Great Basin is known as a "cold desert" because it receives most of its precipitation as snow from winter storms (MacMahon, 1988). The Reserve averages 276 mm of precipitation a year with average temperatures of 9° C. However, temperature can be highly variable in this area with extremes from 41° C to -33° C (Morris, 2006a). The soils in the study area are classified as clayey-skeletal, montmorillonitic, frigid Typic and Lithic Argixerolls. The parent material is the alluvium and residuum of mica, schist and quartzite. The sampling sites were from three different soil mapping units including: Birchcreek-Itca complex, the Itca-Birchcreek complex and Poisonhol very stony loam (SCS, 1994).

Site Selection

The City of Rocks has seen similar patterns of increasing size and intensity of wildfires as the rest of the Intermountain West (Morris, 2006b). Using a fire history for the City of Rocks National Reserve, we selected sampling sites that had burned in 1999 and 2000 ("burned sites") and sites that had not burned within the last 100 years ("unburned sites") (Morris, 2006b) (Figure2). The 2000 fire was the most recent for the Reserve and the biggest in its recorded history (Morris, 2006b). The fire started by lightning in August of 2000, consumed 7,125 ha and burned for five days before it was controlled. This wildfire started in Utah, moved north into Idaho and into the City of Rocks where it blackened 846 ha (Morris, 2006b). It was driven by a strong wind from

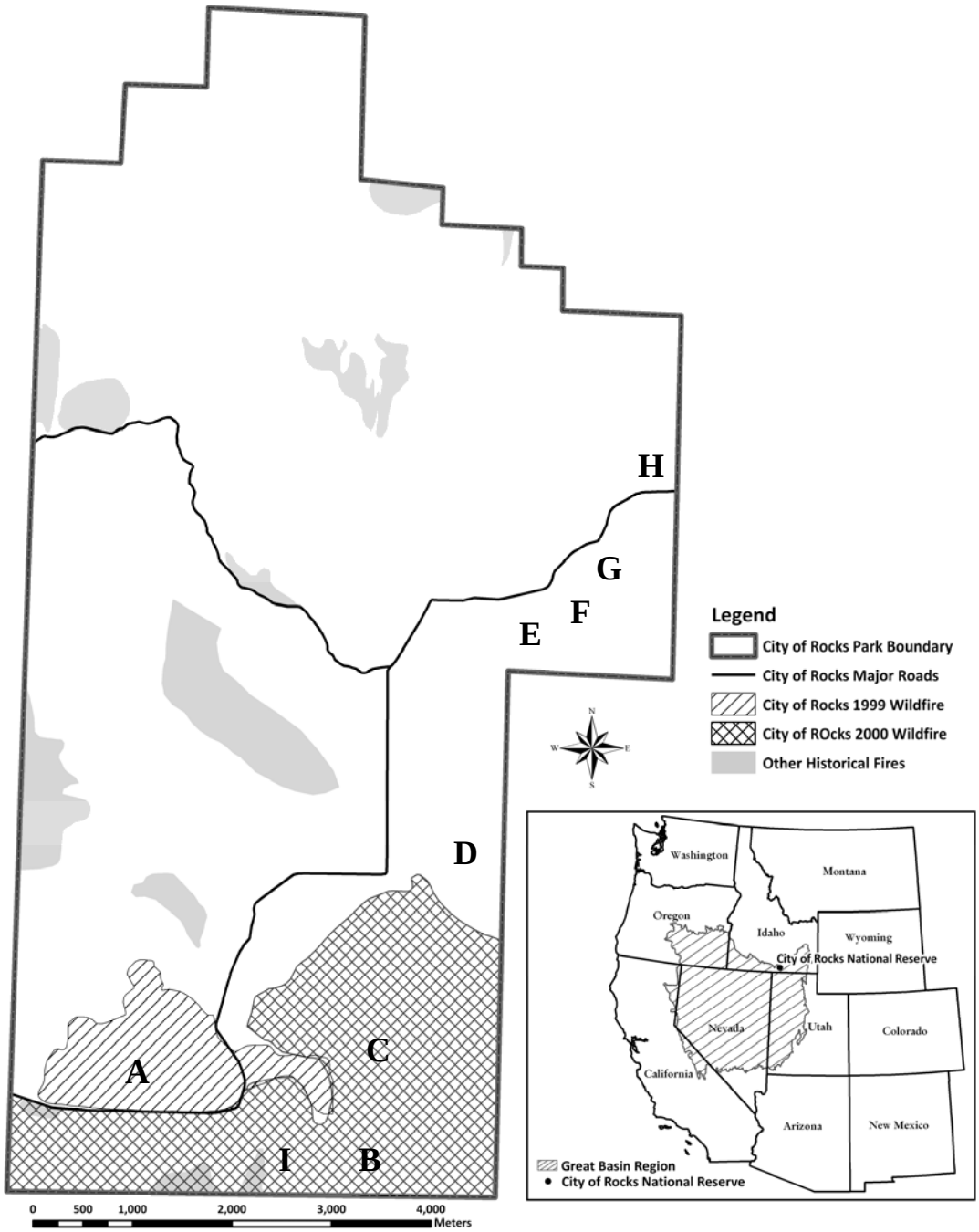

Figure 2 City of Rocks National Reserve showing all mapped fires in study area over the last approximately 100 years (modified from Morris, 2006b). A, B, C, indicate burned site locations from fires in 1999 and 2000. I indicates location of the safe site within the 2000 burn. D-H indicate unburned site locations.

the South and was finally contained within the Reserve through the use of backfiring and bulldozing fire breaks (BLM, 2000). Knowledge of this prevailing south wind was used in our selection of sites with an increasing northward distance from this fire.

We used a total of nine sites in this study: three burned sites (Sites A, B, C), one "safe site" of unburned vegetation within the 2000 fire boundary (Site I), and five other unburned sites (Sites D, E, F, G, H) (Figure 2). Previously published Burned Phytolith Index (BPI) data from surface samples at five of our sites (Sites A, B,C, D and H) are included in our analysis to show the variation across the landscape and within sites (Morris et al., in press). In 2006 and 2007, we collected soil cores from five sites (A, E, F, G, and H) at 10 to 20 cm in total depth. The soil cores were divided into approximately 1cm increments for analysis.

We conducted a pilot carbon dating study on several soil cores in our study area in 2006 to determine which segments to use for analysis. The pilot study revealed information regarding the depth to which different sites should be cored in order to reach sediments that were not mostly "modern" carbon (>95% 1950 carbon ratios). Some sites were modern only to approximately 5 cm in depth and others were modern all the way to 10 cm in depth. Therefore, we cored only to 10 cm at some locations and to 20 cm at others based on pilot carbon dating. Each sampling site is discussed in more detail below. Since the sampling locations for the previously published data (Morris *et al*., In press) were not described in detail before, we have included that information as well.

Sampling Sites

Of the nine sites, A, B, C were located in burned areas (Morris, 2006b) (Figure 2). Site A was formerly pinyon-juniper invaded sagebrush steppe that burned in 1999. It was in a broad valley with a south facing aspect on an 8° slope. Our soil core at this location was at least 22 cm deep and we processed three segments for our analysis: the surface (0-1 cm), 14-15 cm and 19-20 cm. We collected only surface samples from Sites B and C in the area that burned in the fall of 2000. Site B was formerly a pinyon-juniper woodland with a north facing aspect on a 10° slope. Site C was also formerly a pinyon-juniper woodland with a south facing aspect on a 10° slope. We collected surface samples from the safe site (a remnant of unburned pinyon-juniper) (Site I). Site I was sampled under a juniper tree on a 15° slope with a north facing aspect.

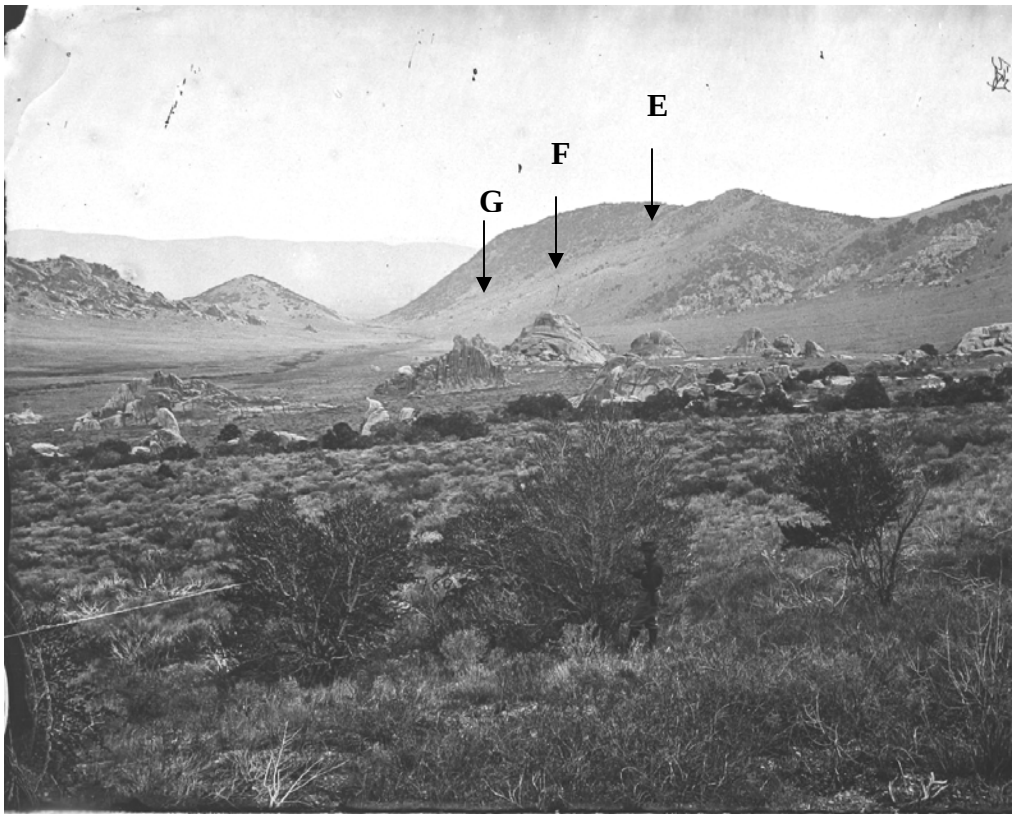

Figure 3 Photo of City of Rocks National Reserve taken in 1868. The old fire scar is on the distant slope in the right center background. The approximate locations of the historic burn sites (Site E, F, and G) are indicated with arrows. (Photo by Timothy O'Sullivan, 1868, Courtesy of the National Archives and Records Administration)

Site D was an unburned area in a pinyon-juniper woodland across a canyon about 402 m from the northern edge of the 2000 fire. It had a south facing aspect on an approximately 10° slope. We collected and processed only soil surface samples from this site.

Sites E through G were sites that had not burned in the last 100 years but that from photo interpretation (Figure 3) we believe burned over 150 years ago ("historic burn sites") (Morris, 2006a; Morris, 2006b). Site E was located very near the top of the ridge on this historic burn site with a 25° slope and a northwest aspect. It was about 2.8 km from the northern edge of the 2000 fire. We collected a soil core from this location to a depth of 10 cm and we processed three segments: 0-1 cm, 4-5 cm, and 9-10 cm. The site was dominated by old growth pinyon pine. Site F was at a slightly lower elevation on that ridge, with a 60° slope and a north facing aspect within pinyon-juniper cover. It was about 3.2 km from the edge of the 2000 fire. Our soil core at this site was 15 cm deep and we processed three segments: 0-1 cm, 4-5 cm, and 9-10 cm. Site

G was lower in elevation where juniper begins to dominate over the pinyon pine on a 30° slope and a north facing aspect. It was about 4.0 km from the northern boundary of the 2000 fire. Our soil core at this location was 13 cm deep and we processed three segments: 0-1 cm, 4-5 cm, and 9-10 cm.

Site H includes two datasets in our analysis. We included BPI data from previous study conducted on surface samples collected at Site H within a pinyon-juniper community with a south facing aspect on a 10° slope about 4.8 km from the 2000 fire boundary. We also collected a soil core in a nearby sagebrush steppe community at about 4.8 km from the 2000 fire with a south facing aspect on a 5° slope. The soil core was approximately 13 cm deep and we processed two segments: 0-1 cm and the 9-10 cm. This site had not burned in at least 100 years (Morris, 2006b).

Methods

Soil Extractions

Both microscopic charcoal and phytoliths were extracted from the soil samples using a modified wet oxidation and heavy liquid flotation technique (Blinnikov, 1994; Pearsall, 2000). Microscopic charcoal and phytoliths have a similar specific density and can be extracted together using the standard methods for phytoliths (Piperno, 2006). The surface samples and soil core segments were ground with a mortar and pestle to ensure homogeneity and sifted through a 250 µm sieve. Acid digestion of organic material was carried out with a heated 70% HNO_3 solution for one hour using 2 g of sieved soil from the core segments or surface samples. We dispersed clays with a 5% solution of sodium hexametaphosphate. Our heavy liquid for density separation was sodium polytungstate (2.3g cm $^{-3}$). The extractant was placed in a vial, dried at 80° C for 1-2 days.

We radiocarbon dated five core segments in this study from Sites A, E and H. We assumed the dates for Site F and Site G would be similar to those for Site E. The soils for radiocarbon dating were also ground with a mortar and pestle, sifted through a 250 µm sieve, weighed (between 3 to 5 g per sample), placed in glass vials and sent to the National Ocean Sciences AMS labs (NOSAMS) at the Woods Hole Oceanographic Institution for carbon dating. We did not observe any macroscopic charcoal pieces within the soil cores that could be sent for dating.

Counting Procedures

For the charcoal analysis, we used a dissecting needle to place a very small amount (<0.0015g) of the extracted sample onto a slide and weighed it. As with the phytolith analysis, a small portion of Canada Balsam oil was added to the slide, mixed well and then covered with a slip and sealed down using clear fingernail polish. The entire slide was systematically examined under 100x magnification using a BH-2 Olympus microscope. Starting at the top left hand corner of the slide, we counted all charcoal pieces on the entire slide. We identified charcoal as pieces that were opaque and angular or irregularly shaped (Clark, 1988; Piperno and Jones, 2003). To see if there were any interactions between distance from the fire and size of charcoal pieces, we counted three different size classifications: small (5-56 μm), medium (56-120 μm) and large (≥120 μm). A "local fire" should be indicated by anything greater than 125 μm (Gardner and Whitlock, 2001). The final charcoal counts were expressed as total abundance (the number per 1 g of soil) by calculating up from the counts per weight of each slide sample.

Slides for counting phytoliths were made with the same methods as the charcoal except they were not weighed. We used modified counting procedures similar to those developed by Boyd (2002). We counted one hundred phytoliths under 400x magnification from the center top and center bottom of each slide for a total count of 200 per slide. The percentage of dark and light phytoliths per 100 count were averaged to generate the Burned Phytolith Index (BPI) for each sample. We included only clear or darkened recognizable phytoliths in our BPI counts. Boyd (2002) only used long cells from grasses and we used averaged percentages rather than ratios.

Pattern Analysis

The BPI and charcoals counts were used to examine our three research questions. Our first two questions related to the existence and spatial distribution of phytoliths and microscopic charcoal in the soil. We predicted that both the charcoal abundance and the BPI would decrease in the surface samples with increasing distance from the fire in 2000. At burned Site A, we predicted that both the charcoal abundance and the BPI would decrease from the surface with depth to reflect the recent fires and lack of fire in the past. Our prediction for the unburned site H was that the charcoal abundance and the BPI would remain relatively constant with depth since it had not burned in at least 100 years. We predicted the BPI at the unburned safe site (Site I) would be at least as high or even higher than the burned sites for two reasons; because of its

proximity to the fire and because less erosion was expected in a place that retained vegetation cover. Our third question addressed whether a known historic fire could be detected within the soil stratigraphy and was examined on sites E though G on the historic burn. We hypothesized that there would be an identifiable increase in both the charcoal abundance and the BPI with depth in the soil profile that would reflect the historic wildfire.

Results

Charcoal Analysis

The carbon dating results showed that the soils at our sites were well stratified (Table V). In other words, we can assume from these dates that the younger soils are above the older soils in our cores.

No microscopic charcoal was observed in the large category, while only 51 pieces were medium, and 1,922 were small in the total 2,063 pieces of charcoal counted across all samples. Therefore, we did not continue to analyze charcoal size and used only the total counts for each sample. The charcoal abundances followed only part of our prediction. Charcoal in surface samples was most abundant on the burn site, but decreased dramatically and remained fairly consistent from 2.8 km to 4.8 km away from the edge of the burn (Figure 4). Charcoal abundances with depth followed our predictions fairly well at the burned versus unburned sites.

Site	**Depth**	**Radiocarbon Age**	**Calibrated Calendar Age (1 Sigma Ranges)**	**Calibrated Calendar Age (2 Sigma Ranges)**
Site A	14-15cm	695 ± 30	Cal AD 1274-1298 Cal AD 1372-1378	Cal AD 1264-1310 Cal AD 1360-1387
	19-20cm	905 ± 35	Cal AD 1044-1098 Cal AD 1119-1142 Cal AD 1147-1174	Cal AD 1037-1209
Site E	4-5cm	>Modern		
	9-10cm	>Modern		
Site H	9-10cm	410 ± 35	Cal AD 1439-1491 Cal AD 1603-1611	Cal AD 1429-1522 Cal AD 1573-1628

Table V Results from carbon dating segments from soil cores at Sites A, E and H.

The charcoal abundance decreased dramatically with depth to reflect the recent fire at Site A and remained fairly constant with depth at the unburned site H (Figure 5). At the depths we analyzed (0-1 cm, 4-5 cm and 9-10 cm) on the historic burn sites (Site E, F and G), we did not detect an increase in charcoal abundance that would indicate the historic fire at these sites. In fact, the charcoal abundance remained relatively consistent within these depths at all three of the historic burn sites (Figure 6).

Burned Phytolith Analysis

Our BPI results followed fairly well with our prediction for change over distance from the recent fires. In general, the BPI of the surface samples decreased with distance from the recent fire (Figure 7). However, when compared with previously published data from surface samples, unburned sites appeared to have a greater amount of variability in BPI than did the burned sites.

Figure 4 Charcoal abundance (number of charcoal x 10^6 per 1 gram of soil) shown with increasing distance from burned Site A. Distances of Site E through H range from 2.8 km to 4.8 km from the boundary of the 2000 fire.

Previous data from Site A (35%) was almost exactly the same as the current BPI (36%). Burned sites in general ranged from 30% to 49% BPI with an average of 38% (n=4). The safe site, Site I, had a very low BPI of only 1%. Unburned sites, on the other hand, exhibited a great deal of variability. The highest BPI (20%) was from the pinyon-juniper woodland area at Site H. Our BPI from the sagebrush steppe community at this same site was only 3%. In addition, two samples from Site D, the closest unburned site to the recent fires had a BPI of 0% and 10%. The BPI on all unburned sites ranged from 0% to 20% and averaged 6% (n=7).

The BPI analysis with depth only followed one of our predictions. The comparisons of burned Site A and unburned Site H met our expectation and the BPI, in fact, decreased between the surface and two depth samples (14-15 cm and 19-20 cm) at Site A and remained fairly constant between the surface and 9-10 cm in depth at Site H (Figure 8). However, on the historic burn (Sites E, F and G), the BPI was low and remained relatively constant between the surface and the two depths (4-5 cm and 9-10 cm) for all three sites. We had expected to find an increase in the BPI between the surface and/or 4-5 cm level and the 9-10 cm depth that would relate to the historic fire (Figure 9).

Discussion

Charcoal with Distance and Depth

Charcoal was most abundant at the location of the modern fire and decreased by 0.4 km from the edge of the burn. Clark et al. (1998) found in an experimental burn that the charcoal loads declined abruptly at the burn edge and then remained rather constant to distances of 1.0 km from their intense crown fire. Ohlson and Tryterud (2000) found a similar trend of abrupt decrease in their experimental burn. Our charcoal abundance followed this pattern over distances from 0.4 km to 4.8 km from the edge of the 2000 fire. We found no differentiation in size of charcoal with increasing distances from the recent fires as has been found in lacustrine sediments (Whitlock and Millspaugh, 1996). Our lack of size differentiation in the charcoal with distance from the fire sites could be a methodological issue created by grinding the sections with a mortar and pestle. However, we did not observe any macroscopic charcoal prior to this step, in the sieve or during soil core collection in the field.

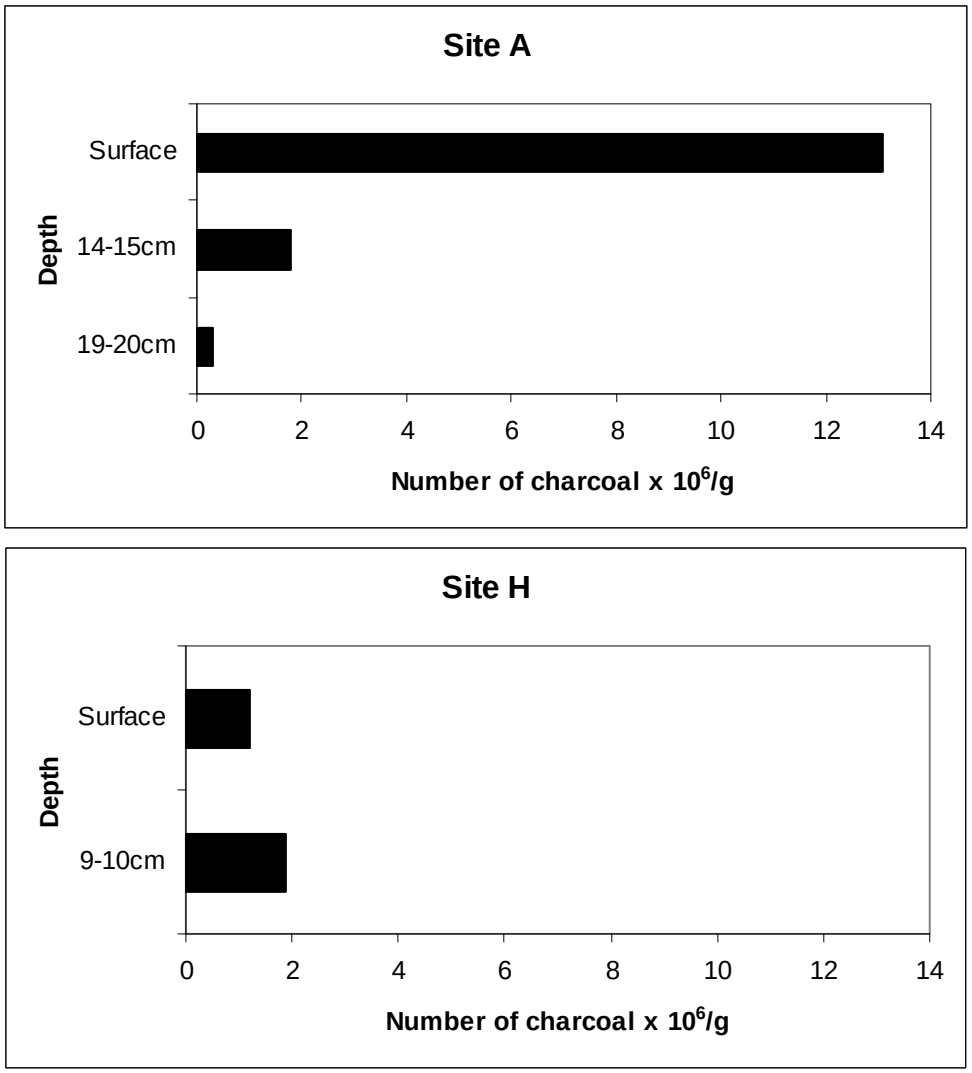

Figure 5 Charcoal abundance (number of charcoal x 10^6 per 1 gram of soil) by depth at a recently burned (Site A) and unburned site (Site H).

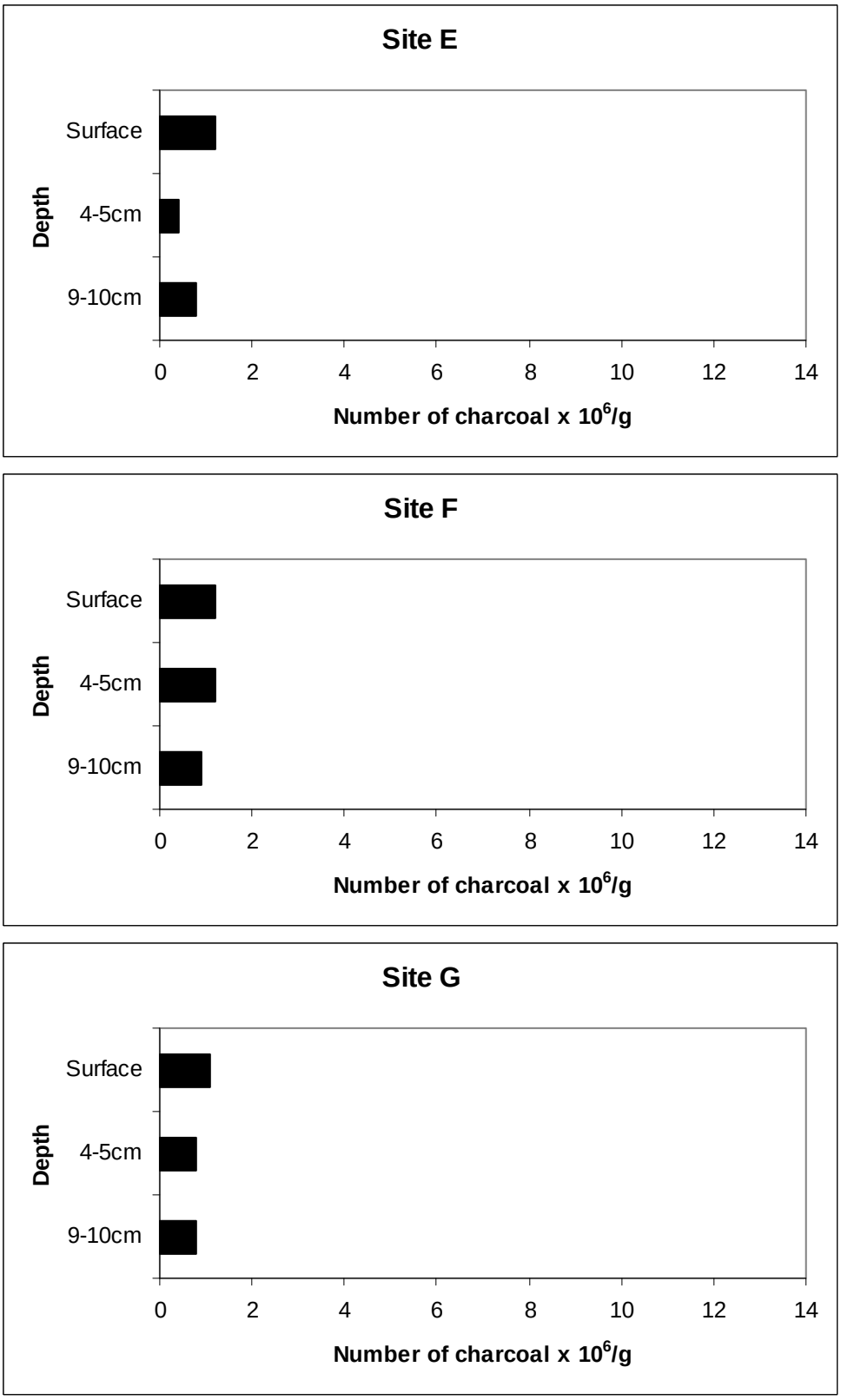

Figure 6 Charcoal abundance (number of charcoal x 10^6 per 1 gram of soil) by depth at the historic burn sites (Sites E-G) that burned over 150 years ago.

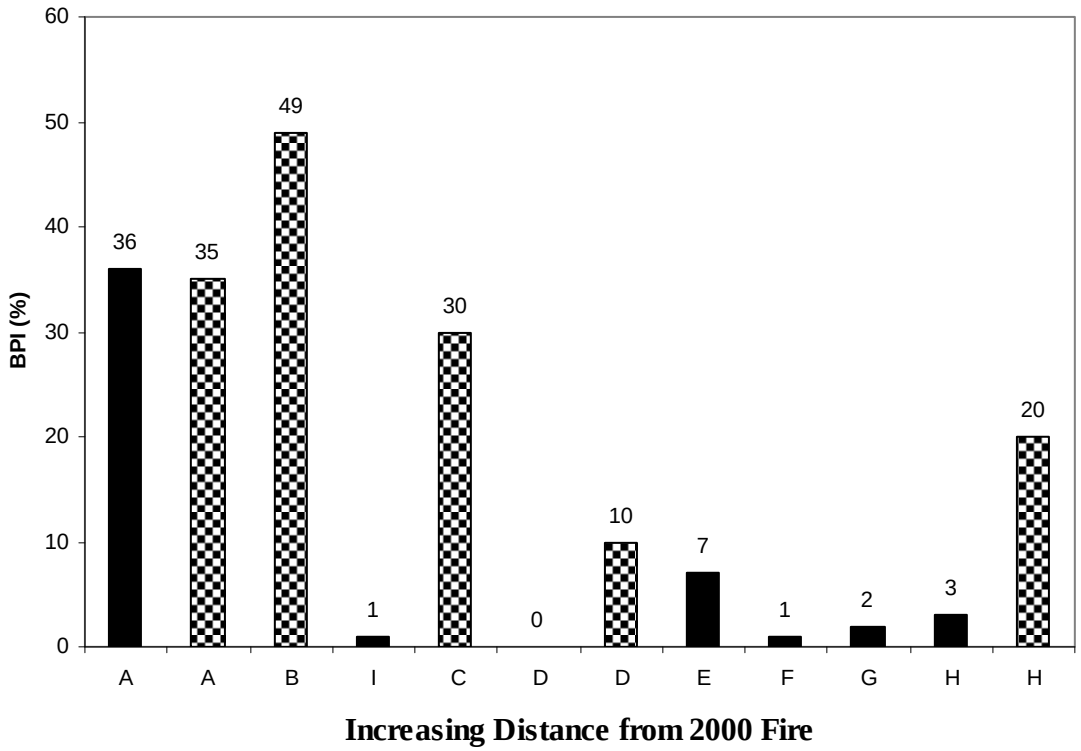

Figure 7 Burned Phytolith Index (BPI) with increasing distance from the 2000 fire. Distances from the nearest edge of the 2000 fire ranged from 0.4 km (Site D) to 4.8 km (Site H). Checkered bars are previously published data (Morris et al., In Press). A, B, and C burned in 1999 and 2000. Sites D-H had not burned in at least the last 100 years. I is the "safe" site of unburned vegetation within the 2000 burn area. A, D, and H are repeated because they were sampled twice. Previously publish data from Site H (with checkered bar) was collected in pinyon-juniper site and the second sample from Site H (solid bar) was collected in sagebrush steppe.

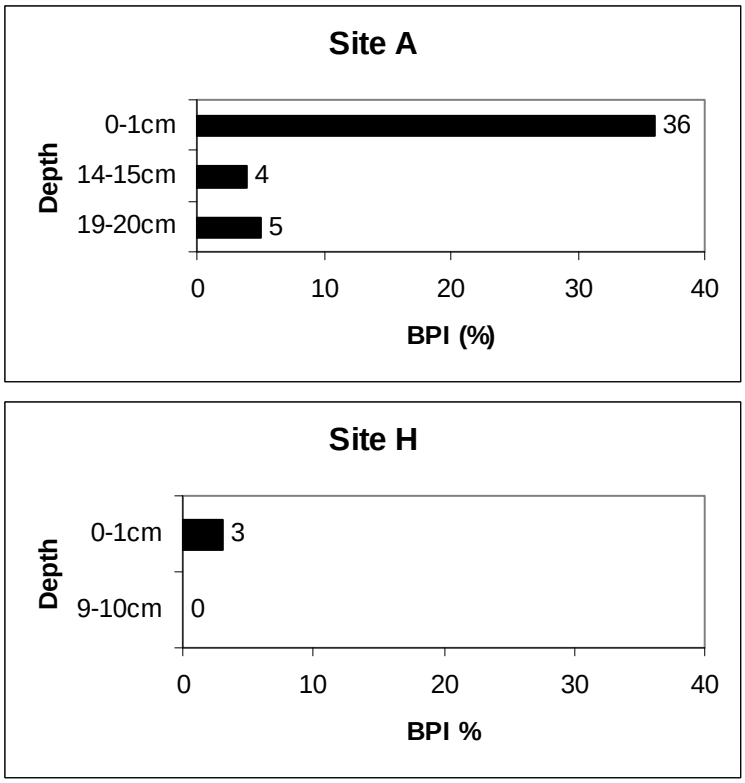

Figure 8 Burned Phytolith Index (BPI) percentages by depth at a burned site (Site A) and unburned site (Site H).

Very little is known about the transportation and incorporation of charcoal into soil sediments following a fire (Ohlson and Tryterud, 2000; Eckmeier et al., 2007). There is good evidence, however, for fragmentation and movement down through the mineral horizons (Preston and Schmidt, 2006). Piperno and Becker (1996) concluded that, in the tropics, the phytoliths were substantially older than the charcoal and that those occurring at the same stratigraphic level cannot be assumed to be the same age. Caracaillet (2001) found that individual pieces of charcoal are not well stratified in alpine and subalpine soils but that charcoal concentrations were. He concluded that in the Alps charcoal particles can migrate through the profile to about 100 cm in less than 500 years (Caracaillet, 2001). Our radiocarbon dates were on bulk soil sediments and we do not know the exact age of the charcoal or the phytoliths within the soil matrix. However, it is interesting to note that the charcoal counts at depth did not differ much from counts at the surface in modern samples unless the site burned. Charcoal abundance was also similar in soil samples close in age. Future research should focus on analysis of soils exposed to fires of known dates to assess how charcoal is incorporated into the soil stratigraphy.

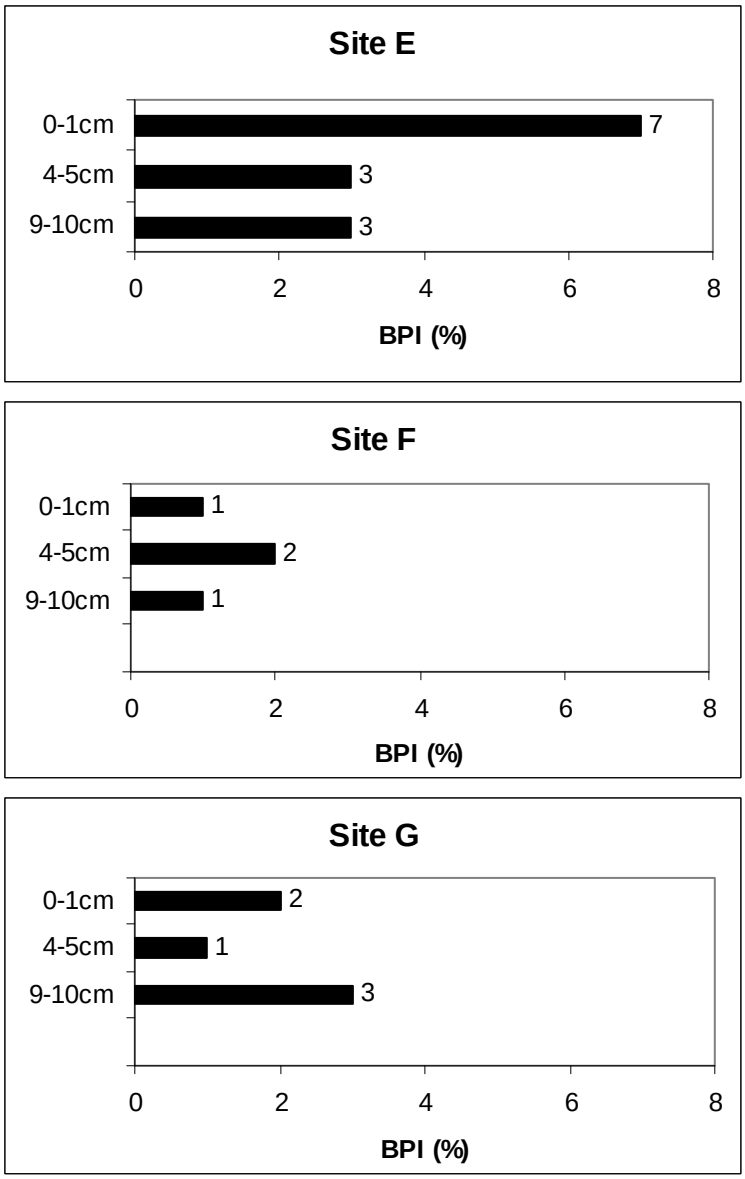

Figure 9 Burned Phytolith Index (BPI) percentages by depth at the historic burn sites (Sites E-G).

BPI with Distance and Depth

The range of our BPIs fall within the range reported for burned areas in other studies. Piperno (1994) reported burned phytolith percentages (burnt/sum of all grass phytoliths) as peaking at 35%. Similarly, Kealhofer (1996) reported burned phytolith percentages in Thailand from 5-29%. Both studies were using lacustrine sediments cores. Boyd's (2002) terrestrial surface samples had an average of 8.2% with the last known fire in the area being in the late 1940s. The buried sediment layer with substantial macroscopic charcoal that he used for

comparison had a BPI of 73%. His study revealed peaks from 60-70% in the BPI with depth and declines all the way to 10% for the uppermost soil layer. The only other study from our region found that, on average, burned sites had a higher BPI (38%, n = 3) than unburned sites (17%, n = 3) (Morris et al., in press). The BPI at our unburned sites was generally lower than reported by Morris et al. (in press) this previous study which may be due to the difference in counting procedures. The study by Morris *et al*. (In press) included soil aggregates, while in this study we counted recognizable phytoliths. When combining results from both studies, surface samples from burned sites had an average 38% BPI (n=4) while unburned sites (n=7) averaged a 6% BPI. Our BPIs might vary from other studies because of vegetation type, topography, climate and sediment type. For example, Boyd (2002), who worked in grasslands and counted grass phytoliths, had the highest BPIs. None of our sampling sites were in grasslands.

Our BPI for Site I on the safe site within the 2000 fire was surprising. Ohlson and Tryterud (2000) conducted an experimental fire to assess the distribution of large charcoal (500-2,000 μm and >2,000 μm) and found that the presence of charcoal was a good indicator of local fire while the absence had to be interpreted more carefully. Even within their experimental fire, some 38 of their 280 traps inside the burn contained no particles >500 μm. Many of the traps without charcoal were located in an area where there was a combination of low fuel loads, low charcoal producing fuels (e.g. grasses) and lower fire intensity. This may also be the case with our safe site where the majority of vegetation that burned around it produced few phytoliths. A recent study of phytolith production in Great Basin species has shown that pinyon pine (*Pinus monophylla*) and juniper (*Juniperus osteosperma*) form only trace amounts or no phytoliths at all (Morris et al., in press).

Because this is the first attempt to use BPI as an indicator of historic fires in these ecosystem types and soils, it is unclear what the threshold BPI should be to indicate an historic fire. Our results on modern fires and distances from them indicated that characteristic BPI of a burn would be around 38%. No site had greater than 30% BPI at any depth. However, we cannot conclude that fire was absent during the time periods that these samples represent because, similar to other studies using charcoal, lower BPIs are actually more difficult to interpret. For example, our safe site within the fire had one of the lowest BPIs in the study. Also, our interpretations are limited because we do not know about the affects of time on this measure. For example, perhaps the BPI of a burned site decreases over time due to post depositional forces on the soil such as wind and

water. There are also issues of inheritance associated with the phytoliths. There were several fires in our study area over the last approximately 100 years (Figure 1) (Morris, 2006b). Each of them could have contributed to the BPI at our unburned sites as well, not just the 1999 and 2000 fires. Future research using BPI on soil profiles at burned sites of varying known ages would be useful.

The BPI of these sites prior to the 1999 and 2000 fires is also unknown. The BPI could be created by the deposition of burned vegetation onto the soils during the fire, by the charring of the phytoliths on the soil surface during the fire, or both. Sites with an accumulation of duff versus those without it could char more phytoliths within the mineral soil layer due to high heat. Temperatures at the ground surface in sagebrush fires can reach peaks of 150-500° C with sustained heating for 5-10 minutes at >100° C and 10-15 minutes at >200° C (Buenger, 2003). In pinyon-juniper woodland fires, ground surface temperatures can peak at 700-800° C with sustained heating at 200-400° C for more than an hour (Buenger, 2003). Large amounts of litter and duff can contribute to deeper soil temperatures up to 94° C (Klopatek et al., 1988).

Finally, the BPI may also be dependent upon grass cover at the time of the fire. Charcoal is generated mostly by woody species while phytoliths in these two systems is mostly from the grasses and some of the herbaceous understory (Chapter 2). Junipers are known to decrease understory vegetation as the cover increases in these woodlands (West, 1991; West, 1999). Most of the fires in this study area occur in late summer and fall when livestock and grazing have worked over the grasses for the season (Morris, 2006b). Therefore, there may simply not be the enough grasses at the time of the fire to contribute to large numbers of phytoliths carried on the wind while they may be present in the mineral soil. Therefore, they might char on site and not be as likely to disperse in the smoke and wind during the fire.

The Historic Burn Site

We did not find a clear indication of the historic fire in our old burn site samples. It could be that the spike in BPI and charcoal on the historic burn site was simply not detected because we sampled modern core segments. Our pilot study dating results indicated that depths of around 9-10 cm could be approximately 190 ± 25 ^{14}C years before present. Therefore, we dated and analyzed core segments at 4-5 cm and 9-10 cm. However, the carbon dates reveal that the segments we processed were modern. We believe this fire occurred over 150 years ago (Morris,

2006b). Given that the soils in our study area have shown to be well stratified in this study, there is good reason to believe that the core segments between the surface and 4-5 cm and from 4-5 cm to 9-10 cm in depth are also modern. Perhaps the charcoal and BPI signal for it was deeper in the soil profile than we sampled. Being on a slope, it is likely that there are buried A horizons deeper in the profile or that much of the soils following the fire in our photo (Figure 3) were eroded away. Or, the soils at this site could be mixed enough to result in a modern date. Finally, it is also possible that there was no fire at this site even though it appears there was one in the past from the photo. Given the ability of the phytolith record to reflect recent fires on lower degree slopes and the presence of both charcoal and burned phytoliths in very old soils, we believe that the method is sound but should be tested in a more stable location in future research.

Conclusion

We have documented that both charcoal and burned phytoliths are present in terrestrial soils dated as old as the late Holocene. We worked with both proxies in a modern analogue study to examine changes in their abundance with distance from modern fires and with depth at sites of modern fires. Our results show that burned phytoliths and charcoal in terrestrial sediments are potential sources for interpreting historic fires in sagebrush steppe and pinyon-juniper woodlands. Both of these important biological proxies were found in sediments dating back to the late Holocene. Information regarding fire from this time period, commonly known as the Little Ice Age, can be important for understanding the historic range of variability of these systems. This is the first attempt that we know to examine these proxies in terrestrial sediments in the region. Our results illustrate the difficulty of defining a clear taphonomy for phytoliths and charcoal in terrestrial sediments after a fire in these two ecosystems. There are many unanswered questions left to explore in future research. However, this study does indicate that charcoal and phytolith analysis have the potential for use in examining questions related to historical fires in pinyon-juniper and sagebrush steppe ecosystems of the Great Basin Desert region.

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CHAPTER 4 - TESTING SOIL PHYTOLITH ANALYSIS AS A TOOL TO UNDERSTAND VEGETATION CHANGE IN THE SAGEBRUSH STEPPE AND PINYON-JUNIPER WOODLANDS OF THE GREAT BASIN, USA

Introduction

Phytolith analysis is becoming an increasingly popular method for determining historic vegetation (Piperno, 2006). Phytoliths are structures formed in plants through deposition and accumulation of silica within and around cell walls (Rovner, 1971; Fredlund, 2001). They are released from plants into sediments through death and decay of plant material where they have been recovered from as early as the Eocene (Stromberg, 2004). These microfossils are most often used along side pollen analysis from lacustrine sediments. But, phytoliths preserve well in terrestrial sediments while pollen grains are more stable in anaerobic conditions (Golyeva, 2001). This is particularly important for arid and semi-arid environments where lacustrine evidence is not as common (Fredlund, 2001). In addition, biological proxies for the more recent past (less than 200 years) are largely limited to the human archive and some dendrochronology evidence (Egan and Howell, 2001) which can be subject to human bias, limited in spatial extent or not appropriate for non-forested systems (Swetnam et al., 1999). Better development of biological proxy methods are needed to understand changes in more arid ecosystems over the recent past. Soil phytolith analysis has the potential to provide this much needed biological evidence.

Several studies have used the phytolith record from natural terrestrial sediments across a variety of regions from the Amazon basin (Piperno and Becker, 1996) to the Rhone valley in France (Delhon et al., 2003). In North America, soil sediments have been used for phytolith studies from the northern prairies of Canada (Boyd, 2002) and in the United States' Columbia Basin in the northwest (Blinnikov et al., 2002), the northern Rocky Mountains between Montana and Idaho (Stromberg, 2004), the Great Plains (Kurmann, 1985; Fredlund and Tieszen, 1997; Stromberg, 2004) and the deserts of southwest US in Utah (Fisher et al., 1995). In each of these studies, one or more buried soil horizons is used as a comparison. Research examining changes in the continuous soil stratigraphy with phytoliths is much more limited. Blinnikov (1994) employed this technique in studies of alpine soils. He sampled every 2 cm to a depth of 10 cm and then every 5 cm to a total depth of 25-40 cm into the lower limit of the soil B horizon. He was able to infer changes in the vegetation for the last half of the Holocene and could reportedly detect the phytolith signal of a severe grazing period in the last several hundred years. Similarly,

Kerns (2001) examined changes between surface (0-2 cm) and subsurface (2-7 cm) soils of the ponderosa pine forests in the southern Rocky Mountains of Arizona.

Diagnostic phytolith morphotypes have been reported at varying taxonomic levels. For example, there are diagnostic phytoliths at the genus (Klein and Geis, 1978) and even species level (Kerns, 2001) within the family *Pinaceae*. However, there need not be a diagnostic form for each taxa for the method to be useful (Piperno, 2006). For example, frequency analysis of morphotypes found in the extant vegetation are often compared to each other as a way of determining which type or set of morphotypes provide a signal for a species, community or even a climate regime (Kerns, 2001; Carnelli et al., 2004; Blinnikov, 2005). Furthermore, since many tree species do not produce diagnostic forms or many phytoliths overall, previous studies have used the mass or percent weight of extracted silica as a proxy for forb dominated vegetation (Kalisz and Boettcher, 1990) versus forest cover in the past or changes in grasslands over time (Fisher et al., 1987). In areas where conifers or other forest species generate recognizable phytolith morphotypes, relative abundance has been used (Blinnikov et al., 2002). Blinnikov (2005) identified a blocky phytolith morphotype useful for signaling *Artemisia* and, therefore, sagebrush steppe ecosystems.

Our analysis in Chapter 2 of the phytolith production and morphotype frequencies in native and introduced species of the Great Basin has demonstrated that pinyon-juniper woodlands do not have a recognizable phytolith assemblage due to the lack of production by the dominant woody species, *Pinus monophylla* (pinyon pine) and *Juniperus osteosperma* (Utah juniper). This work suggested that extraction weights may be a more appropriate method for differentiating between these woodlands and grasslands or sagebrush steppe communities. In addition, this study demonstrated important differences in morphotype production frequency between native and introduced grass species as well as within these groups. In particular, the most common introduced grass species in their study area produced almost half the frequency of rondel morphotypes as native grass species (Chapter 2).

Our objective in this study was to examine the utility of soil phytolith analysis to reflect vegetation changes over the period of about 200 years in two common ecosystem types of the Great Basin, sagebrush steppe and pinyon-juniper woodlands. The sensitivity of phytoliths as a record for the more recent past can be tested by sampling in locations where vegetation changes are known to have occurred based on human records. Results from previous environmental

history work in our study area (Morris, 2006a) show that over the past two centuries, the vegetation has changed in two major ways. First, there are more woody species including denser sagebrush and increased cover and density of pinyon and juniper as these woodlands have encroached down slope and into the valleys. Second, there has been an overall loss of native grasses and an increase in introduced grasses, particularly *Bromus tectorum* (cheatgrass) and *Agropyron desertorum* (crested wheatgrass) (Morris, 2006a). These known changes are used to test the sensitivity of the soil phytolith stratigraphy to record such events. We employed both a multi-core approach and detailed core analysis to examine three questions.

1) Do extraction weights from soils reflect the reduction of grasses over time with an increase in woody vegetation either from sagebrush or pinyon-juniper woodlands across the landscape?

2) Do the relative abundances of total rondels from soil sediments reflect the change over time to dominance of introduced grasses over native grasses across the landscape?

3) Do phytolith assemblages change over time at a fine scale (1 cm increments) in continuous sampling analysis of cores?

We hypothesized that the extraction weights would be less in the surface segments due to the historic reduction of grasses with high phytolith production being replaced by woody species with very low phytolith production. In addition, we predicted that total rondel percentages would be less in the surface segments than in deeper segments within multiple cores due to the increasing dominance of introduced grasses. Finally, we hypothesized that the overall phytolith assemblage would change with depth over time along continuous sampling of 1 cm segments in a core and reflect known vegetation changes.

Study Area

City of Rocks National Reserve

The City of Rocks National Reserve (CIRO) contains approximately 5,800 ha of the Great Basin Desert Region in the Albion Mountains of southern Idaho. The elevation reaches from 1,646 m in the valley to 2,702 m on Graham Peak (Daugherty, 1988). The vegetation includes sagebrush steppe in the valleys and pinyon-juniper woodlands along the slopes and lower mountains with mountain mahogany chaparral and limber pine forest at the highest elevations.

The sagebrush steppe is the largest of the North American temperate semi-desert types (West, 1983). The ecosystem gets its name from the historically equal dominance of shrubs from the genus *Artemisia* and various species of bunchgrasses (West, 1983). The major tree species in the Great Basin pinyon-juniper woodlands are *P. monophylla* and *J. osteosperma* . The understory species are highly variable across the region but are usually made up of the flora found in adjacent forests, shrub steppes or grasslands (West et al., 1975; West, 1999).

Precipitation trends in the Great Basin generally show a marked pattern of winter maximum and summer minimum due to winter storms that develop off the Pacific coast (Miller et al., 1994; WRCC, 2006). The City of Rocks, however, is part of the eastern portion of Idaho that shows maximum monthly amounts in summer and minimums in the winter due to moisture from storms originating from the south in the Gulf of Mexico and the Caribbean region (WRCC, 2006). The average total monthly precipitation peaks during the months of April, May and June (Morris, 2006a). This increased proportion of April-September precipitation in the eastern portion of the sagebrush steppe region has been used to explain the predominance of grass species in some areas (Stoddart, 1941). The mean annual precipitation is 276 mm (Morris, 2006a). Temperatures can be highly variable in this region. The annual mean temperatures at the site range from 41° C to -33° C with average temperatures of 9° C (Morris, 2006a).

CIRO is an excellent location for developing these sensitivity tests because it has a very long and well recorded history from European emigration and settlement in the mid 1800s to present. The City of Rocks contains segments of two important routes of the California Trail from the era of overland emigration in the USA between the 1840s through the 1870s (HRA, 1996). CIRO has also been an important area for livestock grazing and homesteading. Commercial herds of sheep and cattle were trailed through the City of Rocks beginning in the 1850s (Little, 1994). The area was first used as a home base for a livestock grazing in the late 1860s (Little, 1994; HRA, 1996). By the late 1880s several large livestock operations from Nevada and Utah were grazing cattle through the Reserve and surrounding lands (Little, 1994). Extremely harsh winters and droughts in the 1890s devastated the cattle barons (Young and Sparks, 2002). After that, most of the livestock grazing in the area was from more local farms and ranches which supplemented livestock with hay or grain in the winter. The first homesteader arrived within the City of Rocks in 1882 but homesteading and dry land farming were most active in the CIRO from 1909 to 1920. Again, droughts in the 1920s and into the 1930s drove many out of business

and the settlers began to move away, reportedly due to failing springs and other water sources (HRA, 1996). In the 1950s, a push to increase forage production in the most productive sagebrush steppe areas left fallow since the dry farming era and devastated from droughts and overgrazing meant clearing the land once again and drill seeding with the introduced forage grass, *Agropyron desertorum*. More details concerning the environmental history of the study area are available in Morris (2006a).

European exploration and settlement of the American West coincided with the end of the period known as the Little Ice Age. The Little Ice Age was a generally cool period in the Northern Hemisphere from approximately 1300-1850 AD (Millar and Woolfenden, 1999; Miller and Tausch, 2001). Though the difference in average temperature was only estimated to be 1° C, it had marked impacts upon ecosystems in North American, Europe and other parts of the globe (Roberts, 1998). The Little Ice Age was the wettest and coolest period of the Late Holocene (Miller and Tausch, 2001). Since then, the general trend has been one of continual warming and aridity in the much of the Great Basin region (Miller and Wigand, 1994; Miller and Tausch, 2001). Because this climatic shift coincided with the arrival of European settlers and the introduction of new disturbances from agricultural development, livestock grazing and invasive plant species, it is difficult to tease apart the so called "natural" climatic shifts in vegetation from those driven by human influence (Millar and Woolfenden, 1999). Whatever the mechanism, the changes in the vegetation have been very distinct over this time period making the CIRO an excellent location for testing the sensitivity of the soil phytolith record.

Site Descriptions

An understanding of the history and land uses in the study area was crucial for developing hypotheses to be tested as well as determining sampling sites that have had a relatively stable soil profile over the time period of interest (e.g. unplowed sites). The widespread history of dry farming in the early 1900s and seeding projects later in the 1950s left very few sites within the valleys that were potentially stable enough for sampling. Six soil sampling sites were located using the mapped historical information gathered from the human archive (Morris, 2006a; Morris, 2006b). At each site, the following information was collected: GPS coordinates, slope, aspect, recently burned/unburned in the last 100 years, community type, and characterization of the present vegetation. The present character of the vegetation (percent cover) was assessed

using point line transect method for shrub steppe and understory vegetation and line intercept method for woodlands (Bonham, 1989).

The soils in the study area are classified as clayey-skeletal, montmorillonitic, frigid Typic and Lithic Argixerolls. The parent material is the alluvium and residuum of mica, schist and quartzite. The pH ranges from 6.6-7.3 at all sampling locations. The sampling sites were from three different soil mapping units that included: Birchcreek-Itca complex, the Itca-Birchcreek-Rock outcrop complex and Poisonhol very stony loam (SCS, 1994). The Birchcreak-Itca complex soils are a mix of moderately deep to shallow well drained very stony loams on north-facing mountainsides with potential natural plant communities of *P. monophylla*, *J. osteosperma*, *Artemisia tridentata ssp. vaseyana* (mountain big sagebrush) and *Pseudoroegnaria spicata* (bluebunch wheatgrass). The Itca-Birchcreek-Rock outcrop complex is composed of shallow to moderately deep well drained soils on south-facing mountainsides with potential natural vegetation of *P. monophylla*, *J. osteosperma*, *A. tridentata ssp. vaseyana*, *P. spicata* and *Festuca idahoensis* (Idaho fescue). The Poisonhol very stony loam units are typically moderately deep and well drained soils with a potential natural vegetation of *A. tridentata ssp. vaseyana* and *P. spicata* (SCS, 1994). Each sampling location is described in detail below.

Site 1A was in a pinyon-juniper woodland within the Itca-Birchcreek-Rock outcrop complex with a south facing aspect on a 10° slope. The site had not burned in at least 100 years (Morris, 2006b). Total cover of the woodland was 47% with *J. osteosperma* making up 34% and *P. monophylla* was the remaining 13%. The understory cover was 38% grasses, 4% forbs, 9% shrubs and 49% bare ground. The dominant grasses remaining in the understory were *Poa secunda* (sandberg bluegrass) and *Poa pratensis* (Kentucky bluegrass).

Site 1B was in a sagebrush steppe community with a south facing aspect on a 5° slope. The site had not burned in at least 100 years (Morris, 2006b). This was the only sampling location in the Poisonhol very stony loam unit. Total cover of the vegetation on site was 22% grasses, 6% forbs, 51% shrub and 21% bare ground. While dominated by the shrub, *A. tridentata*, the grasses at this site included *Hesperostipa comata* (needle and thread grass), *P. secunda* and *B. tectorum*.

Site 2 was in a pinyon juniper community within the Birchcreak-Itca complex a north facing aspect on a 2° slope. The site had not burned in at least 100 years (Morris, 2006b). Total cover of the woodland was 56% with 18% of the cover from *J. osteosperma* and 38% from *P. monophylla*. The understory cover was 27% grass, 29% forb, 13% shrub and 31% bare ground.

This site had a substantial number of forbs in the understory in comparison to the other sites such as *Mertensia oblongifolia* (sagebrush bluebell), *Phlox longifolia* (longleaf phlox), and *Taraxacum officinale* (dandelion). The dominant grass was *P. secunda*.

Site 3 was in a burned pinyon-juniper woodland within the Itca-Birchcreek-Rock outcrop complex with a south facing aspect on an 8° slope. This site burned in 1999 (Morris, 2006b). Total cover of the former woodland could not be calculated as there were only scattered standing dead trees. The current cover at the site was 48% grasses, 23% forbs, 13% shrubs and 16% bare ground. Both forb and grass cover was dominated by introduced species such as *Alyssum desertorum* (desert alyssum) and *Descurainea sophia* (flixweed tansy mustard) as well as the introduced grass, *B. tectorum*.

Site 4 was formerly a pinyon-juniper woodland within the Birchcreak-Itca complex on a north facing aspect with a 10° slope. The site burned in 2000 and the previous woodland cover was unknown (Morris, 2006b). The current cover of the understory vegetation consisted of 38% grasses, 43% forbs, 6% shrubs and 13% bare ground. This site had a relatively diverse forb community in comparison to other sites. However, up to 29% of vegetation cover from forbs was from the introduced *Alyssum desertorum*. The introduced *B. tectorum* was the dominant grass and the shrub component was mainly the fire resistant *Chrysothamnus viscidiflorus* (rabbit brush).

Site 5 was formerly a pinyon-juniper woodland within the Itca-Birchcreek-Rock outcrop complex a south facing aspect on a 10° slope. The site burned in 2000 and the previous cover for the woodland was unknown (Morris, 2006b). The current cover of the understory vegetation consisted of 51% grass, 26% forbs, 1% shrubs and 22% bare ground. Although relatively high in grasses and forbs, this site was dominated by introduced and weedy species. The majority of grasses at this site were the introduced *B. tectorum* and the site's forbs were mainly introduced mustards, *Alyssum desertorum* and *Sisymbrium altissimum* (tumble mustard).

Methods

Soil Sampling

Soil sampling began in June 2006 and continued through October of 2007. At least two soil cores from the A horizon of the soil (approximately 10 to 20 cm in depth) were collected from each of the sites as near to vegetation transect tape as practical. Distance between cores was no

more than 10 m and care was taken to core in locations that did not appear to be recently disturbed by burrowing animals. The soil cores were divided into approximately 1 cm increments. Given the relatively short time period of interest, we believed the small increments should better reflect changes in phytolith assemblage. We did not assume a constant rate of soil development over that time. The 1 cm increment was the smallest stable section that could be effectively obtained from the soil cores. Depths should be considered relative to each core rather than absolute because some compaction occurred during the sampling.

Carbon Dating

One of the first assumptions we had to address was if the soils in our study area were stable and well stratified enough to examine questions of vegetation change over the period of interest. We conducted a carbon dating pilot study in 2006 on our initial soil cores. A set of four samples from two depths (5 cm and 10 cm) in two cores representing the two watersheds in the study area were sent to the National Ocean Sciences Accelerator Mass Spectrometry Facility (Woods Hole, MA, USA) for radiocarbon dating. Carbon dating samples were prepared by grinding the core segment with a mortar and pestle, removing coarse material through a 250 μm sieve, weighing out between 3 to 5 grams of soil for each sample, and placing it in a labeled glass vial.

The results were useful indicators for locating the appropriate depth in our cores that would potentially represent our time period of interest. An additional set of eight samples were then sent to the same facility for radiocarbon dating. This additional radiocarbon dating was used to determine which soil segments to process and how to frame the time period of interest between the present and the Little Ice Age within our cores.

Extraction of Phytoliths from Soils

Phytoliths were extracted from soil core segments in the laboratory. We selected segments of the cores for processing based upon the carbon dating results so that surface segments could be compared with those from the Little Ice Age first. We then selected one site in each watershed in the study area that demonstrated overall site stability and that had more than one carbon date available to frame the timeline in the core for detailed processing of each 1 cm segment.

The phytoliths were extracted using a modified standard wet oxidation and heavy liquid flotation methods outlined by previous researchers (Blinnikov, 1994; Pearsall, 2000). Acid digestion of organic material was carried out with a heated 70% HNO_3 solution for one hour on 2 g of soil sifted through a 250 µm sieve. We dispersed clays with a 5% solution of sodium hexametaphosphate. Our heavy liquid for density separation was sodium polytungstate (2.3 g cm^{-3}). The extractant was placed in a vial, dried at 80° C for 1-2 days. The extractant was stored dry in the vial.

The extracted material was weighed and recorded to four decimal points. Percent weight was determined by dividing the final extracted weight by the dry soil weight (2 g) and multiplying by 100 for each segment. The extractant weights are not solely from phytolith mass. The extractant includes some microscopic mica, quartz sand and charcoal because these materials have similar specific densities as phytoliths and float out with phytoliths during the extraction process (Piperno, 2006). The extractant also includes whole and broken portions of diatoms and sponge spicules that are also constructed of silica and, therefore, come out with the same density fraction as phytoliths. Some researchers have adjusted for the impurities in their sample weights by estimating the percentage of other material and subtracting that from the overall extractant weight (Evett *et al.*, 2007). We did not apply any "correction estimations" to the extractant weights because we felt these could introduce error that could obscure the overall pattern revealed by the total weights. This pattern and reasoning are covered more thoroughly in the results and discussion sections.

We used multiple cores from all six sites in the extraction weight analysis. Part of the reason we sampled three recently burned (since 1999) areas and three unburned (in the last 100 years) areas was to make sure that extraction weights were not influenced by the one time massive deposition event during recent fires. Even though the sites that had burned were formerly pinyon-juniper woodlands which do not generate phytoliths, we wanted to see if the microscopic charcoal generated or phytolith deposition from all remaining grasses on the site during the fire would influence the weight.

Phytolith Identification and Counting

Identification of morphotypes used in this study was based on a reference collection of 143 species of common Great Basin native and introduced plants (Chapter 2). That study examined

the relative frequencies of phytolith morphotypes in common native and introduced species of grasses (Tables III and IV). Their frequency analysis showed that introduced grasses produced nearly half (15%) of the total rondel frequency compared to native grasses (28%) (Table VI). They also reported on the typical phytolith types found in forbs, shrubs and trees. Some common forms in forbs included hairs, hairbases, and silicified epidermal sheets. These forms are typically not well preserved in sediments (Piperno, 2006) although they have been recovered from soils in sagebrush steppe sites in the Columbia Basin by Blinnikov (2005). The dominant trees in our study site, pinyon and juniper do not produce identifiable phytoliths (Chapter 2). However, as mentioned previously, *Artemisia tridentata*, a very common shrub in our study area produces a recognizable "blocky" form (Blinnikov, 2005; Figure 1n). Even so, grass phytoliths usually dominate phytolith counts even in sagebrush steppe sites (Blinnikov, 2005). "Stipa types" (Figure 10.a) have a bilobate shape in top view with a trapezoidal bottom in cross section and are produced in the grasses from the Stipeae tribe (Fredlund and Tieszen, 1994; Blinnikov, 2005). In Chapter 2, we also noted that the long wavy plate morphotype in *F. idahoensis* usually had deep lobes (Figure 10.c).

Therefore, based upon previous morphotype frequency work in the Great Basin (Chapter 2) and the Columbia Basin sagebrush steppe ecosystem type (Blinnikov, 2005), we counted fourteen morphotypes that we believed would be useful for identifying changes in the grass community, changes from native to introduced grass species, and representation of *Artemisia* (Figure 10). The nomenclature used for the fourteen morphotypes in this analysis follows the work in Chapter 2 and of Blinnikov (2005) who examined phytolith morphotypes in the nearby Columbia Basin. Their descriptions according to the International Code for Phytolith Nomenclature 1.0 were provided in Blinnikov (2005) and are not repeated here.

The morphotype differences between C_4 and C_3 grasses have been known for some time and used for understanding shifts in dominance of these grasses worldwide (Kaufman et al., 1985; Twiss, 1992; Fredlund and Tieszen, 1994). Most of the grass species in the study area are cool season bunch grasses with a C_3 photosynthetic pathway. Of the 66 grass species known to exist in the study area (John, 1995), only 5 are C_4 grasses. One of those is the introduced *Echinochloa crus-galli* (John, 1995) which has had a controversial grouping with the native *Echinochloa muricata* in the past (Gould et al., 1972) (Chapter 2). The only native C_4 grasses in the study

Species Name	Bilobate	Cross	Stipa Type	Plate wavy short	Plate wavy long	Long cell smooth	Long deeply indented	Long cell indented	Plate rectangular	Square-based hair	Round-based hair	Oblong knobby hair	Papillae	Pyramidal rondel	Keeled rondel	Horned rondel	Total Rondel	Other	Total
Native Grasses																	27		
Achnatherum hymenoides	0	0	39	1	0	28	1	1	5	1	8	0	0	1	1	10	13	1	136
Achnatherum nevadense	0	0	15	13	1	4	0	0	1	1	1	3	1	0	0	0	0	47	165
Hesperostipa comata	0	0	8	0	0	3	3	1	0	0	5	16	2	11	12	32	55	2	130
Elymus lanceolatus	0	0	0	0	0	6	1	6	1	1	2	0	0	13	45	24	82	3	120
Poa secunda ssp. juncifolia	0	0	0	2	6	20	6	13	1	6	1	0	0	8	7	4	18	25	109
Poa secunda ssp. secunda	0	0	0	5	1	14	5	9	1	0	11	0	15	4	21	0	24	14	111
Pseudoroegneria spicata	0	0	0	2	15	22	1	11	0	18	4	0	0	10	9	0	19	8	123
Festuca idahoensis	0	0	0	0	50	10	15	3	1	0	0	1	0	0	18	3	20	0	120
Hordeum brachyantherum	0	0	0	0	5	7	33	0	2	0	11	2	0	4	31	5	40	0	132
Elymus elymoides	0	0	0	6	14	9	17	2	4	1	14	0	1	14	6	0	20	13	112
Leymus cinereus	0	0	0	0	0	6	18	21	1	0	8	15	0	9	17	0	25	4	156
Introduced Grasses																	15		
Agropyron desertorum	0	0	0	0	0	0	22	22	0	12	2	2	0	10	11	1	22	11	139
Bromus inermis	0	0	0	0	0	6	1	0	0	1	3	0	71	2	2	1	4	14	126
Bromus japonicus	0	0	0	1	47	26	0	2	1	0	3	2	0	1	2	0	3	7	124
Bromus tectorum	0	0	0	0	18	18	9	1	1	1	19	0	19	1	2	0	3	10	136
Dactylis glomerata	0	0	4	7	45	18	2	2	0	0	0	0	0	2	5	0	7	15	130
Echinochloa crus-galli	59	18	0	11	0	3	0	8	0	0	0	0	0	2	0	0	1	0	111
Elytrigia repens	0	0	0	0	0	7	23	10	3	0	8	6	0	13	25	0	37	0	126
Phleum pratense	0	0	0	0	0	1	26	14	1	0	0	0	32	3	16	0	19	7	107
Poa bulbosa	1	0	0	3	23	34	17	4	2	0	1	0	0	8	4	0	12	0	113
Poa pratensis	0	0	0	1	7	16	13	0	1	0	6	0	0	2	19	23	44	8	119

Table VI Morphotype frequencies (expressed as percentages of total counted) of the ten native and introduced grasses in CIRO.

area were: *Distichlis spicata*, *Muhlenbergia richardsonis*, *Sporobolus aeroides* and *Sporobolus cryptandrus*. None of our sampling sites contained these species presently or were typical sites where they would have occurred in the potential natural vegetation. We believe, therefore, that finding distinctive C_4 morphotypes (e.g. bilobates) may be useful indicators of introduced grasses, vegetation change, historical land uses and as time markers in the soil profile since their timeframe of introduction is known (Chapter 2). We scanned our slides for these types but did not include them in the sum.

A small standard amount of the soil phytolith extract was suspended in Canada Balsam oil to enable three dimensional viewing, placed under a cover slip and sealed with clear fingernail polish for morphotype counting (Pearsall, 2000) using an Olympus BH-2 microscope. Typically, phytolith analysts count between 200 to 300 particles per slide (Piperno, 2006). We counted at least 200 phytoliths at 400x magnification by beginning at the left hand corner and working systematically down, across and up on each slide. We included the fourteen recognizable morphotypes in the total sum (Figure 10). We completed a full scan of the slides at 100x magnification to note any other morphotypes though they were not included in the sum (e.g. C_4 bilobates and forb hairs). We did not include phytoliths that were broken or partially dissolved so that the primary characteristic of identification could not be found. The level of dissolution was noted for each core.

We used the four sites (Sites 1B, Site 3, Site 4 and Site 5) that were dominated by introduced species (particularly *B. tectorum*) to test for the increase of rondels in older segments as a signal for native grass domination of the site in the past. We used the cores from Site 1A and at Site 3 for detailed analysis. These cores were selected for analysis because they were located on sites that appeared to be stable and well stratified. In addition, they shared several key characteristics such as soil type, slope, aspect, potential natural vegetation and recent invasion by pinyon-juniper woodlands. Both of these sites were also located in areas very near the historic overland emigration trail system and, therefore, shared similar grazing histories throughout the modern period (Morris, 2006a). One potentially important difference for phytolith composition was the current dominance of *Poa* species (with a moderately high total rondel frequency) at Site 1A and the current dominance of *B. tectorum* (with minimal total rondel frequency) at Site 3. The counting procedures and morphotypes were the same for both sets of analysis but only the total

percent rondel count is reported for the Sites 1B, Site 3, Site 4 and Site 5. The entire phytolith assemblage is reported for the detailed analysis in Sites 1A and Site 3.

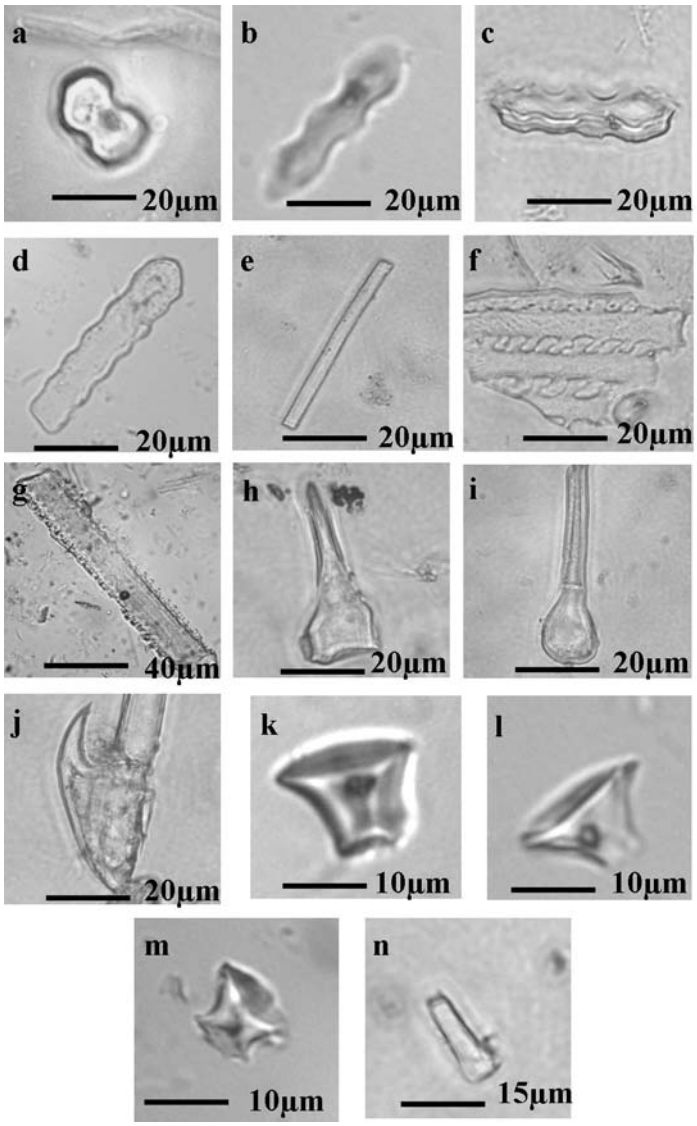


Figure 10 Morphotypes used in phytolith assemblage analysis; (a) stipa type (b) plate wavy short (c) plate wavy deep lobes (d) plate wavy long (e) long cell smooth (f) long deeply indented (g) long cell indented (h) square-based hair (i) round-based hair (j) oblong knobby hair (k) pyramidal rondel (l) keeled rondel (m) horned rondel (n) blocky.

Results

Carbon Dating

Our carbon dating results were useful at demonstrating that the soils in these pinyon-juniper woodlands and sagebrush sites were well stratified and relatively stable over the period of interest (Table VII). In other words, based on these results we can assume that the youngest soils were on top and the oldest soils were below. A date of ">modern" was assigned by the lab to samples with at least 95% of the radiocarbon concentrations from calendar year 1950 to present. Kerns et al. (2001) referred to her surface samples as "modern" and her subsurface samples, that were also mostly modern carbon, as "pre-modern" to reflect the assumption of younger soils on top even if they were both ">modern". This language seems appropriate for our results as well. We will, therefore, refer to the surface of the core (0-1 cm) as "modern" and the subsurface sections including the >modern dated segment as "pre-modern". All of the other radiocarbon dates fell within the Little Ice Age (250 ± 35 to 905 ± 35 ^{14}C years B.P.). We can then frame our time period of interest between modern, pre-modern and Little Ice Age soil segments within the cores.

Extraction Weights

The overall pattern across our multiple cores demonstrated a reduction in extraction weights in the modern core segments compared to the Little Ice Age segments. Both cores from each of the six sites were processed with the exception of Site 2 where one of the cores was found to be mislabeled. Therefore, a total of 11 cores with 32 core segments were processed. Twenty four of the segments were from 1 cm increments and eight of the segments came from 3-5 cm increments in the deepest part of the core.

There was variation in extraction weight between the sites as well as within sites from unburned (Figure 11) and burned sites (Figure 12). The burned areas tended to have more among site and within site variation as is shown in the differences in extraction weights at all three sites (3, 4 and 5). Sites 5 had the most variation between cores. Even so, the modern segments had lower extraction weights than the dated Little Ice Age and deeper segments in 5 out of the 6 cores from burned sites. Only the first core from Site 5 was essentially unchanged in extraction weight between modern and Little Ice Age and deeper segments. The unburned sites,

Site	Depth	Radiocarbon Age	Calibrated Calendar Age (1 Sigma Ranges)	Calibrated Calendar Age (2 Sigma Ranges)
Site 1A	9-10cm	> Modern		
	14-15cm	370 ± 25	Cal AD 1458-1515 Cal AD 1598-1617	Cal AD 1449-1524 Cal AD 1558-1631
Site 1B	9-10cm	410 ± 35	Cal AD 1439-1491 Cal AD 1603-1611	Cal AD 1429-1522 Cal AD 1573-1628
Site 2	4-5cm *	>Modern		
	9-10 cm	510 ± 30	Cal AD 1410-1435	Cal AD 1328-1341 Cal AD 1395-1445
Site 3	4-5 cm*	> Modern		
	9-10cm*	> Modern		
	14-15cm	695 ± 30	Cal AD 1274-1298 Cal AD 1372-1378	Cal AD 1264-1310 Cal AD 1360-1387
	19-20cm	905 ± 35	Cal AD 1044-1098 Cal AD 1119-1142 Cal AD 1147-1174	Cal AD 1037-1209
Site 4	9-10cm	540 ± 30	Cal AD 1329-1340 Cal AD 1396-1426	Cal AD 1317-1354 Cal AD 1389-1437
Site 5	9-10cm	250 ± 35	Cal AD 1529-1547 Cal AD 1634-1688 Cal AD 1781-1798	Cal AD 1519-1593 Cal AD 1619-1681 Cal AD 1738-1753 Cal AD 1762-1802

Table VII Results from radiocarbon dating bulk sediments from soil cores at all sites. Calibration of calendar ages from Stuiver, M., Reimer, P. J., and Reimer, R. W. 2005. CALIB 5.0. (http://calib.qub.ac.uk/calib/). * Data from pilot study cores.

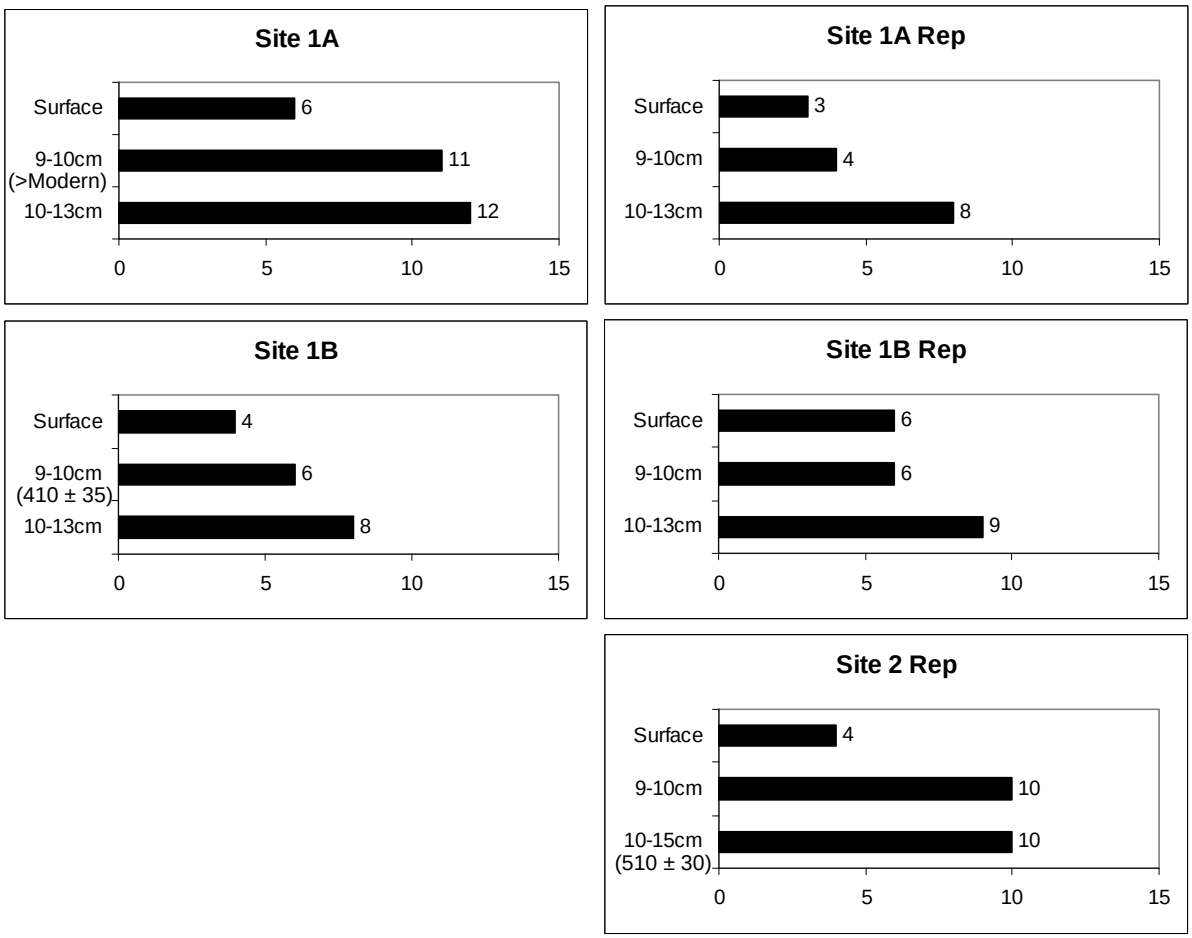


Figure 11 Percent extraction weights for core and replicate core for sites that had not burned in at least 100 years (Morris, 2006b). The first core for Site 2 was destroyed during mishandling in the laboratory. Radiocarbon dates in years before present are presented parenthetically when available.

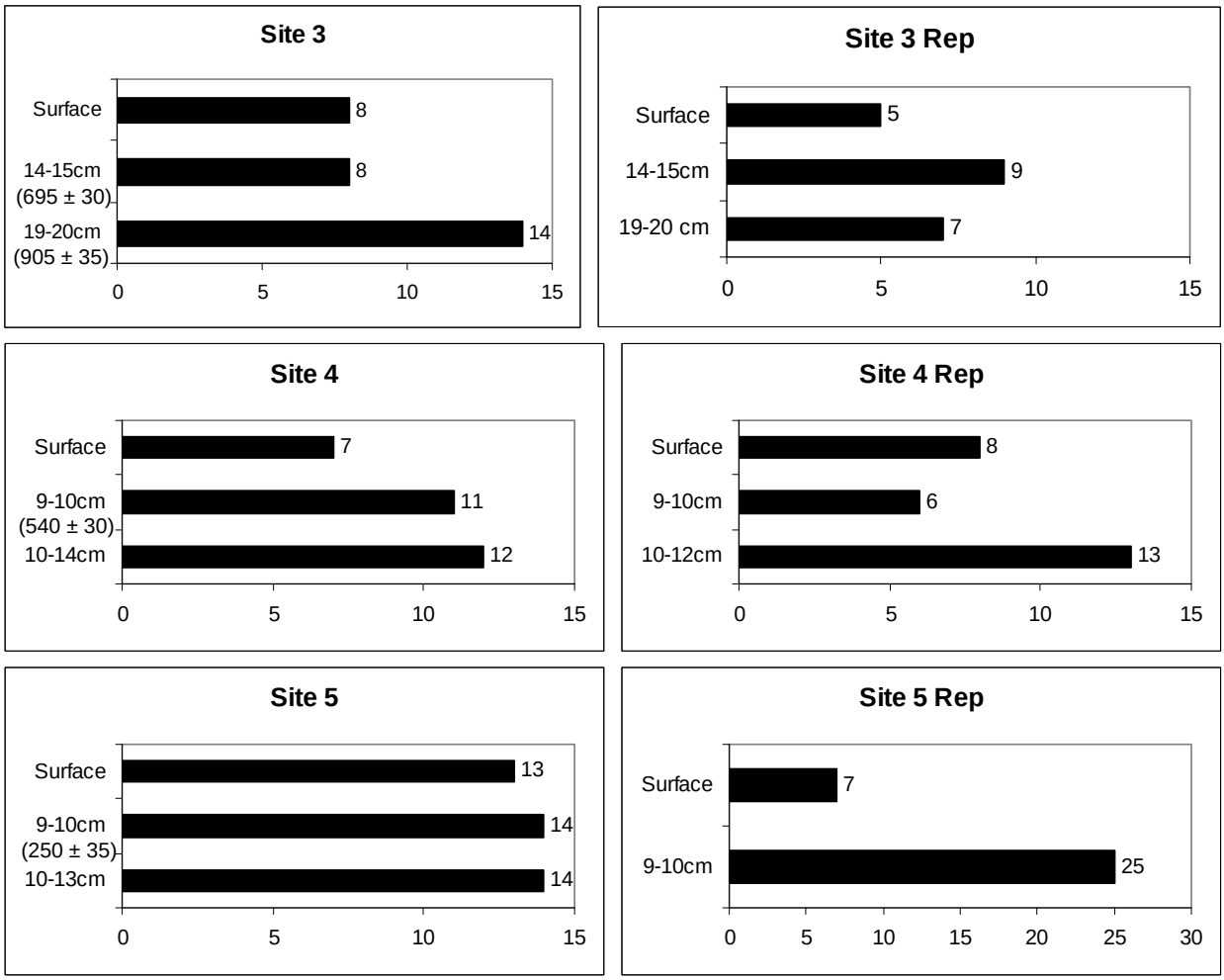


Figure 12 Percent extraction weights for sites that burned in 1999 and 2000 (Morris, 2006b). Radiocarbon dates in radiocarbon years before present are presented parenthetically where available.

on the other hand, had more consistent extraction weight patterns across and within sites. Typically, the lowest extraction percentage was in the modern segment and it increased with depth to the dated Little Ice Age and deeper segments. The reduction in percent extractant weight was almost half of the highest weight in the oldest segments at most unburned sites.

Total Rondel Counts

The results from phytolith analysis of the total rondel counts were consistent with our prediction at only two of the four sites dominated by *B. tectorum* (Figure 13). Site 1B and Site 3 both showed a marked reduction in total rondel percentage in the modern segments compared to

the Little Ice Age segments. In fact, total rondel percentages were reduced by nearly half at these two sites. Site 4 and Site 5, on the other hand, were not consistent with our prediction. The total rondel percentages at these sites were essentially unchanged between the modern and Little Ice Age segments.

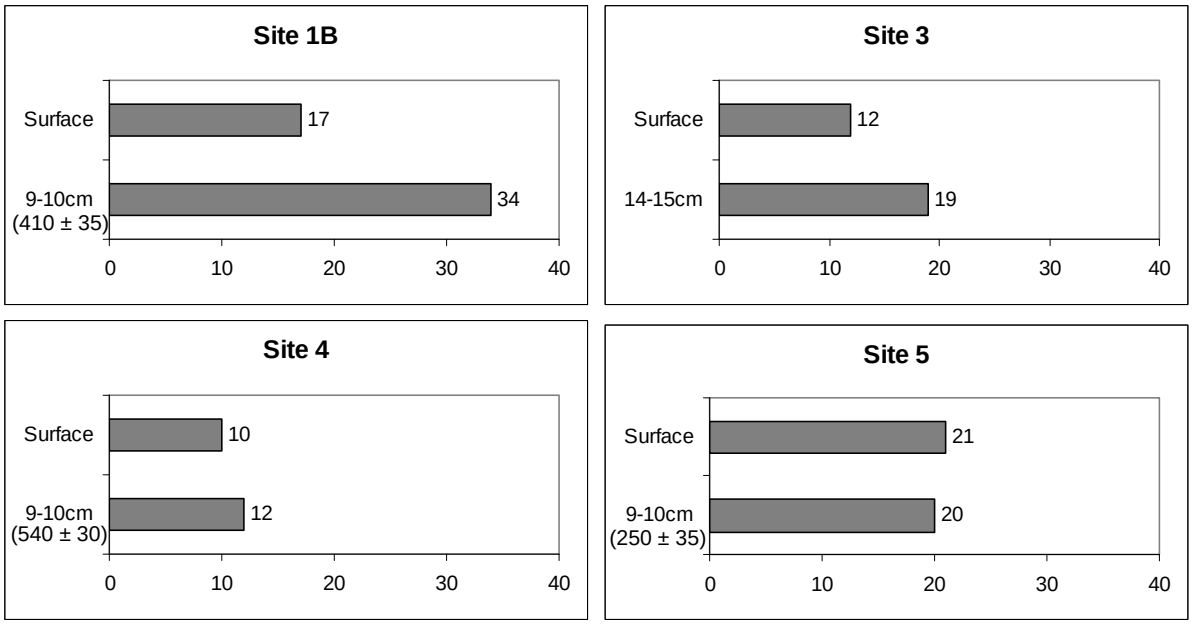
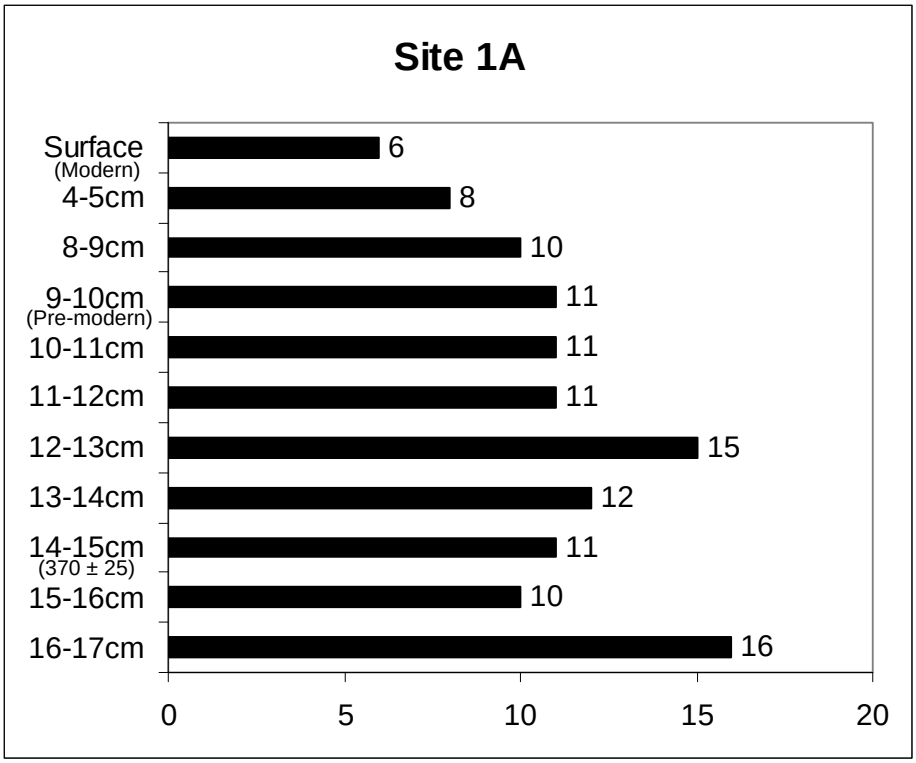


Figure 13 Percent rondels at four sites that were dominated by the introduced grass, *Bromus tectorum.* The information is expressed as all rondels counted, divided by the sum of all grass morphotypes multiplied by 100 to give percent rondels. Dates in radiocarbon years before present are present parenthetically.

Detailed core analysis

Detailed core analysis of each centimeter segment between dated portions in two of the cores from Site 1A and Site 3 revealed additional information regarding extraction weights (Figure 14), total rondel counts and soil phytolith assemblages (Tables VIII and IX; Figures 15 and 16).

The extraction weights at Site 1A varied throughout the core from 6-16% (Figure 14). There were two segments in the core where the extractant weights peaked: at 16-17cm (16%) and 12-13 cm (15%). The pattern seemed to follow our prediction that extraction weight would reflect the overall decrease in grasses at the site over time because the extraction weights dropped by nearly half from the 14-15 cm segment (370 ± 25 ^{14}C years B.P.) to the modern surface sample. By the beginning of the pre-modern segments (9-10 cm), the extractant weights had not gone



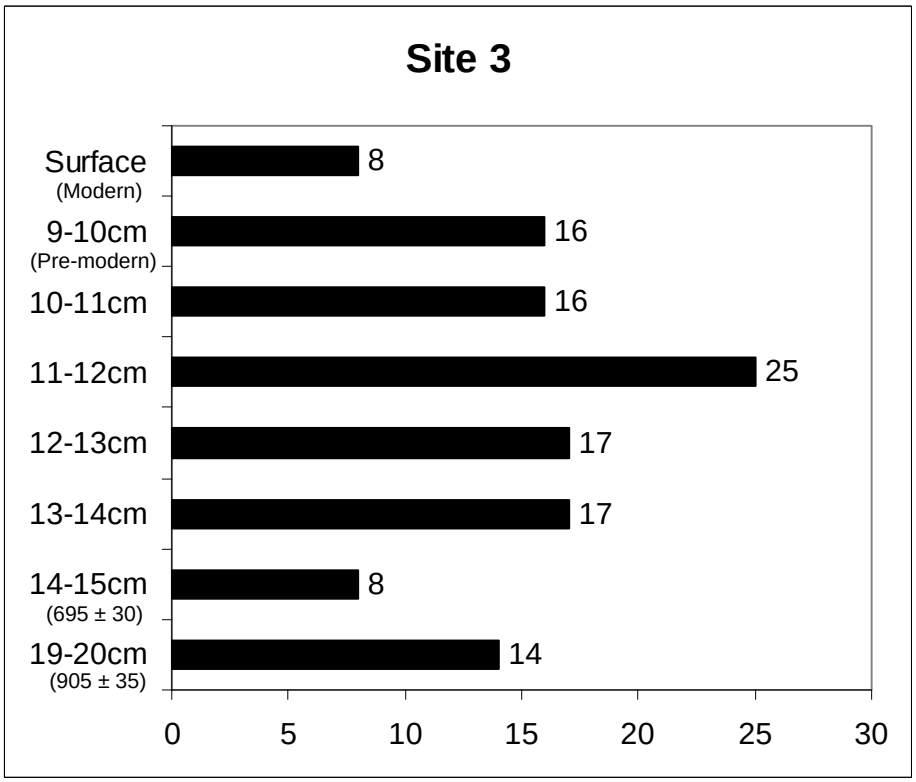


Figure 14 Percent extraction weights for detailed analysis cores. Site 1A is in pinyon-juniper woodland and Site 3 is in a former pinyon juniper woodland that burned in 1999 and is now dominated by introduced grasses and forbs. Segment ages are provide parenthetically where available. See Table II and text for details on radiocarbon dating.

below their historic range. However, the weights showed a steady decline through the sampled pre-modern segments beginning in the 8-9 cm segment (10%) and into the modern segment (6%).

The total rondel percentages also varied throughout the core in Site 1A (Table VIII and Figure 15). Total rondel percentages throughout the core ranged from 20% to 31%. The highest values for total rondels (25-31%) were in the four deepest segments (13-14 cm to 16-17 cm). Total rondel percentages declined abruptly between the 13-14 cm (31%) segment and the 12-13 cm segment (21%). The total rondel counts for the segments from the 12-13 cm and the 10-11 cm segment remained at lower percentages (20-22%) than the deepest four segments. Similarly, the pre-modern segments (9-10 cm to 4-5 cm) remained at percentages (20-24%) that were lower than the deepest segments. Site 5 and Site 1A were on similar soils with the same aspect and the same slope. The total rondel percentage at Site 1A from the 9-10 cm to 12-14 cm segments ranged from 20-22% where Site 5 at the 9-10 cm segment (250 ± 50 ^{14}C years B.P.) had 20% total rondels.

The soil phytolith assemblage at Site 1A also changed through each segment within the core and over time (Table VIII and Figure 15). Grass phytoliths dominate the record with blocky forms from *Artemisia* making up 1-7% of the total sum. The blocky forms of *Artemisia* fluctuated in the Little Ice Age segments (12-17 cm) from 1-4% and then dropped abruptly between 13-14 cm segment (6%) and the 12-13 cm segment (2%). The blocky forms increase just as abruptly back to 7% by the 11-12 cm segment and then remain consistent at 6% into the pre-modern and modern segments. As with the total rondel percentages, there were changes in the representation of several key morphotypes that began to shift between the 12-13 cm and 13-14 cm depths. It was here that the stipa type peaked, going from 1% to 4%, the wavy plates with deep lobes dropped from 12% to 5% and remained low, long wavy plates increased from 18% to 25%, keeled rondels decreased from 17% to 2%, horned rondels dropped from 9% to 6% and pyramidal rondels increased from 5% to 12%. Finally, it is at this 12-13 cm depth that the blocky morphotypes drop to a low of 2% and then quickly jump and maintain a higher level through to the modern segment. The long wavy plate with deep lobes, indicative of *F. idahoensis* (Chapter 2) was relatively more abundant in the deeper portions of the core (7-13%) and declined into the pre-modern segments. The long indented cells and keeled rondels also increased throughout the pre-modern segments from 10% to 16%. We observed a great deal of

Segment Age	Depth in centimeters	Extraction weight	Stipa type	Plate wavy short	Plate wavy deep lobes	Plate wavy long	Long cell smooth	Long deeply indented	Long cell indented	Square-based hair	Round-based hair	Oblong knobby hair	Pyramidal rondel	Keeled rondel	Horned rondel	Total rondel	Blocky (*Artemisia*)	Grass Total	Sum
Modern	**0-1cm**	6	1	4	5	18	23	2	16	3	2	4	10	10	3	23	6	215	228
	4-5cm	8	0	3	3	27	25	1	14	1	4	1	10	8	1	20	6	205	219
	8-9cm	10	3	4	3	20	28	0	12	2	3	1	6	12	6	24	6	212	226
Pre-Modern	**9-10cm**	11	2	2	3	27	31	0	10	0	3	1	15	5	2	22	6	213	227
	10-11cm	11	3	1	4	26	29	0	8	1	4	1	9	10	4	22	5	216	227
	11-12cm	11	3	4	7	22	26	0	13	1	2	1	9	7	4	20	7	216	233
	12-13cm	15	4	4	5	26	26	0	8	2	2	1	12	2	6	21	2	204	209
	13-14cm	12	1	3	12	25	18	0	7	0	1	0	5	17	9	31	6	204	217
370 ± 25	**14-15cm**	11	3	7	13	18	19	0	10	1	3	0	6	10	9	25	4	211	220
	15-16cm	10	2	3	13	14	23	0	9	0	2	0	11	11	9	31	1	203	206
	16-17cm	16	2	2	7	18	24	1	10	1	4	1	9	14	7	30	2	221	226

Table VIII Detailed core analysis results from Site 1A. Relative abundance of phytolith morphotypes expressed as a percent of the grass total for grass morphotypes and expressed as a percent of the total sum for the blocky (*Artemisia*) morphotypes. See Table II and text for details on segment ages. Extraction weights are expressed as percents of total sample weight (2 g).

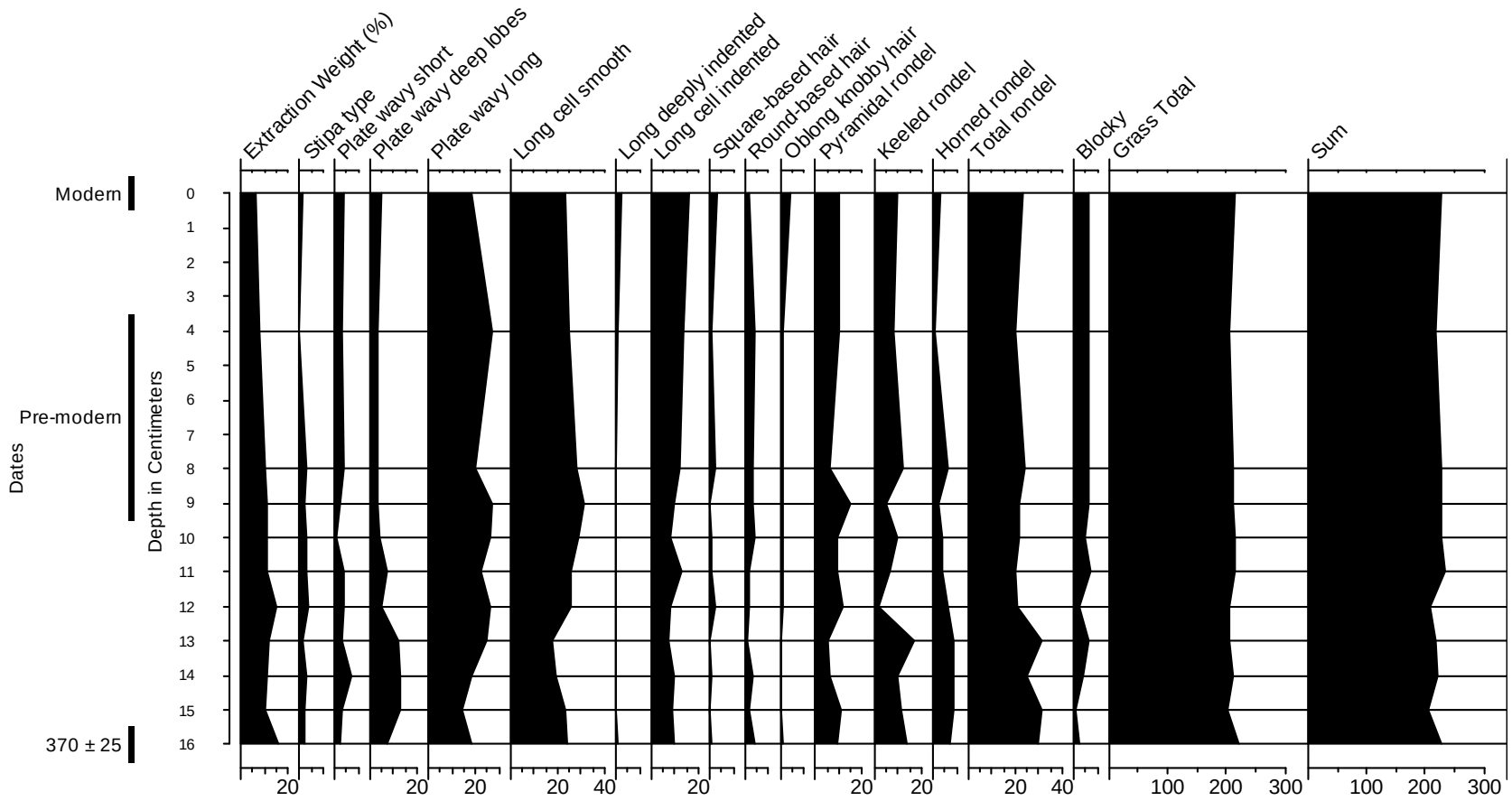


Figure 15 Phytolith percent diagram from detailed core at Site 1A.

dissolution and breakage of the phytoliths in this core beginning with the surface segment and progressing through the core.

Site 3 also had variable extractant weights throughout the entire core (Figure 14). The extractant weights ranged from 8-25%. Extractant weights were the same between the modern surface segment and the 14-15 cm segment (695 ± 30 ^{14}C years B.P.). However, the oldest segment at 19-20 cm (950 ± 35 ^{14}C years B.P.) had nearly twice as much extractant weight (14%) than the modern surface segment (8%). The oldest segments did not have the greatest extraction weights in the core, and this pattern did not appear to support our prediction that the lowest extraction weights would be in the modern samples and the highest in the Little Ice Age segments. However, it does still appear to follow our prediction of loss of grasses at the site with pinyon-juniper woodland encroachment in the more recent sediments. In fact, the extractant weight peaked at the 11-12 cm segment (25%) and then declined again in the next segment (16%) and through the pre-modern segment (9-10 cm). The extraction weights dropped by nearly half between the oldest segment (19-20cm) (14%) and the modern surface (8%) and between the pre-modern segment (16%) to the modern surface (8%). This was similar to patterns in the multiple core weight analysis (Figure 11).

Site 3 also appeared to support our prediction regarding the reduction in total rondel percentages at sites that were dominated by the introduced species of grass, *B. tectorum* (Table IX and Figure 16). Total rondel counts in this core ranged from 13% to 30%. The total rondel percentages were highest (27-30%) in the deepest three segments including the Little Ice Age segment (695 ± 30 ^{14}C years B.P.). Total rondel percentages declined from 30% to 23% between the 12-13 cm and 11-12 cm segments. They remained fairly consistent (23-26%) between 11-12 cm segment and the pre-modern segment at 9-10 cm. Then, they decreased by nearly half from the pre-modern segment (26%) to the modern surface segment (13%). Total rondel percentages declined by similar amounts across the different cores from Site 3 at the same depth (Figure 12 and Table IX). The detailed core total rondel percentage went from 27% at the 14-15 cm segment to 13% in the modern surface segment while the 14-15 cm segment from the multiple core study went from 19% to 12% in the modern surface segment.

The overall soil phytolith assemblage also changed over time throughout the core at Site 3 (Table IX and Figure 16). Grass phytoliths dominated the record with the blocky forms of *Artemisia* making up 3-8% of the total sum. Similar to the results in Site 1A, representation of

Segment Age	Depth in centimeters	Extraction weights	Stipa Type	Plate wavy short	Plate wavy deep lobes	Plate wavy long	Long cell smooth	Long deeply indented	Long cell indented	Square-based hair	Round-based hair	Oblong knobby hair	Pyramidal rondel	Keeled rondel	Horned rondel	Total rondel	Blocky (*Artemisia*)	Grass total	Sum
Modern	**0-1cm**	8	2	2	6	33	26	0	11	2	2	3	3	7	3	13	4	214	222
Pre-Modern	**9-10cm**	16	2	2	6	22	29	0	10	2	2	0	8	9	8	26	8	202	220
	10-11cm	16	8	1	8	20	24	1	10	0	3	1	3	10	11	24	5	225	238
	11-12cm	25	9	3	8	18	23	0	10	1	4	1	5	9	10	23	3	222	228
	12-13cm	17	5	2	7	18	24	0	7	2	2	0	6	16	8	30	4	228	237
	13-14cm	17	4	1	8	25	24	0	5	2	1	1	8	12	8	28	5	212	222
695 ± 30	**14-15cm**	8	5	3	8	16	24	0	12	0	3	0	7	10	9	27	4	229	238

Table IX Detailed core analysis results from Site 3. Relative abundance of phytolith morphotypes expressed as a percent of the grass total for grass morphotypes and expressed as a percent of the total sum for the blocky (*Artemisia*) morphotypes. See Table II and text for details on segment ages. Extraction weights are expressed as percents of total sample weight (2 g).

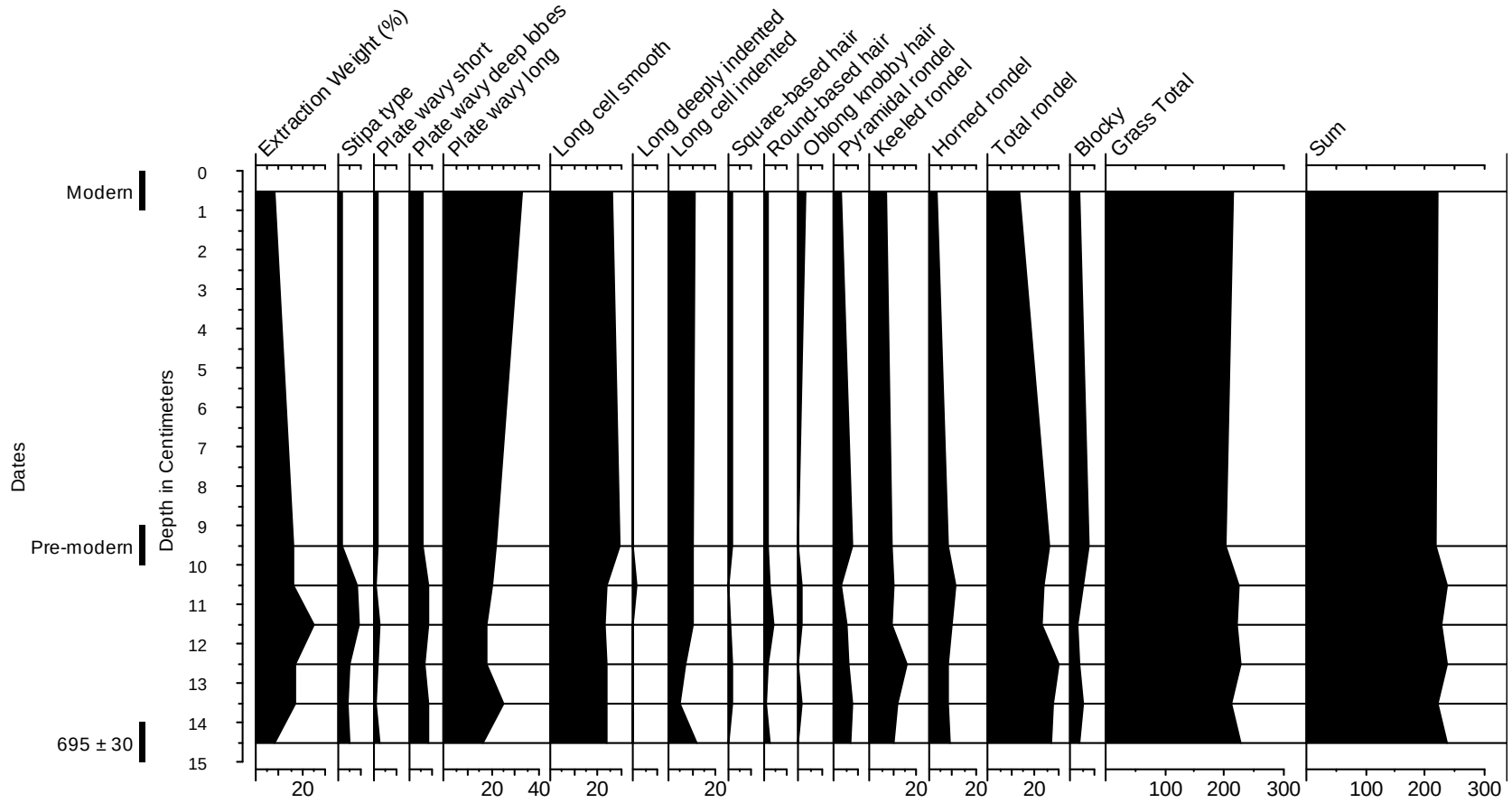


Figure 16 Phytolith percent diagram from detailed core at Site 3.

several key morphotypes began to shift between the 11-12 cm and 12-13 cm segments. It was here that the stipa types reached a peak from 5% to 9%, keeled rondels declined 16% to 9%, horned rondels increased slightly from 8% to 10% followed by a decline in the pre-modern and modern segments. Pyramidal rondels and wavy plate with deep lobes did not change as much as in Site 1A. In this core, the wavy plates with deep lobes were generally lower (6-8%) throughout all segments. However, like Site 1A, between the 11-12 and 12-13 cm segments, the total rondel percentage dropped by nearly 10% and blocky types for *Artemisia* also reached a low. The blocky types then jump to 8% in the pre-modern segment and drop again to 4% in the modern surface segment. Stipa types began declining into the pre-modern segment. Pyramidal rondels, keeled rondels and horned rondels all declined from the pre-modern to modern segment. The phytoliths in this core become progressively broken and weathered with depth in the core.

We did not encounter any of the phytoliths typically associated with native or introduced forb species in the Great Basin (Chapter 2) including hairs, hair bases, or silicified epidermal cells during the counts and scans for the detailed cores. Nor did we see any of papillae that were dominant in the frequency analysis (Tables III and IV). We observed the hairs of the introduced *Alyssum desertorum* in surface samples from Site 3 used in multiple core analysis. We also encountered two bilobate morphotypes that appeared to be from introduced C_4 grasses at the surface of Site 3 and at Site 1A in segment 12-13 cm. Other hairs (e.g. square-based and oblong knobby hairs) that were common in the frequency analysis were encountered and included in the sum, however, there were not any interpretable patterns linked with grass species that we could detect.

Discussion

Extraction weights

The results from our extraction weight analysis appeared to support our prediction that increases in woody vegetation over grasses would be reflected in extraction weight due to limited production of phytoliths in the woody species. The extraction weights from the multiple core study showed decreases of nearly 50% in weight from the surface to the Little Ice Age layers at most sagebrush sites and those recently dominated by pinyon-juniper woodland. Since most of our sampling locations were in areas where pinyon-juniper woodlands had recently encroached and dominated the site, more sampling should be done to examine extraction weights and

sagebrush cover. However, the decrease in extraction weights seemed to be strongly linked to the recent increase in pinyon-juniper woodlands. Evidence for this claim comes from the multiple core results as well as connections with extraction weight coupled with the information from the detailed core analysis.

The extraction weights in the detailed core at Site 1A reached maximum in the segments where the blocky phytoliths indicating *Artemisia* were the lowest percent of the sum. As *Artemisia* representation increased, the extraction weight actually decreased. This would be expected if the increased in woody vegetation was replacing the grasses. However, the extraction weights continue to decrease even though the *Artemisia* percentages did not change in the pre-modern and modern segments of the core. What was likely represented in this pre-modern and modern timeframe was increasing cover and density of the pinyon-juniper woodlands as well as increased grazing pressure (Morris, 2006a).

Likewise, the detailed core analysis at Site 3 showed a similar connection with pinyon-juniper woodland density. The extraction weight in the core at Site 3 also peaked at the time in which *Artemisia* representation was the lowest in the sum. The extraction weights continually decreased with increasing *Artemisia* representation, but the lowest extraction weight does not correspond with the highest percentage of sagebrush. In addition, the extraction weights and the *Artemisia* representation currently match the Little Ice Age segment (695 ± 30 ^{14}C years B.P.). However, the extraction weights followed the same pattern as Site 1A and decreased over time in the pre-modern to modern segments. Again, this change seems to correspond to an increase in pinyon-juniper woodland cover and potentially combined with increasing grazing pressure (Morris, 2006a). Increasing pinyon and juniper cover is known to suppress understory vegetation including sagebrush (Everett et al., 1983; West, 1991; West, 1999). The impacts come from not only above ground cover and duff accumulation, but also from dominance of the soil resources by the roots of *J. osteosperma* (Everett et al., 1983; West, 1991; West, 1999).

The pattern of extraction weights is consistent with increasing pinyon-juniper woodland cover in the recent past. However, more information is still needed to interpret the fluctuating extraction weight patterns in the deepest portions of both cores. Although they may appear to represent alternating pinyon-juniper woodland and grass domination at the sites, there is no evidence to support woodland encroachment during the Little Ice Age. In fact, woodland densities over the past approximately 200 years are generally three times greater than they were

at the end of the Little Ice Age (Tausch, 1999). Expansions of these woodlands in the just the last 130 years exceed anything that is found in other proxy records (e.g. woodrat middens and pollen) in the last 5,000 years (Miller and Wigand, 1994; Tausch, 1999). Since there are no recognizable phytoliths for *P. monophylla* or *J. osteosperma*, we cannot demonstrate that these were the cause of fluctuation in weight. Connections to other biological proxy records are needed for more interpretation in this matter.

Our extraction weights were higher than the "corrected" percent weights reported in other studies (Fisher et al., 1987; Kerns et al., 2001; Evett et al., 2007). The soils in the City of Rocks are formed on granitic parent material containing mica, schist and quartzite that come out in the same density fraction as biogenic silica. We did not use counts or percent cover of impurity estimations as others have done because we did not want to introduce a potential estimation error into the data. Our uncorrected extraction weights matched the ratios reported in other studies even if not their "corrected" values (Fisher et al., 1987; Fredlund and Tieszen, 1997). For example, Fisher et al. (1987) reported corrected mean percent weights in their forested sites (0.53 ± 0.035 se) that were half of those in their prairie sites (1.05 ± 0.018 se). Although there are variations in soils types, deposition variables and preservation rates across ecosystem types, this was the closest analogue to our study using weight analysis. Furthermore, we examined the potential for a one time deposition event of fire to increase extraction weights. We found that fire did not increase extraction weights and that microscopic charcoal impurities were not overshadowing the weights. Therefore, we believe that the higher values of our weights showed the influence of the soil parent material and that the ratios of our extractant weights were consistent with those reported in the literature.

Total Rondel Percents

We predicted that total rondel percentages would be less in the surface segments than in older subsurface segments across the multiple cores due to the increased dominance of introduced grasses. The relative abundances of total rondels did reflect the change in dominance from native to introduced grasses over time if the soils have been relatively stable. This pattern was especially pronounced at sites that were presently dominated by the invasive grass *B. tectorum*. This change was evident at two sites in the multiple core study. Total rondel percentages in the surface segments at Site 1B and Site 3 were nearly half those in the older,

deeper segments. This change coincides with the frequency analysis of rondel production between native and introduced grasses showing native production is nearly twice that of introduced grasses. However, the pattern did not hold for the other two sites. We believe that the surface soil segments at Site 4 and Site 5 experienced erosion and mixing following the recent fire in 2000. The variation of the extraction weights between cores and the lack of variation in total rondel counts support this conclusion. The similarity of total rondel counts at similar depths across the cores at Site 5 and Site 1A suggested that only the surface sediments mixed and the deeper portions remained stable.

The pattern of reduction in total rondel percentages was evident in the detailed core analysis as well. In the core used for detailed analysis at Site 3, the total rondel count decreased by 50% from the pre-modern segment to modern surface segment and was also nearly half of the total rondel percentages in all the deeper (and older) segments. Declines in total rondel percentages were also similar in the different cores from Site 3. The total rondel percentage declined in the detailed core at Site 1A but not as much as at sites dominated by *B. tectorum*. This was probably due to the fact that Site 1A is currently dominated by *Poa* species which also tend to produce moderately high percentages of rondels (Table III).

We observed that areas with the greatest cover of *Agropyron desertorum* had been seeded in the past (unpublished data). Since we had to sample from untilled areas, we did not directly test changes in total rondel percentages under dominance of this species. Even so, this and other species of introduced grass in the study area could influence the phytolith record through wind transport and livestock dung. This grass, as well as the other common introduced species will spread easily in these ecosystem types, but none has been as widespread dominant an invader as the *B. tectorum* (Bradley and Mustard, 2005). *Bromus tectorum* was the most common invasive grass species on sites with no cultivation (Morris, 2006a).

Evidence of Vegetation Change in the Detailed Core Analysis

The detailed analysis of soil cores by one centimeter segments demonstrated that phytolith assemblages changed over time at a very fine scale with continuous sampling. These phytolith assemblages also appeared to be linked to known vegetation changes and they shared commonalities across cores.

The phytolith assemblages at Site 1A changed from the bottom of the core, representing the Little Ice Age (~ 500 cal. years B.P.), to the pre-modern and modern segments. The phytolith assemblages from approximately 13 to 17 cm in depth were consistent with what would be expected during generally cooler and wetter conditions of this time period. For example, the total rondel percentages were the highest we found (25-31%). Blinnikov (2002) reported that total rondel percentages in the Columbia Basin in the range of 30% were indicative of *F. idahoensis,* and also implied cooler, wetter conditions. The long wavy plates with deep lobes, also indicative of *F. idahoensis* (Chapter 2), were also relatively more abundant in these deeper portions of the core. Finally, keeled rondels, also produced with relatively high frequency in *F. idahoensis* (Table III), were relatively high in the deeper portions of the core.

There was an apparent shift in the phytolith assemblage between the 12-13 cm and 13-14 cm segments at Site 1A where *Artemisia* blocky forms, deeply lobed (*Festuca*) morphotypes, keeled and horned rondels, and the total rondel percentage all decreased while the stipa types increased. This shift suggests a drying period at the site (Blinnikov et al., 2002). The morphotypes for both *Festuca* (e.g. long wavy with deep lobes and keeled rondels) and Stipeae tribe grasses (*A. hymenoides*, *A. nevadense* and *H. comata*) declined after this segment. Long wavy plate morphotypes began to increase around the same time that the *Festuca* deep lobed wavy plates dropped. This could reflect an increase in the *P. spicata* at the site as it is also a common producer of this morphotypes (Table III). *Festuca idahoensis* is commonly replaced by *P. spicata* and Stipeae grasses when moisture decreases or there is strong grazing pressure (USDA, 2007).

Grass composition also changes in the pre-modern to modern segments. The stipa types peaked at 12-13 cm segment then decrease steadily into pre-modern and modern portions. Coincident with the decrease in Stipeae grasses were the indications of an increasing contribution of the *Poa* species from long indented cells and keeled rondels. This loss of the Stipeae grasses is consistent with what is known about both grazing pressure and increasing pinyon-juniper cover at the site. While Stipeae grasses (e.g. *H. comata* and *A. hymenoides*) and *Poa* species are all palatable to livestock, *Poa secunda* is more resistant to grazing, trampling and increasing cover and duff from of pinyon-juniper woodlands (Everett et al., 1983; Monsen et al., 2004). *Poa* species now dominate grass cover under the canopy at this site.

The phytolith assemblages at Site 3 also changed from the bottom of the core, representing the Little Ice Age (~ 700 cal. years B.P.) to the pre-modern and modern segments. In this core, the bottom three segments from 12-15 cm also seemed to reflect the generally cooler and wetter climate during the Little Ice Age. As in Site 1A, the total rondel percentage were much higher in these segments and were within the 30% range that Blinnikov (2002) said represented *Festuca* dominated, cooler and wetter sites. The wavy plate with deep lobes, typical of *F. idahoensis* (Chapter 2), remained fairly consistent in this core. Dissolution and breakage may have played a role here. The deep lobes on this morphotype can be broken or worn down. The deepest segments in this core were older and had a great deal of breakage and dissolution. However, the keeled rondel morphotypes, also produced in high frequency in this grass (Table III) were highest in these lower sections of the core.

Similar to the core in Site 1A, there was an apparent shift in the phytolith assemblage that occurs between two segments. In Site 3, this shift occurred between the 11-12 cm and the 12-13 cm segments. As was observed at Site 1A, there was a drop in the total rondel percentage, keeled rondels and the *Artemisia* blocky types between these depths. In addition, the stipa types increased sharply. Horned rondels, also produced with great frequency in Stipeae grasses, began to rise. Again, this shift suggested a change to a drier climate at the site around this time. This could represent the end of the Little Ice Age.

Vegetation also changed in the time represented by the pre-modern segment and modern segments. After the spike in representation of the stipa type and horned rondels indicative of the Stipeae grasses, these types declined over time into the pre-modern segment. Across the same segments, the representation of the *Artemisia* blocky form increased. This pattern appeared to reflect the known increase in sagebrush cover, loss of native grasses, and finally encroachment of pinyon-juniper onto the site. These changes could be from increasing grazing pressure, drought and encroachment of the pinyon-juniper woodland. The decline by 50% in the representation of the total rondels seemed to support the increasing dominance of the invasive *B. tectorum* at the site. Unlike Site 1A, this site burned in 1999 and was dominated by invasive grasses and forbs.

Our interpretations of the changes in these phytolith assemblages were similar to other findings from soil sediments. Blinnikov (1994) was the only study that we are aware of in which fine scale continuous sampling (0-2 cm segments to 15-30 cm total depth) of natural soil sediments was used to examine vegetation change. His study was conducted in alpine soils of

the Northwestern Caucasus, Russia (Blinnikov, 1994). He also found that the soil phytolith assemblages changed over time with fine scale continuous sampling. Increases in the morphotype associated with *Nardus stricta* in the upper segments, a grass typically avoided by sheep, was interpreted to reflect historic overgrazing. Kerns et al. (2001) found changes the phytolith assemblage between surface segments (0-2 cm) they called "modern" and subsurface segments (2-7 cm) they called "premodern". They observed a decrease from surface to subsurface samples in a crenate morphotype (similar to our wavy types) that were typical of two native grasses, *Koeleria macrantha* and *Bromus ciliatus*. Because these grasses are palatable forage species, they suggested that the decrease could be related to excessive grazing. In addition, these researchers pointed to the negative impacts of duff buildup under forest canopies to grass production as a related cause. Their findings and explanations are consistent with ours.

Effectiveness of Phytolith Morphotypes in the Detailed Core Analysis

Some of the morphotypes that made up a substantial portion of the frequency analysis (Table III) were not useful in interpreting the soil phytolith assemblage. Although the different types of grass hairs appeared to be important indicators for different native and introduced species in the frequency analyisis, their patterns within the soil were not useful. For example, the oblong knobby hair was produced with great frequency by *H. comata* but its representation within the sums did not fit with any of the other patterns demonstrated throughout the cores. Likewise, pyramidal rondels were not a useful indication of vegetation change. Long deeply indented cells that can be prevalent in the Triticeae tribe of grasses (e.g. *Hordeum brachyantherum* and *Elymus elymoides* and *Agropyron desertorum*) were negligible and not used in our interpretation.

Other researchers have pointed to morphotypes such as papillae (Blinnikov et al., 2002) or long hairs (Fisher et al, 1995) as indicative of the introduced grass species *B. tectorum*. Our frequency analysis also showed highest frequencies of papillae in *Bromus.* Fisher et al (1995) reported significant decreases between surface samples and buried horizons in the long hair morphotypes as a sign of current dominance of this invasive grass. Blinnikov et al. (2002) also recovered hairs, hair bases and epidermal sheets typical of herbaceous plants from modern soils, loess, and paleosols. We did not count any papillae, long hairs or epidermal sheets in our samples. We observed hairs in our sediments but very few of the types found in herbaceous plants in our reference collection. Our use of a 250 μm sieve should not have excluded all of

them from our slides and our methods of extraction and counting closely followed Blinnikov et al. (2002). Perhaps differences in preservation rates in the soil types between our study sites were a factor in the absences of these phytoliths in our samples. Dissolution and breakage of the phytoliths seemed high in both cores especially at the surface of the younger segments in Site 1A. It may also be more effective to separate the silt and sand fractions as others do in forested systems to help increase counts of large, rare morphotypes like hairs (Piperno, 2006).

We did observe several of the bilobate morphotypes associated with introduced C_4 grasses at two sites at different depths. At Site 3, they were observed in the surface segments as would be expected if these morphotypes were an indication of introduced species. They were also observed at Site 1A in the 12-13 cm segment where the overall phytolith assemblage begins to shift and the extraction weight peaks. This observation could represent the beginning of overland emigration in the area or the introduction of livestock. Both could have transported C_4 grass morphotypes in dung, mud, fur, boots and the like. However, this is purely speculation at this point and should be explored in further sampling.

Evaluation of the Method

In general, our results indicated that soils in pinyon-juniper woodlands and sagebrush steppe can be stable and stratified well enough to reflect some changes in vegetation over time using soil phytolith analysis. This seemed to be the case for both the historic period (~200 years) and the Little Ice Age. However, an understanding of the site history was crucial for choosing a sampling location selection and interpretation with this method because many areas containing these ecosystem types have been plowed historically (Morris, 2006a). As can be seen from the variations in extraction weight between cores at burned sites and the insensitivity of total rondel percentages, areas that have not burned recently may be preferable sampling locations. This is particularly true if the analysis will include portions of the pre-modern soils because there could be more mixing from erosion in the upper segments associated with the fire. We did not do any additional sampling between the pre-modern and modern surface segments at Site 3 because of this.

Our results also showed the importance of using multiple cores. This type of analysis helped locate more stable sites and provided more rigor for the interpretation as comparisons could be made within sites and across them. It would be useful to test for a few known changes in the

vegetation as we have done here before embarking on detailed core analysis. Also, our pilot study for carbon dating from several different cores was very useful for narrowing down the portions of the cores for further dating and analysis. The detailed core analysis of continuous segments in 1 cm increments was most useful for conducting detailed vegetation change studies. Clearly, there was more to be learned from the transitions in between the Little Ice Age, pre-modern and modern segments than 2-3 samples per core could provide.

Conclusion

This is the first study to examine the use of soil phytoliths in a continuous core sampling method in these ecosystem types. We found that these soils can be stable and well stratified enough to record changes in the vegetation if the sampling is done with care to find unburned sites with gentle slopes outside of cultivated areas. The utility of soil phytolith analysis was tested by looking for known vegetation changes in the soil stratigraphy such as increased cover of woody species like sagebrush and pinyon-juniper woodlands. Extraction weights tracked increases in pinyon-juniper woodland cover and density in the recent past. Phytolith assemblages in the soil stratigraphy also reflected increasing dominance of invasive grass species like *B. tectorum*. Finally, detailed analysis at a fine scale of extraction (1 cm increments) revealed shifts in soil phytolith assemblages that suggested connections to changes in climate, vegetation and land uses from the Little Ice Age to present. Soil phytolith analysis appears to hold promise as a biological proxy for understanding historic and prehistoric environmental conditions and deserves further exploration and research.

We interpreted our phytolith assemblages from the detailed cores using frequency analysis of phytolith production in extant plants and from modern analogues in the literature that relate assemblages to present vegetation in reference areas. Future research should seek more information about historic plant communities in these ecosystem types through modern analogue studies of reference areas. Reference sites for this type of modern analogue study were not available in the City of Rocks particularly in the valleys where a great deal of historic soil disturbance occurred with dry farming and forage seeding in the past. Based on our findings, soil phytolith analysis is a useful biological proxy for examining vegetation changes since European settlement as well as into the Little Ice Age. More work should be done combining the

human archive and soil phytolith analysis as modern analogue studies from within the Great Basin region to explore its utility.

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