1Article Type: Original Article

2Title: *Phytolith Concentration and Morphotypes in Modern Soils of the Columbia Basin,*

3*USA as Indicators of Vegetation Composition and Cover*

4Authors: Reyerson, P.E.[a, 1], corresponding author

5   Affiliation Address:

6   [a]Department of Geography

7   St. Cloud State University

8   Stewart Hall 344

9   720 4th Ave South

10   St. Cloud, MN 56301

11   USA

12   Present Address:

13   [1]Department of Geography

14   University of Wisconsin-Madison

15   160 Science Hall

16   550 North Park Street

17   Madison, WI 53706

18   USA

19   Phone: 320-260-0624

20   Email: reyerson@wisc.edu

21   Research interests: Quaternary vegetation dynamics, paleoenvironments,

22   biogeochemical cycles

23   Blinnikov, M.S.[a]

24   Affiliation Address:

25   [a]Department of Geography

26   St. Cloud State University

27   Stewart Hall 344

28   720 4th Ave South

29   St. Cloud, MN 56301

30   USA

31   Phone: 320-308-2263

32   Email: msblinnikov@stcloudstate.edu

33   Research interests: Quaternary paleoecology, phytolith analysis

34   Busacca, A.J.[b]

35   Affiliation Address:

36   [b]Department of Crop and Soil Sciences

37   Washington State University

38   245 Johnson Hall

39   P.O. Box 646420

40   Pullman, WA 99164

41   USA

42   Phone: 208-885-7505

43   Email: busacca@wsu.edu

44   Research interests: Pedology, geomorphology, paleoclimatology

45   Gaylord, D.R.[c]

46   Affiliation Address:

47   [c]School of Earth and Environmental Sciences

48   Washington State University

49   1146 Webster Physical Sciences Building

50   Pullman, WA 99164

51   USA

52   Phone: 509-315-8127

53   Email: gaylordd@wsu.edu

54   Research interests: Quaternary eolian-climatic interactions; clastic

55   sedimentary environments

56   Rupp, R.[b]

57   Affiliation Address:

58   [b]Department of Crop and Soil Sciences

59   Washington State University

60   405 Johnson Hall

61   Pullman, WA 99164

62   USA

63   Phone: 509-335-2381

64   Email: richard_rupp@wsu.edu

65   Research interests: remote sensing, GIS

66   Sweeney, M.R.[d]

67   Affiliation Address:

68   [d]Earth Sciences Department

69   University of South Dakota

70   414 East Clark Street

71   Vermillion, SD 57069

72   USA

73   Phone: 605-677-6142

74   Email: mark.sweeney@usd.edu

75   Research interests: Geomorphology, sedimentology, paleoclimatology

76   Zender, C.S.[e]

77   Affiliation Address:

78   [e]Department of Earth System Science

79   University of California-Irvine

80   3200 Croul Hall

81   Irvine, CA 92697

82   USA

83   Phone: 949-824-2987

84   Email: zender@uci.edu

85   Research interests: Climate, surface-atmosphere interaction

86

87**ABSTRACT**

88The goals of this paper are to assess feasibility of using total concentration (TPC) of

89phytoliths in modern soils and morphotypes in soil assemblages to infer paleovegetation

90cover and composition. We sampled from undisturbed grassland sites with different

91values of shrub and grass cover in the Columbia Basin, interior Pacific Northwest, USA.

92Phytolith concentration in soils were measured and all morphotypes counted. Estimates

93of vegetation cover were obtained using NDVI values derived from multispectral digital

94imagery. Linear regression was used to predict NDVI values based on TPC in soils.

95Linear regression revealed a direct positive relation between vegetation cover and TPC

96(R^2 = 0.49). Estimates of vegetation cover averaged over multiple years may increase it's

97relation with TPC. CCA was used to assess the degree of similarity between field plots.

98The morphotypes-species correlations for the axes are moderately high (r=0.863 and

99r=0.660 for the first two axes, respectively), suggesting that phytoliths reflect vegetation

100plot compositions with moderately high certainty. We conclude that phytoliths reflect

101modern vegetation in grasslands and shrublands on the Columbia Basin. Estimates of

102vegetation cover reflect annual and inter-annual trends, while the phytolith assemblages

103from modern soils reflect the vegetation averaged over a decadal to centennial scale.

104

105**Keywords**

106Grasslands, modern analogs, phytoliths, morphotypes, Columbia Basin, Palouse

107

108**INTRODUCTION**

109The Columbia Basin is located in a semi-arid portion of the U.S. Pacific NW behind the

110rain shadow of the Cascade Mountains (Fig. 1). The Columbia Basin is a structural and

111topographic low and subprovince of the Columbia Intermontaine Physiographic Province

112(Freeman et al., 1945; Baker et al., 1991). The Columbia Basin lies south of the

113maximum extent of the Cordilleran Ice Sheet, and largely south and east of the Columbia

114River. The total area of the basin exceeds 160,000 km^2. Large portions of the Columbia

115Basin in SE Washington State are blanketed by thick layers of Quaternary loess

116(windblown silt). Known informally as the Palouse Loess, these deposits have been

117molded into rolling hills that dominate the topography of much of eastern Washington

118(Baker et al., 1991; Busacca and McDonald, 1994). Modern soils that developed on the

119loess are mostly Mollisols or Aridisols (Baker et al., 1991). These surface soils form

120along a strong climatic (primarily moisture) gradient that correlates with a decrease in

121precipitation across the Columbia Basin from NNW to SSE (Bolig et al., 1998) (Fig. 1).

122   Because of the semi-arid climate, few sedimentary repositories have existed on

123the Columbia Basin during the Late Pleistocene to Holocene that have favored either

124pollen or macrofossil preservation. Lakes are scarce, and the majority are less than

12510,000 years old (Mack et al., 1976). Minckley and Whitlock (2000) presented a regional

126modern pollen assemblage dataset from which they assessed the spatial variability of

127pollen influx across the Pacific Northwest; but their data came primarily from sites closer

128to the Cascade Mountains, and not from the lower, drier Columbia Basin.

129   In the absence of a pollen record, phytoliths have emerged as a powerful proxy

130for determining vegetation composition in arid and semi-arid regions in North America

131(Fredlund and Tieszen, 1994; Fearn, 1998; Kelly et al., 1998; Kerns, 2001; Blinnikov et

132al., 2001, 2002; Parker et al. 2004; Blinnikov, 2005). Many taxa (particularly grasses,

133forbs, shrubs, and trees) produce phytoliths in their cell walls and intercellular spaces.

134Phytolith production is taxonomically specific and genetically controlled (Hodson et al.,

1352005). The abundance and persistence of phytoliths in soil are considered by many

136researchers to be directly related to the plant biomass of silica-producing species and the

137amount of time the vegetation existed at the site (Bartoli and Wilding, 1980; Fredlund

138and Tieszen, 1994; Alexandre et al., 1997b; Blinnikov, 2005; Blecker et al., 2006). In

139temperate, semi-arid areas such as the Great Plains or the Columbia Basin, phytoliths can

140persist for thousands of years in soils under a variety of pH and moisture conditions

141(Kelly et al., 1998; Blinnikov et al., 2001; Blinnikov et al., 2002; Reyerson, P.E.).

142   Working in the Loess Plateau of China, Lu et al. (2005) provided compelling

143evidence that phytolith morphotypes can be used to reliably estimate mean annual

144precipitation, temperature and other climate variables on regional scales. While the Loess

145Plateau is a semi-arid region, it does receive climatically driven dust influx from the Gobi

146Desert. Thus, phytolith reconstructions in regions such as the Loess Plateau can supply

147valuable data in regard to global drylands. Phytolith analysis has been used within deserts

148as well, for paleovegetation (Parker et al. 2004), and archaeological (Albert et al. 2008)

149reconstructions.

150   Blinnikov et al. (2002) used the modern analog method to reconstruct

151paleovegetation of the interior Pacific Northwest (Columbia Basin) from an

152approximately 100,000 yr record of phytoliths preserved in the Palouse loess. However,

153the modern dataset used in that study did not provide adequate quantitative estimates of

154the vegetation cover. Further, Blinnikov et al. (2002) chose to distinguish forest,

155grassland and shrubland vegetation of the large region, not specific grassland types.

156   In this paper, we refer to 'vegetation composition' as the presence and abundance
157of certain silica-producing plant species and 'vegetation cover' as the percentage of plant
158canopy cover, which is estimated by the normalized difference vegetation index (NDVI).
159Many studies have demonstrated that vegetation composition influences, at the very least,
160the presence and abundance of specific phytolith morphotypes (Verma and Rust, 1969;
161Blinnikov et al., 2002; Reyerson, P.E.). However, few studies have focused on the
162relation between vegetation cover and total phytolith concentration in modern soils
163(which we term 'total phytolith concentration', or TPC, expressed as a percentage of dry
164weight of extracted phytoliths from the dry bulk soil).

165   Two specific research questions are explored in this paper. First, to determine if
166assemblages of phytolith morphotypes from modern soils collected on standard
167vegetation plots (6 x 6 m) within a relatively small geographical area (ca. 30,000 km^2)
168reliably reflect modern grassland and shrubland vegetation composition. By focusing on a
169relatively limited area of study we believe we can more confidently resolve local-scale
170differences in vegetation cover and composition than has been done previously. Second,
171if measures of TPC in modern topsoil can be used to predict estimated plant percent
172cover obtained through remote sensing (e.g., NDVI) on the same plots. The results from
173this study will be used to constrain the accuracy of paleobotanical data we will provide to
174numerical climate modelers.

175   In paleovegetation reconstructions, it is prudent to calibrate estimations of the
176paleoecological make-up of the area in question when possible for greatest accuracy.
177Modern phytolith assemblages and distributions for a given region must be recognized
178before paleoenvironmental reconstructions can be undertaken with any certainty
179(Bowdery, 1998; Carnelli et al., 2001; Lu and Liu, 2003; Blinnikov, 2005). Hence, this
180study is an important first step toward measuring and understanding the late Pleistocene
181and Holocene paleoenvironments of the Columbia Basin. Such reconstructions can be
182used to establish vegetation boundary conditions for input into numerical paleoclimate
183models. Such paleobotanical boundary conditions are necessary to estimate dust flux
184rates from the paired (sand: silt/clay) eolian system since the last glacial maximum
185(LGM) (Mahowald et al., 2006), when episodes of heightened eolian activity, including
186loess generation and deposition, have been recorded (Sweeney et al., 2005).

187   The results of this study can be used in any environment where phytolith
188accumulation in soils is common. While this study uses phytolith assemblages from
189grasslands and shrublands, the techniques presented here are directly applicable to arid
190environments (sensu Parker et al. 2004).

191

192**METHODS**

193

194**Field data collection**

195

196A total of 37 modern soil samples were collected across the Columbia Basin (Fig. 1;
197Table 1). Sample sites were chosen primarily on the basis of their undisturbed nature.
198Very few such natural sites exist in this heavily agricultural region, which greatly limited
199our choices. We eventually chose four nature preserves along a roughly north to south
200transect, with distinct temperature and precipitation gradients (Fig. 1; Table 1). Mean
201annual precipitation decreases from NNW to SSE, and mean annual temperature
202increases from north to south across the study area (Fig. 1). As a result, Lindsay Prairie
203and Boardman preserves are drier and warmer sites, while Marcellus and Kahlotus Ridge
204are cooler and wetter.

205   The northernmost Marcellus preserve north of Ritzville, WA is located within the
206*Artemisia tridentata–Festuca idahoensis* association of Daubenmire (1970, 1972) and is
207cooler and wetter than the Kahlotus Ridge site. The Marcellus site also has the highest
208percentage of shrubs and *Festuca* cover. The Kahlotus Ridge preserve north of Kahlotus,
209WA is located in the middle of a grassland immediately north of the Snake River in
210*Agropyron–Festuca* association of Daubenmire (1970, 1972) and has very few shrubs.
211Boardman preserve, OR is a large grassland area south of the Columbia River, and it is
212more arid than the northern preserves. It contains high percentages of *Stipa* and
213*Agropyron* bunchgrasses and some *Artemisia* shrubs on canyon slopes. The soils are
214more sand-enriched compared to Marcellus and Kahlotus Ridge. Lindsay Prairie, OR is a
215small preserve south of Boardman, similar to the Boardman preserve and the Kahlotus
216preserve in that both contain sandy soils and relatively high proportions of *Stipa* and
217*Agropyron* grasses and some shrubby plots. Lindsay Prairie has some unique

218communities present such as *Oryzopsis* communities not found in the other preserves
219examined in this study. Lindsay Prairie has a similar climate to Boardman Preserve.

220   As stated above, each plot evaluated in this study was considered separately. In
221this way, each plot could be compared to other plots, regardless of proximity. Each
222sample plot was selected for its own distinctive vegetation attributes in order to maximize
223overall variability of vegetation cover and composition. Preserves in the north were
224relatively cooler and wetter, while those in the south were warmer and drier. Two field
225sites were located in southeastern Washington (Marcellus and Kahlotus Ridge preserves
226of the Washington Department of Natural Resources), and two in northeastern Oregon
227(Lindsay Prairie and Boardman Preserves of the Nature Conservancy).

228   All samples were collected on plots covered by pre-agricultural vegetation.
229Despite our best efforts to utilize pristine sites, all preserves contain some invasive
230species, most notably annual cheat brome (*Bromus tectorum* L.). However, due to its
231relatively recent introduction, *B. tectorum* is expected to have a minimal impact on the
232modern phytolith record. Our reasons for this assumption are twofold. First, soil phytolith
233assemblages are the products of gradual accumulation over many growing seasons that
234may encompass hundreds of years (Fredlund and Tieszen, 1994). Second, while the mean
235residence time for phytolith persistence in the soil (Fredlund and Tieszen, 1994) is not
236known for our study areas, recent studies have suggested that the rate of phytolith
237dissolution may be very high in temperate grasslands (Alexandre et al., 1997; Derry et al.,
2382005; Blecker et al., 2006). Therefore, sizeable accumulations of *B. tectorum* phytoliths
239should take many growing seasons.

240   Each soil sample was obtained within a 6x6 m square plot. Each plot was larger
241than 4 m^2 plots used in Daubenmire (1970), so that they could be located from the aerial
242surveys conducted as part of this study. While the plots were clustered geographically
243into 4 nature preserves, we assumed each plot to be an independent sample. To achieve
244this, we attempted to maximize the vegetation variability within each preserve to include
245as many combinations of grassland and shrubland types and cover as possible in our
246plots. Each square plot was aligned to the magnetic north with a Brunton compass.

247   The UTM coordinates of the southwest corner of each study plot were recorded
248using a professional mapping grade handheld Trimble GPS receiver with differential

249correction to the nearest permanent station, which allowed us to achieve about 1 m

250horizontal positional accuracy. Next, a permanent spike with a tag was placed on the

251southwest corner of the plot. The linear boundaries were then entered into a GIS polygon

252layer.

253   Overhead color images of each study plot were obtained using a hand-held

254camera mounted on a 12-ft. tall pole to create a permanent archive of plant cover and

255composition. Each species was identified in the field at the peak of the flowering season

256(mid-May 2003) (Table 2). Due to budget constraints, airborne surveys of the same plots

257were flown only in May, 2004 using a digital multispectral camera with 10cm on-the-

258ground resolution. All evident plant species that had been identified and recorded in May,

2592003 were deemed appropriate given the similarity in growing seasons between the two

260years of sampling. Each plant was assigned to one of four functional groups (shrub, grass,

261forb or legume). The region of study has very few C_4 grasses and none were encountered

262on field plots; thus, all the grasses in this study are C_3.

263   Ten random pinches of topsoil were taken from each study plot, placed in a

264plastic bag and thoroughly mixed. These samples were collected from plant detritus-free

265surfaces to a depth of less than 2 cm. Any evident plant detritus was manually removed

266before sampling the soil. The total amount of sample procured from each plot was

267approximately 50 g. No attempt was made to subsample within each plot.

268

269**Phytolith processing**

270

271   To achieve total phytolith concentrations (TPC) for soil samples, phytoliths were

272extracted using the modified wet oxidation technique of Pearsall (2000) (Appendix A).

273Visual inspection of the resulting phytoliths under a light microscope verified that the

274extraction was reasonably pure (less than 5% of observed fragments were not biogenic in

275origin). Steps were taken to recover as much phytolith matter from the samples as

276possible, and to avoid any loss. Microscopic analysis of the decanted liquid in a few

277samples did not reveal significant loss of phytolith material. The ratio between the

278resulting dry weight of retrieved phytoliths and the original dry soil weight yielded the

279TPC and is expressed as a percentage in Figure 2.

280   Individual opal phytolith shapes (morphotypes) were counted systematically using
281a Leica optical microscope model DMLB, at 400x magnification mounted in immersion
282oil type A, which permitted the rotation and movement of the phytoliths on the
283microscope slide to augment the estimation of true three-dimensional shapes. Twenty-six
284distinct morphotypes were identified and recorded for each sample (Fig. 3). Digital
285images and permanent slides were created for future reference. Morphotypes were
286scanned in a row-like fashion, from left to right and from top to bottom of each slide. A
287total of 300 grains were counted for each sample. Any object whose size was between 5
288µm and 50 µm was counted, and was assumed to be biogenic silica in origin, unless it
289was apparent that it was not (e.g., dark organic material, volcanic glass, or distinctly
290shaped thin mica plates). Morphotype classes were modified from Blinnikov (2005). At
291the conclusion of the counting, seven of the originally defined morphotypes were
292removed from consideration because they occurred only in trace amounts. These
293morphotype classes were not considered statistically significant because they occurred in
294such low numbers as to have little impact. For example, only 7 saddle (SA) morphotype
295grains were counted for the entire study, out of a total of over 11,000. Further, these
296morphotypes were not considered primarily diagnostic; that is, their presence or absence
297did not indicate the presence or absence of a key species. See Table 3 for final
298morphotypes, nomenclature and species associations. See Figure 3 for morphotype
299images.
300
301**Image processing**
302
303Estimates of vegetation cover/biomass were obtained by measuring Normalized
304Difference Vegetation Index (NDVI) on bands 4 and 3 of color-infrared digital aerial
305imagery, using a standard algorithm (Jensen, 1996, p. 182). A chartered plane was flown
306in May 2004 to obtain GPS-referenced digital images with 4 channels (blue, green, red,
307and near-infrared) comparable in spectral sensitivity to the first four bands of Landsat
308ETM+. Image resolution was approximately 0.16 m^2 on the ground per pixel. GPS-
309obtained vector files of the sample plot boundaries were matched to the existing digital
310orthoquads of the four nature preserve areas to extract 37 grids of pixels corresponding to

311the 37 plots (Fig. 4). NDVI values were estimated for each plot by averaging pixel values

312(from about 250 pixels per plot) to yield a mean NDVI value for each plot.

313

314**Statistical Methods**

315

316Two statistical methods were used to compare phytolith assemblages to recorded

317vegetation cover and composition. First, linear regression was utilized to determine if

318there is a relation between total phytolith concentration (TPC) in soils and vegetation

319cover. Second, Canonical Correspondence Analysis (CCA) (ter Braak, 1986; McCune et

320al., 2002; run in PC-ORD) was utilized to evaluate the overall relations between the plots

321(rows) and morphotypes (columns) in the main matrix and plots (rows) and percent cover

322by plant taxa (columns) in the environmental matrix. We chose 10 morphotypes for this

323analysis including straight rectangular plates, two types of rondels (pyramidal and keeled

324or horned), short wavy trapezoids, *Stipa*-type bilobates, grass seed epidermis long cells,

325regular long cells (rods), silicified hairs and trichomes, epidermal non-grass phytoliths,

326and blocky forms. This level of phytolith classification was sufficiently broad to allow

327unambiguous identification of all of these forms. More detailed classifications could be

328used, but would result in much longer time necessary to count a statistically valid number

329of grains. The plant taxa used were *Agropyron spicatum*, *Bromus tectorum*, *Festuca*

330*idahoensis*, *Poa secunda*, *Stipa* spp., Asteraceae forbs, and shrubs. Together, these

331accounted for about 95% of all plant cover, with the remainder mostly in representatives

332of Liliaceae and Fabaceae families, which do not produce phytoliths.

333   CCA was chosen because it allows simultaneous ordination of morphotypes

334(species) and plots with plant taxa (environmental variable) and plots in a single analysis.

335This method also allows quick visualization of relations between morphotype and plant

336taxa data in a single graph. We did not attempt to use CCA to investigate actual

337environmental (climate or soil) variables in this study given the limited coverage of

338suitable pristine sample sites in the Columbia Basin.

339

340**RESULTS**

341

342 Estimates of Vegetation Cover and Total Phytolith Concentration

343

344   Modern vegetation cover values on the study plots range from 9% to 98% (Table

345 2). Grasses are the most dominant functional group, averaging 34% of composition by

346 cover. Of the four preserves, Kahlotus Ridge reported the highest overall vegetation

347 cover (52%), the highest proportion of grasses (44%) and the lowest proportion of shrubs

348 (4%). Marcellus reported a mean vegetation cover of 51%. Its proportion of grasses to

349 shrubs was more balanced than at Kahlotus Ridge, with 29% covered by grasses and 19%

350 by shrubs. Lindsay Prairie averaged 48% vegetation cover, with 42% grasses and 5%

351 shrubs present. One plot at Lindsay Prairie exhibited the overall highest vegetation cover

352 of any plot in the study, at 98% (L4). This is relevant because it shows the high degree of

353 intra-preserve variability, suggesting a low interrelatedness between the plots. Boardman

354 Preserve's average vegetation cover (32%) was the lowest for any plot; plot B7 from that

355 preserve also exhibited the lowest percent vegetation cover of all plots (9%). The average

356 proportion of grasses and shrubs from Boardman Preserve was 23% and 8%,

357 respectively. As was expected, as mean annual precipitation (MAP) increased and mean

358 annual temperature (MAT) decreased, the percent of vegetation cover also increased.

359   The density of vegetation of each plot is reflected in the total phytolith

360 concentration (TPC). TPC for all 37 modern samples averaged about 2.5% (Fig. 2).

361 Overall, Boardman Preserve and Lindsay Prairie had the lowest TPC values (1.4% and

362 2.2% respectively). Marcellus yielded the highest average TPC at 3.3%, while Kahlotus

363 Ridge reported 3.0%. The highest TPC was observed at M10 (4.3%; Marcellus preserve)

364 and lowest at B9 and B5 (0.99%; Boardman preserve). All TPC values >3%

365 corresponded to plots from either Kahlotus Ridge or Marcellus preserve (the northern

366 preserves), which are characterized by higher vegetation (and grass) cover. Plot L4

367 (Lindsay Prairie) - with the highest vegetation cover reported - had only 2.3% TPC.

368 However, this plot is composed mostly of shrubs, not grasses. Shrubs, overall, tend to

369 produce a lower proportion of phytoliths when compared to grasses. The five plots from

370 which we identified the lowest TPC values were all located in the Boardman preserve.

371 These five plots possessed higher average proportions of shrubs and/or weedy annual

372grass species (*Bromus tectorum*, *Vulfia octoflora*), which likely would have contributed

373less opal to the soils than native grasses.

374   Although we measured vegetation cover in the field, we chose to use aerial

375imagery-based estimations rather than in-field observations. In general, in-field estimates

376of plant cover may be misleading, because they are often based on qualitative visual

377observations and, in our case, only a single visit to each plot in May of 2003. Remote

378sensing analyses, in contrast, can provide an objective measure of photosynthetically-

379active biomass, a factor not detectable by the human eye (Fig. 4). Values of vegetation

380biomass expressed as a normalized difference vegetation index (NDVI) were measured

381from digital aerial images.

382   Utilizing a linear regression, TPC values from modern soils were implemented to

383predict NDVI values. The resulting graph is presented in Fig. 6. The regression equation

384is NDVI = 0.0475(TPC) – 0.432 (R^2 = 0.49, p<0.001). In contrast, we were only able to

385achieve an R^2 of 0.21 when comparing TPC to in-field estimates of vegetation cover. The

386robustness of the correlation between TPC and NDVI should be assessed by applying our

387methods or equivalent techniques in other regions. This predictive relation between TPC

388and NDVI can help reconstruct paleo-NDVI from TPC measurements. NDVI can also be

389used to constrain the vegetation boundary conditions in dust entrainment models (e.g.,

390Zender et al., 2003).

391   Regressions determined for grasses or shrubs alone yielded lower R^2 values (0.14

392for grasses only and 0.07 for shrubs). Despite our best efforts, the ranges of shrub cover

393values were rather inconsistent. Most plots yielded shrub cover values of <10% and only

3945 had values >25%. No plots contained between 12 and 25% of shrub cover. More

395continuous ranges of cover were obtained for grass cover with TPC values falling

396between 8% and 68%, with no major gaps.

397

398**Analysis of Modern Morphotypes**

399

400The majority of the modern samples possessed similar morphotype assemblages (Fig. 5).

401Most morphotypes were found on every plot, but often in different proportions. Most

402assemblages were dominated by plates (PR; 10% to 26%), short trapeziforms (WS; 8% to

403(25%), long cell rods (LR; 5% to 24%), oblong/oval rondels (RO; 4% to 15%), and keeled
404rondels (RK; 2% to 11%), which are all grass phytoliths. The presence of morphotypes
405for non-grasses were likewise similar between the plots, with a greater proportion of
406polygonal forms (EP; 12% to 29%) than blocky forms (BL; 3% to 12%). (Refer to Table
4073 for morphotype nomenclature.) The ubiquitous presence of morphotypes on most plots
408was expected, considering the relatively homogenous species composition on all study
409plots in the study area. All plots were located in non-forested, upland sites with the same
410seven regionally dominant species of grasses and shrubs (*Agropyron spicatum, Festuca
411idahoensis, Poa sandbergii, Stipa comata, Artemisia tridentata,* and two *Chrysothamnus*
412spp., Table 2).

413   Grass phytoliths, which include eleven morphotypes used in this study, made up
414between 62% and 84% of all phytoliths in soil samples (Fig. 5). The PR type accounts for
41510% to 26% of all morphotypes, and is the dominant short cell. However, the PR type is
416common in many grasses and is not diagnostic of any specific plant species or genus. The
417WS (short crenate) type ranges from 8% to 25% of all morphotypes. The third most
418common morphotype in the assemblages was the LR (smooth rod) type, which ranged
419from 5% to 23% of the total morphotype population. The phytoliths of microhairs (HH)
420and trichomes (HT) ranged from 0% to 4%. Non-grass types, made up of EP (polygonal)
421and BL (blocky) forms, range from 24% to 27% of all phytoliths.

422   The eigenvalues for the first CCA axes were $\lambda_1=0.027$ and $\lambda_2=0.004$. The species-
423environment correlations for the axes are moderately high (Pearson correlation
424coefficient r=0.863 for the first, and r=0.660 for the second). In the CCA environmental
425matrix, the first axis appears to be most positively correlated with the *Bromus tectorum*
426and *Stipa* cover (the former is an annual weed, the latter is a native grass associated with
427dry soils). The same axis is negatively correlated with the cover of native mesic grass
428species *Poa, Agropyron* and *Festuca.* Therefore, the axis represents a moisture gradient.
429The second axis was most positively correlated with forbs; *Agropyron* and *Festuca* cover
430and most negatively correlated with *Poa, Stipa* and shrub cover. Thus, the second axis
431represents grassland to shrub steppe gradient. Essentially, both axes capture one complex
432environmental gradient of shrubland-grassland transition across the region based on
433moisture (Fig. 1). A tight clustering appears for the samples on the CCA biplot showing

434two first axes of the main matrix (Fig. 7). The samples from the warmer and drier

435preserves (Lindsay Prairie and Boardman) cluster in the lower right of the biplot, while

436the samples from cooler and wetter preserves (Kahlotus Ridge and Marcellus) tend to be

437grouped more to the upper left. Data from the northern preserves revealed a higher

438abundance of cooler/wetter climate species, such as *Festuca*, while data from the

439southern preserves revealed higher proportions of warm/dry climate adapted *Agropyron,*

440*Artemisia,* and *Stipa* occurring at overall lower densities.

441   Additionally, CCA helped us assess the relative position of each plot with respect

442to different morphotypes from the main CCA matrix. Wavy trapezoids, bilobate *Stipa-*

443type and silicified grass hairs, hair bases and trichomes tend to occur on plots from more

444southern preserves with a higher incidence of *Stipa, Oryzopsis* (a related genus to *Stipa*)

445and *Bromus.* The oval and keeled rondels and plates, on the other hand, are better

446represented in the northern preserves on plots with a high incidence of either *Festuca*,

447*Agropyron*, or both. Epidermal non-grass phytoliths occur on plots with higher

448percentages of shrubs and forbs. Blocky forms occur on plots where *Festuca* and shrubs

449are common, including a few from Marcellus preserve. Overall, the CCA results agree

450well with the expected pattern of phytolith production from modern plants (Table 1;

451Blinnikov, 2005).

452

453**DISCUSSION**

454

455**Total Opal Concentration in Soils Estimates of Modern Vegetation Cover and NDVI**

456

457Total opal concentration (TPC), expressed as percent of extracted plant opal relative to

458the total dry weight of soil, is positively correlated to the observed vegetation cover on

459the plots (as percent ground cover by species and plant functional group). TPC is also

460positively correlated to Normalized Difference Vegetation Index (NDVI) as measured by

461color-infrared aerial imagery. Although many studies use phytolith assemblages to

462reconstruct the composition of vegetation found at a particular site (Bartolome et al.,

4631986; Fisher et al.*,* 1995; Blecker et al.*,* 1997; Fredlund and Tieszen, 1997; Dehlon et al.*,*

4642003; Blinnikov, 2005), few have focused on the TPC in the soil (Prebble, 2003b;

465Blecker et al., 2006). With accurate TPC values, it is possible to reconstruct

466paleovegetation cover, which can lead to a clearer understanding of vegetation ecotone

467dynamics and climate. Indeed, there is precedence for determining TPC values in

468paleoreconstruction studies. As demonstrated by previous investigations, TPC is a

469reliable indicator of paleovegetation, especially when grassland species are the dominant

470vegetation, but temperate deciduous and coniferous forests were also applicable (Verma

471and Rust, 1969; Wilding and Drees, 1971). These two papers revealed that TPC values

472from grassland prairie sites in Minnesota and Ohio, contained 3 to 10 times, respectively,

473the TPC values of forest top soils. Paleovegetation cover in the Columbia Basin is an

474important factor to measure because it so strongly influences eolian activity and soil

475formation. Vegetation cover also may directly reflect soil moisture (Morrow and Friedl,

4761998). Several studies have linked sand dune reactivation and loess deposition with

477drought (Muhs et al., 2000; Mason et al., 2004; Sweeney et al., 2005; Miao et al., 2007,

478Sweeney et al., 2007). Others have linked increased eolian deflation to reduced

479vegetation cover (Snelder and Bryan, 1995; Arens et al., 2001; Mason et al., 2001;

480Engelstaedter, 2003; Sweeney et al., 2007) and decreased root mass (Dong et al., 2001;

481Wang et al., 2003). Increased surface roughness owing to a higher percentage of

482vegetation cover also can increase drag on the wind, and protect soils from deflation

483(Mason et al., 1999; Dong et al., 2003; Crawly and Nickling, 2003). Studies have shown

484that increased soil moisture and vegetation cover leads to increased rates of pedogenesis

485(Huang et al., 2001; Wolfe et al., 2001; Gustavson and Holliday, 1995).

486   Regression analysis revealed a significant positive trend. As TPC values

487increased, the percent of vegetation cover also rose (Fig. 6). Thus, our TPC values helped

488us predict the modern vegetation cover on our sample plots. Although we treated all plots

489as independent samples, the plots in southern preserves (Lindsay Prairie and Boardman),

490that evolved under warmer and drier conditions had lower overall vegetation densities

491and also lower TPC values than their counterparts to the north. Thus, we do observe the

492regional signal in the TPC values.

493   A note about the robustness of the methods should be mentioned here. We feel

494that an R^2 value of 0.49 is a significant relationship considering the many factors which

495can potentially influence vegetation cover and TPC. These factors include disease,

496herbivory, fire, and invasive species on the vegetation side. Factors influencing TPC

497include interference from mineral forms of silica (such as volcanic glass), fragments of

498phytoliths <5 μm, and dissolution of phytoliths into soil water (or partial dissolution such

499that remaining phytoliths are unrecognizable). We suggest two techniques to minimize

500the uncertainty introduced by these factors. First, the use of aerial imagery from several

501growing seasons will effectively mitigate the effects of short-term vegetation fluctuation.

502Second, the use of chemical silica extraction methods (DeMaster 1981, Koning 2002)

503will result in more accurate and precise biogenic silica (phytolith) estimates. Phytolith

504fragments can be especially troublesome, as some authors have estimated that these can

505account for up to 65% of the phytolith pool (Wilding and Drees 1971, 1974).

506   When the TPC value for a given plot is over-predicted (such as B2) or under-

507predicted (such as L4), the disparity may be the result of short-term fluctuation in

508biomass at the site. For example, analysis at plot L4 revealed a vegetation cover of 98%,

509yet its TPC value was only 2.3%. TPC values reflect an averaging of vegetation densities

510temporally. Therefore, the regression equation predicted the vegetation cover on L4 at

51145%. However, 40% of the vegetation cover on L4 is explained by exotic annual *Bromus*

512*tectorum*. While *B. tectorum* produces phytoliths, its contribution to the assemblage per

513unit of covered area is likely to be much lower than for native bunchgrasses (e.g., *A.*

514*spicatum* or *F. idahoensis*), given its much smaller biomass and tendency towards

515interannual fluctuations in growth. If *B. tectorum* cover is ignored, the predicted value

516(45%) is closer to that observed (58%). However, the full ramifications of ignoring

517invasive species in a plot have not been thoroughly researched, and should be approached

518with caution. Plot B2, with 13% observed cover, yielded a TPC value of 2.1%, which is

519roughly the median value for the entire dataset. This overabundance of TPC may suggest

520that the observed plant cover is lower than suggested by phytoliths. Therefore, there may

521be some inheritance of phytoliths on the plots from earlier growing episodes.

522   NDVI linear regression yielded a stronger correlation with TPC than that based on

523visual observation of plants in the field. In both cases (NDVI and visual inspection)

524measurements were performed within a single day (no repetitive estimates of cover or

525NDVI). NDVI captures the difference in photosynthetic rates of plants as opposed to

526recording plants covering a certain percentage of the ground surface. Higher

527photosynthetic activity results in more active growth of plant tissues and should translate
528into overall higher silica deposition in plants as well. Two sources of uncertainty play a
529role in estimating NDVI in our study: imprecise georeferencing of the aerial photos and
530seasonality. The first is easier to estimate, because we were able to match the aerial
531imagery with our rectified in-field square plot boundaries in a GIS. Since the
532georeferencing positional accuracy is around 1 m, an offset by 1 m linearly in both X and
533Y directions would allow 11 m^2 out of the total 36 m^2 of the plot be excluded from the
534pixel count, and an additional 11 m^2 to be brought in from the surrounding plot
535vegetation. All of our plots, however, were chosen inside a larger patch of similar,
536homogenous vegetation, so this effect was probably not very pronounced. The second
537source of error is the fact that only one digital fly-over image was available per plot taken
538on a specific day at the height of vegetative season for all preserves. We do not have
539multidate or multiyear samples. However, the reasonably high linear relationship between
540TPC and NDVI suggests that this was not a significant problem.
541

542**Modern Morphotypes Distinguish Shrublands from Grasslands and Dry Grasslands**
543**from Mesic Grasslands**
544

545The overall diversity of phytolith morphotypes in our samples was relatively low. We
546deliberately chose to use only a few broad categories of phytoliths in this study. While
547more detailed morphotype classifications can be tested, our goal was to assess the broad
548applicability of the method to resolve significant differences in plant cover and
549composition. Most samples were dominated by the same seven morphotypes: plates (RP),
550short trapeziforms (WS), keeled and oval rondels (RK and RO, respectively) and long
551cell rods (LR) from grasses and blocky (BL) and epidermal polygonal (EP) forms from
552shrubs and forbs (Fig. 5). This is not surprising, given the relatively few dominant species
553that are phytolith producers in the region (Blinnikov, 2005). No panicoid or chloridoid
554species of Poaceae are dominant in the region. Thus, essentially all phytoliths in our
555records originate from Fectucoid native (*Agropyron, Festuca, Poa*) and non-native
556(*Bromus tectorum*) grasses. The bilobate forms of *Stipa* are not "true bilobates", but
557rather trapezoids of transitional type (Mulholland, 1989). A handful of true bilobates and

558saddles were identified in the record and most likely were also contributed by *Stipa*

559and/or *Oryzopsis*.

560   This study focused on a narrow environmental gradient ranging from dry

561sagebrush communities to moderately mesic grasslands within a relatively small

562geographic area. The much higher variability of morphotypes documented in the Great

563Plains (Fredlund and Tieszen, 1994) and across China (Lu et al*.,* 2005) is consistent with

564the continent-spanning gradients in those studies. However, we did find important

565differences in our assemblages highlighted in the CCA study.

566   CCA revealed that there is a good agreement between the vegetation growing on

567the plots and morphotypes found in soil (Fig. 7). For example, plots with *Stipa*-type

568bilobate phytoliths in soils are also the ones that support *Stipa* today. Plots with a high

569incidence of silicified hairs (HT) corresponded with a high concentration of *Bromus*

570*tectorum*, which has heavily silicified hairs. Plots with a high incidence of epidermal

571polygonal phytoliths from shrubs are the ones with high shrub content today. Contrary to

572our expectations, there was less correspondence between shrub cover and blocky forms.

573Blinnikov (2005) reported that blocky forms occur primarily in *Artemisia* and perhaps in

574other shrubs from Asteraceae family in the region. However, 'blocky' is a catch-all

575category for phytoliths that are large in size and 3-dimensional in appearance. Certain

576types of grass bulliform cells also may resemble these. Keystone-shaped bulliforms,

577which are very distinct, were not found in this study, but some blocky forms may have

578been contributed by grasses. Also, our collection of forbs from the area is far from

579complete. It is possible that some yet unstudied taxa contribute blocky forms in non-

580shrub communities.

581   The most encouraging result from our research was that plants above ground seem

582to contribute morphotypes in situ. Few studies exist that prove this connection (Kerns et

583al*.,* 2001). Generally, phytoliths are expected to provide a rather local signal, since it is

584assumed that there is little post-depositional translocation (Piperno, 1988). Fredlund and

585Tieszen (1994), however, found that in the Great Plains, only about 50% of phytoliths

586from modern soils could be considered truly local (i.e., from within a few meters of a 4x4

587m plot); the rest had been transported in from the surrounding one hectare. We

588acknowledge that transport may be a legitimate problem, however our dataset indicates it

589was not a major issue in our study. It seems that there is a strong correspondence between

590the presence of certain phytolith producers with distinct shapes (e.g., *Stipa*) in our plots

591that do deposit these primarily locally (within 6x6 m plots). In most cases, we did not

592find a large number of foreign phytoliths that we could not link to the present vegetation.

593   Another issue with phytolith records in soils is inheritance. There were some plots

594in our study where the morphotypes in the soils did not match well with the species

595compositions on the plots. For example, plot B8 (Boardman preserve) yielded a high

596incidence of blocky phytoliths presumably from shrubs, but no shrubs in the surface

597record. However, history of the site (TNC staff, pers. comm.) indicates that a recent fire

598may have destroyed the pre-existing sagebrush on this site, which takes longer to recover

599than grasses. Phytoliths in the upper 2 cm of the soil profile likely accumulated in the

600past few decades, and thus more accurately reflect the longer-term period of vegetation

601on the site, and not necessarily only current vegetation. This longer-term phytolith

602accumulation can cloud the modern-day phytolith record in soils somewhat, but

603acceptable for paleoecological studies where temporal resolutions are much larger

604(Blinnikov et al.*, 2002).

605   We also found that annual exotic weeds (*Bromus tectorum*) may influence

606modern-day phytolith records. Seed phytoliths, presumably from *Bromus,* and silicified

607hairs common in this species were found on plots on which *B. tectorum* occurs with

608regularity. This highlights the detective ability of phytolith analysis, but also dilutes the

609assemblage of morphotypes from native grasses. Although due care was taken to sample

610only native grasslands, the reality is that *B. tectorum* in the Columbia Basin ecosystem is

611an ever-increasing problem, even on the preserves where our study was conducted.

612However, the presence of *B. tectorum* doesn't invalidate our study: this species has not

613been present for a great enough time period to have a significant impact on the phytolith

614record we examined.

615

616**CONCLUSIONS**

617

618The first attempt to quantitatively analyze phytolith soil assemblages and total opal

619concentrations (TPC) in the Palouse area of the Columbia Basin has shown several

620benefits and limitations. Total phytolith concentration (TPC) in topsoils were moderately

621positively related to NDVI values estimated from aerial surveys ($R^2 = 0.49$). Phytolith

622morphotypes in topsoil correspond reasonably well to the above-ground plant taxa on our

6236 x 6 m plots. Our results show that TPC can be an important indicator of past vegetation.

624However we suggest the use of more robust methods to achieve more accurate and

625precise results. These methods include 1) the use of NDVI data averaged over many

626growing seasons to account for short-term fluctuations in vegetation cover; and 2) the use

627of chemical silica extraction methods to measure all sizes and forms of phytoliths

628(including fragments). Morphotype assemblages do reasonably approximate the

629vegetation on a given plot over a timescale of at least a few decades. Short-term

630fluctuations in vegetation attributes are muted (averaged) in the phytolith assemblages.

631Even though exotic weeds (*Bromus tectorum*) have been detected in the modern

632assemblages, it does not change our results. Most assemblages from grasslands and

633shrublands in our area are broadly similar, which is not surprising given the regional

634scale of the study in broadly similar arid habitats. There are no morphotypes that would

635distinguish one vegetation type from another, but overall, existence of even small

636amounts (3-5%) of *Stipa*-type bilobates is a strong indicator that *Stipa* and *Oryzopsis* are

637present in the modern vegetative cover. Likewise, the occurrence of epidermal polygonal

638forms strongly suggests that shrubs are present. Silicified hairs found in the assemblages

639suggest the presence of *Bromus tectorum*, an exotic weed. More mesic grasslands can be

640distinguished from more arid ones on the basis of higher proportions of plates and blocky

641forms in the former, while the arid ones will have a higher incidence of short

642trapeziforms and rods. Very few phytoliths were contributed by *Asteraceae* and other

643forbs, although contribution to the assemblages by these species is expected.

644   The issues of inheritance and translocation of phytoliths in post-depositional

645period were not conclusively resolved in this study. Some of our morphotypes may have

646come from outside the plots or were inherited from previous times (e.g., when shrubs

647were removed in a crown fire), but we did not see significant evidence for truly extralocal

648forms (e.g., no tree phytoliths were found on any plots). The issues should be studied

649further in a series of controlled experiments with long-term mixtures.

650

651 **REFERENCES**

652

653 Albert, R. M., Shahack-Gross, R., Cabanes, D., Gilboa, A., Lev-Yadun, S., Portillo, M.,
654   et al., 2008. Phytolith-rich layers from the late bronze and iron ages at Tel Dor
655   (Israel): Mode of formation and archaeological significance. Journal of
656   Archaeological Science, 35, 57-75.

657 Alexandre, A., Meunier, J., Lezine, A., Vincens, A., Schwartz, D., 1997. Phytoliths:
658   indicators of grassland dynamics during the late Holocene in intertropical Africa.
659   Palaeogeography, Palaeoclimatology, Palaeoecology 136, 213-229.

660 Arens, S.M., Baas, A.C.W., Van Boxel, J.H., Kalkman, C., 2001. Influence of reed stem
661   density on foredune development. Earth Surface Processes and Landforms 26,
662   1161-1176.

663 Baker, V.R., Bjornstad, B.N., Busacca, A.J., Fecht, K.R., Kiver, E.P., Moody, U.L.,
664   Rigby, J.G., Stradling, D.F., Tallman, A.M., 1991. Quaternary geology of the Columbia
665   Plateau, in: Morrison, R.B., (Ed.), Quaternary nonglacial geology; Conterminous U.S.
666   Geological Society of America, The Geology of North America, v. K-2, Boulder, CO.,
667   pp. 215-250.

668 Bartoli, F., and Wilding, L.P., 1980. Dissolution of biogenic opal as a function of its
669   physical and chemical properties. Soil Science Society of America 44, 873-878.

670 Bartolome J.W., Klukkert, S.E., Barry, W.J., 1986. Opal phytoliths as evidence for
671   displacement of native Californian grassland. Madrono 33, 217-222.

672 Blecker S.W., Yonker, C.M., Olson, C.G., Kelly, E.F., 1997. Paleopedologic and
673   geomorphic evidence for Holocene climate variation, Shortgrass Steppe, Colorado,
674   USA. Geoderma 76, 113-130.

675 Blecker, S.W., McCulley, R.L., Chadwick, O.A. Kelly, E.F., 2006. Biologic cycling of
676   silica across a grassland bioclimosequence. Global Biogeochemical Cycles 20,
677   GB3023, doi: 10.1029/2006GB002690.
678

679 Blinnikov, M.S., Busacca, A.J., Whitlock, C., 2001. A new 100,000-year record from the
680   Columbia Basin, Washington, USA., in (Meunier, J.D., Colin, F., Eds.), Phytoliths –
681   Applications in Earth Science and Human History. A.A. Balkema, Rotterdam, pp.
682   27-55.

683 Blinnikov, M.S., Busacca, A.J., Whitlock, C., 2002. Reconstruction of the late
684   Pleistocene grassland of the Columbia Basin, Washington, USA, based on phytolith
685   records in loess. Palaeogeography, Palaeoclimatology, Palaeoecology 177, 77-101.

686 Blinnikov, M.S., 2005. Phytoliths in plants and soils of the interior Pacific Northwest,
687   USA. Review of Palaeobotany and Palynology 135, 71-98.

688 Bolig, M., Frazier, B., Busacca, A., 1998. General soil map of Washington. Washington
689   State University, Pullman, WA.

690 Bowdery, D., 1998. Phytolith analysis applied to Pleistocene–Holocene archaeological
691   sites in the Australian arid zone. British Archaeological Reports International Series no.
692   695. Hadrian Books, Oxford.

693 Busacca, A.J., McDonald, E.V., 1994. Regional sedimentation of late Quaternary loess
694   on the Columbia Plateau: sediment source areas and loess distribution patterns.
695   Washington Division of Geology and Earth Resources Bulletin 80, 181-190.

696 Carnelli, A.L., Madella, M., Theurillats, J.P., 2001. Biogenic silica production in selected
697   alpine plant species and plant communities. Annals of Botany 87, 425-434.

698 Crawley, D.M. Nickling, W.G., 2003. Drag partition for regularly-arrayed rough
699   surfaces. Boundary-Layer Meteorology 107, 445-468.

700 Daubenmire, R., 1970. Steppe Vegetation of Washington. Washington Agricultural
701   Experiment Station, Washington State University, Pullman, WA.

702 Daubenmire, R., 1972. Annual cycles of soil moisture and temperature as related to grass
703   development in the steppe of eastern Washington. Ecology 53, 419-424.

704 Delhon C., Alexandre, A., Berger, J., Thiebault, S.T., Brochier, J.E., Meunier. J., 2003.
705   Phytolith assemblages as a promising tool for reconstructing Mediterranean Holocene
706   vegetation. Quaternary Research 59, 48-60.

707 Demaster, D. J., 1981. The supply and accumulation of silica in the marine environment.
708   Geochimica Et Cosmochimica Acta, 45(10), 1715-1732.

709 Derry, L.A., Kurtz, A.C., Ziegler, K, Chadwick., O.A., 2005. Biological control of
710   terrestrial silica cycling and export fluxes to watersheds. Nature 433, 728-731.

711 Dong, Z., Gao, S., Fryrear, D.W., 2001. Drag coefficients, roughness length and zero-
712   plane displacement height as disturbed by artificial standing vegetation. *Journal of Arid*
713   *Environments*, 49, 485-505.

714 Dong, Z., Liu, X., Wang, H., Wang, X., 2003. Aeolian sand transport: a wind tunnel
715   model. Sedimentary Geology 161, 71-83.

716 Engelstaedter, S., Kohfeld, K.E., Tegen, I., Harrison, S.P., 2003. Controls of dust
717   emissions by vegetation and topographic depressions: An evaluation using dust storm
718   frequency data. Geophysical Research Letters 30, 271-274.

719 Fearn, M.L., 1998. Phytoliths in sediment as indicators of grass pollen source. Review of
720   Palaeobotany and Palynology, 103, 75-81.

721 Fisher, R.F., Bourn, C N., Fisher, W.F., 1995. Opal phytoliths as an indicator of the
722   floristics of prehistoric grasslands. Geoderma, 68, 243-255.

723 Fredlund, G.G., Tieszen, L.T., 1994. Modern phytolith assemblages from the North

724 American Great Plains. Journal of Biogeography, 21, 321-335.

725 Fredlund, G.G., Tieszen, L.T., 1997. Phytolith and carbon isotope evidence for late

726 quaternary vegetation and climate change in the southern Black hills, South Dakota.

727 Quaternary Research 47, 206-217.

728 Freeman, O.W., Forrester, J.D., Lupher, R.L., 1945. Physiographic divisions of the

729 Columbia Intermontaine Province. Annals of the Association of American Geographers

730 35, 53-75.

731 Gustavson, T.C., Holliday, V.T., 1999. Eolian sedimentation and soil development on a

732 semiarid to subhumid grassland, tertiary Ogallala and Quaternary Blackwater Draw

733 Formations, Texas and New Mexico High Plains. Journal of Sedimentary Research 69,

734 622-634.

735 Hodson, M.J., White, P.J., Mead, A., Broadley, M.R., 2005. Phylogenetic variation in the

736 silicon composition of plants. Annals of Botany 96, 1027-1046.

737 Huang, M., Shao, M., Li, Y., 2001. Comparison of a modified statistical-dynamic water

738 balance model with the numerical model waves and field measurements. Agricultural

739 Water Management 48, 21-35.

740 Jensen, J. R., 2005. Introductory digital image processing: A remote sensing perspective.

741 Upper Saddle Rive, NJ: Prentice Hall.

742 Kelly, E.F., Blecker, S.W., Yonker, C.M., Olson, C.G., Wohl, E.E., Todd, L.C., 1998.

743 Stable isotope composition of soil organic matter and phytoliths as paleoenvironmental

744 indicators. Geoderma 82, 59-81.

745 Kerns, B.K., 2001. Diagnostic phytoliths for a ponderosa pine–bunchgrass community

746 near Flagstaff, Arizona. The Southwestern Naturalist 46, 282-294.

747 Kerns, B.K., Moore, M.M., Hart, S.C., 2001. Estimating forest-grassland dynamics using
748   soil phytolith assemblages and $\delta^{13}C$ of soil organic matter. Ecoscience 8, 478-488.

749 Koning, E., Epping, E., & Van Raaphorst, W., 2002. Determining biogenic silica in
750   marine samples by tracking silicate and aluminium concentrations in alkaline leaching
751   solutions. Aquatic Geochemistry, 8(1), 37-67.

752 Kuchler, A. W., 1964. Potential natural vegetation of the conterminous United States.
753   New York: American Geographical Society.

754 Lu, H., Liu, K., 2003. Phytoliths of common grasses in the coastal environments of
755   southeastern USA. Estuarine, Coastal and Shelf Science 58, 587-600.

756 Lu, H., Wu, N., Yang, X., Jiang, H., Liu, K., Liu, T., 2005. Phytoliths as quantitative
757   indicators for the reconstruction of past environmental conditions in china I: Phytolith-
758   based transfer functions. Quaternary Science Reviews 25, 945-959.

759 Mack, R.N., Bryant, V.M., Jr., Fryxell, R., 1976. Pollen sequence from the Columbia
760   Basin, WA: reappraisal of postglacial vegetation. American Midland Naturalist 95,
761   390-397.

762 Mahowald, N.M., Muhs, D., Levis, S., Rasch, P., Yoshioka, M., Zender, C.S., Luo, C.,
763   2006. Change in atmospheric mineral aerosols in response to climate: last glacial
764   period, preindustrial, modern, and doubled carbon dioxide climates. Journal of
765   Geophysical Research 111, D10202, doi:10.1029/2005JD006653.

766 Miao, X., Mason, J.A., Swinehart, J.B., Loope, D.B., Hanson. P.R., Goble, R.J., Liu, X.,
767   2007. A 10,000 year record of dune activity, dust storms, and severe drought in the
768   central Great Plains. Geology 35, p. 119-122.

769 Mason, J.A., 2001. Transport direction of Peoria Loess in Nebraska and implications for
770   Loess sources on the central Great Plains. Quaternary Research 56, 79-86.

771 Mason, J.A., Nater, E.A., Zanner, C.W., Bell, J.C., 1999. A new model of topographic
772 effects on the distribution of loess. Geomorphology 28, 223-236.

773 Mason, J.A., Swinehart, J.B., Goble, R.J., Loope, D.B., 2004. Late-Holocene dune
774 activity linked to hydrological drought, Nebraska Sand Hills, USA. Holocene 14,
775 209-217.

776 McCune, B., Grace, J.B., Urban, D.L., 2002. Analysis of Ecological Communities. MjM
777 Software Design, Gleneden Beach, OR, 284 p.

778 Minckley T., Whitlock, C., 2000. Spatial variation of modern pollen in Oregon and
779 southern Washington, USA. Review of Palaeobotany and Palynology 112, 97-123.

780 Morrow, N., Friedl, M.A., 1998. Modeling biophysical controls on land surface
781 temperature and reflectance in grasslands. Agriculture and Forest Meteorology 92,
782 147-161.

783 Muhs, D.R., Bettis III, E.A., 2000. Geochemical variations in Peoria Loess of western
784 Iowa indicate paleowinds of midcontinental North America during last glaciation.
785 Quaternary Research 53, 49-61.

786 Mulholland, S.C., 1989. Phytolith shape frequencies in North Dakota grasses: a
787 comparison to general patterns. Journal of Archaeological Science 16, 489-511.

788 Parker, A. G., Eckersley, L., Smith, M. M., Goudie, A. S., Stokes, S., Ward, S., et al.
789   2004. Holocene vegetation dynamics in the northeastern Rub' al-Khali Desert,
790   Arabian Peninsula: A phytolith, pollen and carbon isotope study. Journal of
791   Quaternary Science, 19, 665-676.

792 Pearsall, D.M., 2000. Paleoethnobotany: A handbook of procedures. Academic Press,
793 San Diego, CA, 736 p.

794 Piperno, D.R., 1988. Phytolith analysis: an Archeological and Geological Perspective.
795 Academic Press, San Diego, CA, 280 p.

796 Prebble, M., & Shulmeister, J., 2002. An analysis of phytolith assemblages for the

797 quantitative reconstruction of Late Quaternary environments of the lower Taieri Plain,

798 Otago, South Island, New Zealand II. Paleoenvironmental reconstruction. Journal of

799 Paleolimnology, 27, 415-427.

800 Reyerson, P. E., 2004. Phytolith indicators of paleo-vegetation composition and density

801 in eastern Washington state, USA. Unpublished Masters Thesis. St. Cloud State

802 University, St. Cloud, MN, 105 p.

803 Snelder, D.J., Bryan, R.B., 1995. The use of rainfall simulation tests to assess the

804 influence of vegetation density on soil loss on degraded rangelands in the Baringo

805 District, Kenya. Catena 25, 105-116.

806 Sweeney, M.R., Busacca, A.J., Gaylord, D.R., 2005. Topographic and climatic influences

807 on accelerated loess accumulation since the last glacial maximum in the Palouse,

808 Pacific Northwest, USA. Quaternary Research 63, 261-273.

809 Sweeney, M.R., Gaylord, D.R., Busacca, A.J., 2007. Evolution of Eureka Flat: A dust-

810 producing engine of the Palouse loess, USA. Quaternary International 162-163, 76-96.

811 Ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique

812 for multivariate direct gradient analysis. Ecology 67, 1167-1179.

813 USDA Forest Service, 2008. Interior Columbia Basin ecosystem management project.

814 Retrieved 06/20, 2008, from http://www.icbemp.gov/.

815 Verma, S.D., Rust, R.H., 1969. Observations on opal phytoliths in a soil biosequence in

816 southeastern Minnesota. Proceedings-Soil Science Society of America 33, 749-751.

817 Wang, X., Qian, Y., Jiang, J., Lei, J., Zhang, W., 2003. The distribution of ephemeral

818 vegetation on the longitudinal dune surface and its stabilization significance in the

819 Gurbantunggut Desert. Acta Geographica Sinica 58, 605-609.

820 Western U.S. climate historical summaries. Retrieved November 28, 2004 from Desert

821   Research Institute website Western Region al Climate Center. Web site:

822   http://www.wrcc.dri.edu/index.html.

823 Whitlock, C., Sarna-Wojcicki, A.M., Bartlein, P.J., Nickmann, R.J., 2000. Environmental

824   history and tephrostratigraphy at Carp Lake, southwestern Columbia Basin,

825   Washington, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 155, 7-29.

826 Wilding, L. P., Drees, L. R., 1971. Biogenic opal in Ohio soils. Proceedings of the Soil

827   Science Society of America 35, 1004-1010.

828 Wilding, L. P., & Drees, L. R., 1974. Contributions of forest opal and associated

829   crystalline phases to fine silt and clay fractions of soils. Clays and Clay Mineralogy,

830   22, 295-306.

831 Wolfe, S.A., 2001. Eolian activity. Bulletin of the Geological Survey of Canada 548,

832   231-240.

833 Zender, C.S., Bian, H., Newman, D., 2003. Mineral Dust Entrainment And Deposition

834   (DEAD) model: Description and 1990s dust climatology. Journal of Geophysical

835   Research 108, 4416, doi: 10.1029/2002JD002775.

836

837 **ACKNOWLEDGEMENTS**

838

844**FIGURES AND TABLES**

845**Figure 1.** Map of the Columbia Basin, vegetation zones including nature preserve sites,
846and climate data. Vegetation zones are from Kuchler's potential natural vegetation map
847(1964) as reproduced by the Interior Columbia Basin Ecosystem Management Project
848(www.icbemp.org). Mean annual precipitation (MAP) data modified generated by
849PRISM model (PRISM precipitation data, courtesy of ICBEMP project,
850www.icbemp.gov). Full metadata is available at http://www.icbemp.gov/spatial/metadata/
851atm/741.htm. ArcMap was used to generate 250 mm precipitation contours from the
852underlying PRISM raster dataset.
853
854**Table 1.** Location of preserves and climate data. Mean annual temperature (MAT) and
855mean annual precipitation (MAP) data modified from Desert Research Institute, Western
856U.S. Climate Historical Summaries (2004).

	Preserve	Coordinates	MAT, ºC	MAP, mm
857				
858	Marcellus (M)	47º.23N, 118º.41W	9.06	301 mm
859	Kahlotus Ridge (K)	46º.70N, 118º.55W	10.39	258 mm
860	Boardman (B)	45º.65N, 119º.92W	11.89	172 mm
861	Lindsay Prairie (L)	45º.59N, 119º.65W	11.70	187 mm

862

863**Table 2.** Observed total and functional groups' vegetation cover (%, measured visually in the field) on 37 modern plots ranked

864   by decreasing total cover.

865 Plot 866	Total	*Agropyron spicatum*	*Festuca idahoensis*[1]	*Poa sandbergii*[2]	*Stipa*[3] *tectorum*	*Bromus* sum	Poaceae sum	Asteraceae sum	Forbs[4] sum	Shrubs
867 L4	98	15	0	3	10	40	68	2	3	25
868 M10	87	1	40	5	0	0	46	1	4	36
869 B3	76	5	2	0	1	40	48	1	2	25
870 M5	75	0	10	1	0	1	12	3	5	55
871 K6	73	30	26	3	0	5	64	2	3	4
872 L1	71	10	0	3	2	50	65	5	1	0
873 M3	71	0	30	2	0	1	33	2	3	33
874 K5	70	15	45	0	0	0	60	2	3	5
875 K2	60	0	40	7	0	1	48	1	3	8
876 B5	59	15	6	0	0	25	46	1	1	11
877 M1	58	0	16	2	0	1	19	5	4	30
878 M4	57	0	50	5	0	0	55	0	2	0
879 K4	55	0	40	3	0	0	43	6	5	1
880 L5	52	10	0	5	20	10	45	3	3	1
881 K1	51	0	41	5	0	0	46	1	3	1
882 K3	51	0	30	5	0	0	35	1	3	12
883 L2	50	15	0	1	1	30	47	2	1	0
884 K7	49	25	10	5	0	0	40	1	7	1
885 B1	48	5	1	0	1	10	17	0	1	30
886 K8	44	5	31	2	0	0	38	0	4	2

887K9	44	20	12	5	0	3	40	0	3	1
888L6	42	0	0	3	5	20	28	5	6	3
889L3	41	0	0	2	5	20	27	2	4	8
890M8	36	0	15	5	0	0	20	1	4	11
891M7	35	0	20	5	0	0	25	0	2	8
892M9	33	0	26	1	0	0	27	1	3	2
893M2	31	0	25	1	0	0	26	0	2	3
894M6	30	0	20	1	0	0	21	0	3	6
895B8	27	4	5	1	6	10	26	1	0	0
896K10	27	0	21	1	0	0	22	0	3	2
897B10	26	8	0	1	5	5	19	1	3	3
898B6	24	10	0	2	2	5	19	0	0	5
899L7	22	1	0	2	3	10	16	2	3	1
900B4	22	3	0	0	0	10	13	1	1	7
901B9	19	6	0	1	4	5	16	1	2	0
902B2	13	6	1	0	1	2	10	1	1	1
903B7	9	1	0	1	5	0	8	1	0	0

904

905[1]Also includes *Festuca rubra* (M9) and *F. octoflora* (M1, K1, K6, K8, K9, K10, B1, B3, B5, B8)

906[2]Also includes *Poa bulbosa* (M3, L1, L3, L4, L6, L7) and *P. juncifolia* (M1)

907[3]Stipa-group includes mainly *Stipa comata*, as well as *S. occidentalis* (B3) and *Oryzopsis hymenoides* (B7, B8, L7)

908[4]Also includes legumes

909 **Figure 2.** TPC for sample plots. Bars represent percentage of total. TPC is percent of dry

910   weight of extracted opal relative to the bulk soil dry weight.

911**Table 3.** Individual morphotype nomenclature used in this study and plant species they derive from. Modified in part from

912 Blinnikov (2005).

913

Abbreviation	Description following International Code of Phytolith Nomenclature	Taxa in Which Observed
915PR	Plate, short trapeziform in 3D, rectangular in 2D, epidermal short cells (ESC)	Grasses
916WS	Short trapeziform in 3D, lobate <4 lobes on each side in 2D, sinuate margin, ESC	*Poa, Koeleria*
917WL	Long trapeziform in 3D, lobate >4 lobes on each side in 2D, sinuate margin, ESC	*Stipa, Calamogrostis*
918LR	Rod, very long trapeziform in 3D, mostly smooth on each side in 2D, epidermal	Grasses, most heavy in long
919	cells (ELC)	*Festuca* and *Agropyron*
920LD	Rod, serrated, very long trapeziform in 3D, mostly aculeate, serrated in 2D, ELC	*Festuca, Agropyron*
921SD	Elongated, flat, dendriform, epidermal from seed, ELC	*Bromus,* domesticated cereals
922RO	Rondel, oblong/oval: short trapeziform in 3D, oblong in top view 2D, ESC	*Agropyron*
923RP	Rondel, pyramidal: truncated pyramidal in 3D, square top view 2D ESC	*Agropyron, Stipa*
924RK	Rondel, keeled: short trapeziform in 3D, oval in top view 2D ESC	*Agropyron, Festuca, Stipa*
925BS	Bilobate *Stipa*-type: trapeziform in 3D, two lobes on each side in top view, ESC	*Stipa, Oryzopsis*
926BB	Bilobate: two lobes with shaft both in top and side view	*Stipa,* Panicoid grasses
927SA	Saddle: concave in top view, concave in side view, ESC	*Stipa* (in our region)
928HT	Trichome: acicular/lanceolate psillate epidermal appendage (trichome)	Grasses, forbs (multicell
929		trichomes in
930*Asteraceae*)		
931HH	Hair, hair base	Grasses, forbs and shrubs
932BL	Blocky: cubic or globose, mesophyll and possibly epidermal	*Artemisia* and other shrubs
933EP	Polygonal: irregular polygonal in top view, very flat on the side	Forbs and shrubs

934

935 **Figure 3.** Phytolith morphotype depictions. PR – Plate rectangular; WS – short

936   trapeziform; WL – long trapeziform; LR – long smooth trapeziform (rod); LD –

937   long serrated tapeziform (rod); SD – seed epidermal long cell; RO – Rondel

938   oblong/oval; RP – Rondel pyramidal; RK – Rondel keeled/horned; BS – Bilobate

939   short trapeziform *Stipa*-type; BB – "True" Bilobate; SA – Saddle; HT –

940   Trichome; HH – Hair/Hair base; BL - Blocky; EP – Epidermal non-grass. Refer to

941   Table 3 for the morphotype nomenclature and the list of taxa in which these forms

942   are observed.

943

944 **Figure 4.** Black and white example of a digital color infrared aerial image showing field

945   plots in Marcellus preserve. Pixel resolution is 0.16 m^2, for a total of 250 pixels

946   per plot.

947

948 **Figure 5.** Sample plot phytolith assemblages. Bars represent percentage of total. Refer to

949   Table 3 and Fig. 3 for morphotype descriptions.

950

951 **Figure 6.** Regression scatterplot of NDVI values derived from the digital aerial images

952   predicted by total opal concentration (TPC) in topsoil. The regression equation is

953   NDVI = 0.0475(TPC) – 0.0475 (R^2=0.49, p<0.001). TPC is measured in percent

954   of dry weight of extracted opal relative to bulk soil dry weight. NDVI is the mean

955   value for each plot as measured from approximately 250 pixels per plot on

956   multispectral aerial digital imagery.

957

958 **Figure 7.** Canonical Correspondence Analysis scatterplot (Ter Braak, 1986; PC-ORD) of

959   first two axes showing position of morphotype assemblages from modern plots

960   and morphotypes as the main matrix and abundance of selected plant taxa as the

961   environmental matrix. Refer to Table 3 and Fig. 3 for individual morphotype

962   descriptions and illustrations. Refer to Fig. 5 for morphotype percentage data per

963   plot.

36

964**APPENDIX A**

965Soils were left in a drying oven at approximately 80 ºC overnight and then weighed and 966placed in 100 ml beakers. Carbonates and most organics from the soil were removed by 967digesting with 10% HCl for 15 minutes and then boiling in 70% HNO_3 with a pinch of 968$KClO_3$ for 1.5 hours. After deflocculation in 5% $(NaPO_3)_6$ solution, the samples were 969floated in a heavy liquid solution of ZnI_2 calibrated to a specific gravity of 2.3 g cm^{-3}. 970This step was repeated at least three times to ensure that most of the opal in the sample 971was retrieved.