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ORIGINAL ARTICLE

Phytolith assemblages in modern top soils under plant communities of Northern and Western Altay, Russia

M. Yu. Solomonova, M. S. Blinnikov, N. Yu. Speranskaja, N. V. Elesova, M. M. Silantyeva

Altai State University, 61 Lenina prospect, Barnaul, 656049, Russia.
E-mail: ngi_geo@mail.ru

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We investigated 120 assemblages of phytoliths from modern top soils of 40 different plant communities of Northern and Western Altay region of Russia. The samples were collected from elevations between 360 m and 2360 m above sea level. Using statistical analyses, it was discovered that many communities produce sufficiently distinct assemblages based on standard morphotypes. Specifically we studied 6 kinds of forests (larch, spruce, fir, pine, cedar pine and birch-dominated), 3 kinds of steppes (true, meadow and petrophytic), 5 kinds of meadows (steppe-like, upland dry, wet floodplain, subalpine, alpine), alpine tundra, and mountain shrubland communities. The communities were not evenly sampled, with more redundancy in some types than in others. Using PCA, it was possible to reveal the few morphotypes most responsible for distinguishing different communities, e.g., low conical rondels, rondel sum, long cell sum, lanceolate cells with massive base, and bulliform cell sum.

Key words: Phytoliths; Modern soils; Temperate zone; Plant communities; Eurasia

Introduction

Phytolith analysis is one of a few rapidly developing methods of paleoenvironmental analysis in world science. New and improved studies of subrecent phytolith assemblages formed in top soils under plant communities allow to detect subtle changes in their taxa composition. It is thought that for many communities that are stable an assemblage would develop over a period of a few decades to about a century (Blinnikov et al., 2012).

Although distinct phytoliths (plant opal or hydrogenated silica bodies) form in many taxa (Wallis, 2003; Katz, 2014; 2015; An, 2016), the most abundant and best studied are those produced in grasses (Poaceae) (Golyeva, 2001, 2007; Madella et al., 2005; Piperno, 2006; Strömberg, 2011; Blinnikov et al., 2013) and some other monocots (Ollendorf, 1992; Benvenuto et al., 2015; Bobrov et al., 2016; Stevanato et al., 2019). Many recent studies focus on grasses primarily (Kiseleva, 2006; Fredlund, Tieszen, 1994; Carnelli et al., 2001; Piperno, 2006; Blinnikov et al., 2013; Shakoor, Bhat, 2014; Sperankaya et al., 2018; Lada, Gavrilov, 2016; Neumann et al., 2017), however, there is a constant need to further refine our understanding of phytolith production in various plants. A major challenge is overcoming both redundancy (same form in many taxa) and multiplicity of forms (many forms in the same taxon) (Tsartsidou et al., 2007; Out, Madella, 2016).

Kamanina (1992) and Blinnikov (1994) were among the first in Russia to use a method of analyzing subrecent phytolith assemblages in soils instead of relying on indicator forms. Golyeva (2001, 2007) further refined and added to this approach by analyzing phytoliths across a few nature zones in Russia and applying it to paleoecological and archaeological investigations (Khokhlova et al., 2019 (a,b); Solomonova et al., 2017).

Our research in the south of Western Siberia have analyzed ecological and systamtic specificity of certain morphotypes (Silantyeva et al., 2018). For example, the Northern Altay yielded diverse and divergent assemblages of 20 different plant communities (Solomonova et al., 2019). This paper adds 20 additional communities to the results of that previous research. We have additional plots in Northern and Western Altay of Russia that have been investigated.

Methods

We studied modern topsoils of 40 plant communities (forty sites) from eight mountain ranges of the Russian Altay (Anuy, Bashchelak, Iolgo, Korgon, Kuminsky Belki, Seminsky, Tigirekskiy, and Cherginsky) from the elevations between 360 and 2360 m a.s.l. At each site a standard geobotanical relevee was and aggregated soil samples were collected in triplicate at 0-5 cm below the surface (the very top of A horizon, but not O horizon).

The soil samples were processed using the method of Goleva (2001): Approximately 40 g of soil was boiled in 15% hydrochloric acid for 1 hour to destroy carbonates and most organics. After that, the residue was cooled to 20°C and sand was removed by rapid sieving through a 250 micron sieve and settling for 30 seconds to the 15 cm depth. The residue below the 15 cm mark near the bottom and on the sieve was mainly sand fraction and was discarded. The remaining suspension of clay and silt was then subjected to a few cycles of gravity sedimentation and decantation to remove suspended clays near the top (after 3 hours, repeated 3-7 times) (Tanner and Jackson, 1947). Phytoliths were floated in heavy liquid solution of CdI2 and KI at 2.3 g/cm^3. The samples were mixed thoroughly with a glass rod and centrifuged for 10 minutes at a slow speed (approximately 1000 rpm). The floated phytoliths were collected by a Pasteur pipette from the top 5 mm of the solution, transferred to clean test tubes and sunk by adding distilled water in proportion of 3:1, and dried. The phytolith-rich residue was stored dry in glass vials.

Phytoliths were studied under an optical microscope Olympus BX-51 equipped with Olympus XC-50 digital camera and using cellSens Standart software under 200x magnification. In total, we counted morphotypes in 120 samples (3 per each of the 40 sites). On average between 500 and 600 morphotypes were counted in each sample. The statistical analyses were carried in STATISTICA 8 package to obtain basic statistics and to apply Principal Components Analsysis for ordination and to reveal important factors influencing grouping of individual assemblages.

The production of phytoliths in plants depend to a large extent on their anatomy, and the latter may in turn be dependent on the local environment. We used 54 different morphotypes in our analyses based on Solomonova et al. (2019) and percentages of their presence in each sample.

Results

Morphotypes are not evenly distributed across different community types. The greatest differences were observed for wavy plates (crenates), polylobates, pseudo-bilobates (aka Stipa-type), low trapezoid and conical rondels, lanceolate forms with long awn, and a few different long cells and plates (Figure 1).

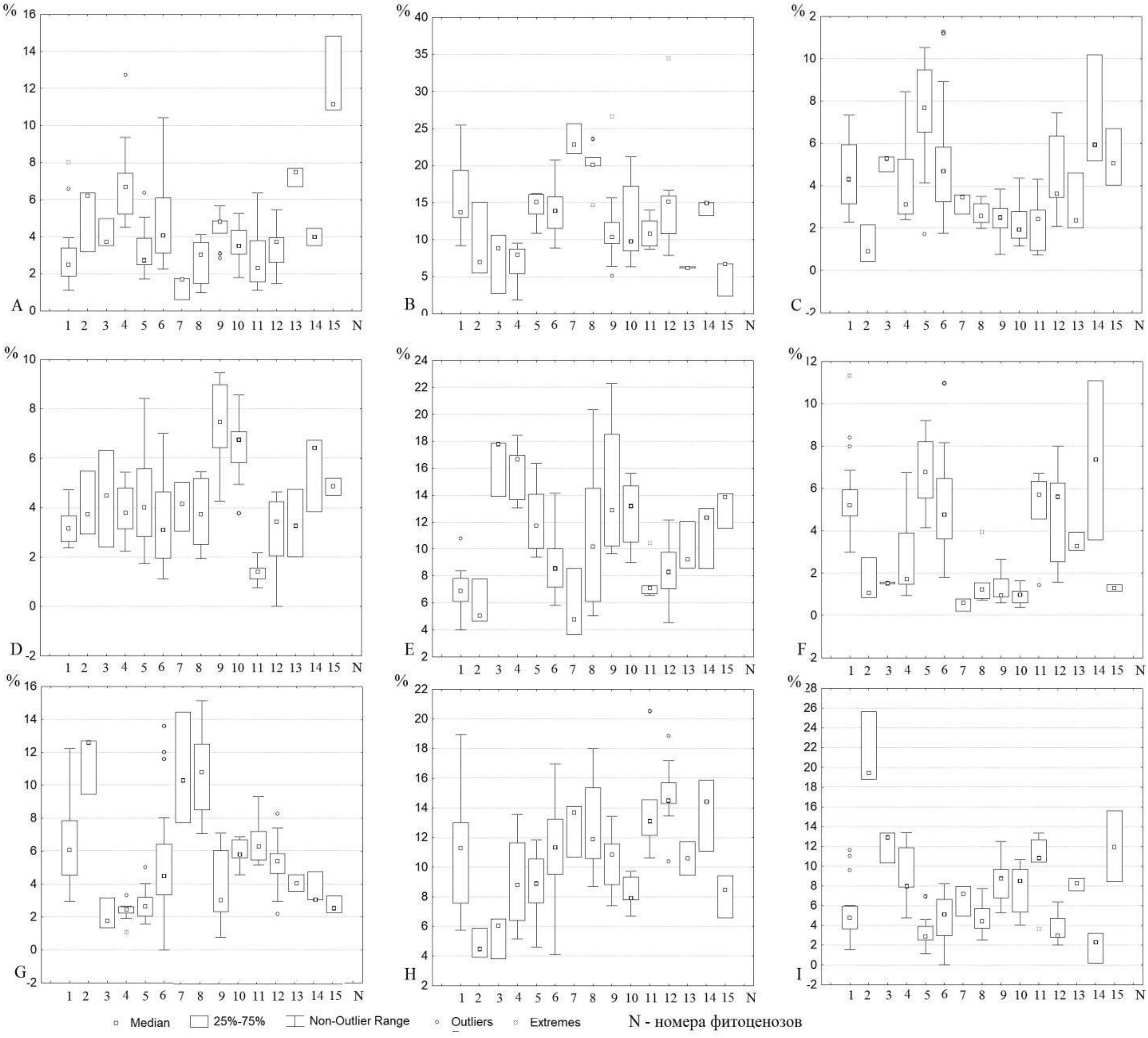
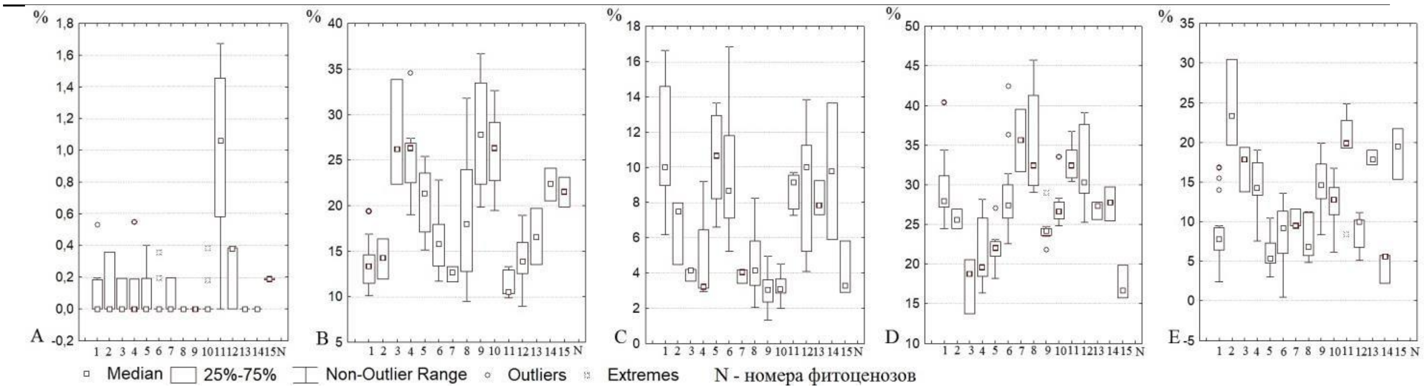


Figure 1. Indicator morphotypes of the Northern and Western Altay. Morphotypes: A – Wavy plates (crenates); B – Poilylobate trapezoids; C – Pseudo-bilobate trapezoids; D – Low trapezoidal rondels; E – Low Conical rondels; F – Lanceolates with a long awn; G – Oval long cells; H –Ribbed long cells; I –Irregular plates (non-grass). Plant communities: 1 – Larch forests, 2 – Spruce forests, 3 – true steppes, 4 – Meadow steppes and steppe meadows, 5 – Pine forest, 6 – Upland meadows, 7 –Subalpine meadows, 8 – Siberian cedar pine forests, 9 – Alpine meadows, 10 – Alpine tundras, 11 – Floodplain meadows, 12 – Birch forests, 13 – Shrublands, 14 – Fir forests, 15 – Petrophytic steppes. Among the sums, the following five displayed major differences across the studied communities: bulliforms, rondels, lanceolates, long cells and plates (Figure 2).



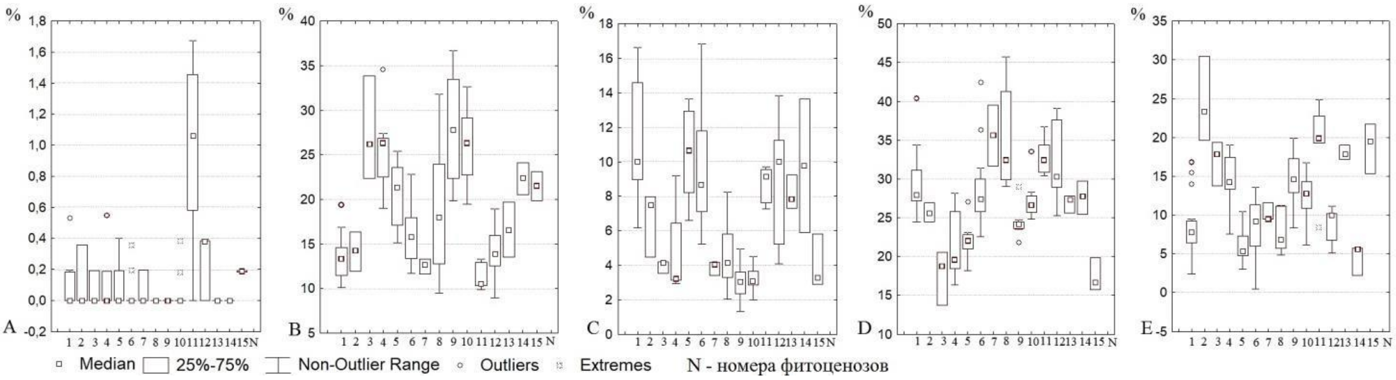


Figure 2. Summary values for diagnostic groups of phytolith morphotypes for 15 plant community types from the Northern and Western Altay. Morphotypes: A –Bulliform sum; B –Rondel sum; C –Lanceolate sum; D –Long cell sum; E –Plates sum (not including crenates of grasses). Plant communities: 1 – Larch forests, 2 – Spruce forests, 3 – True steppes, 4 – Meadow steppes and steppe meadows, 5 – Pine forest, 6 – Upland meadows, 7 –Subalpine meadows, 8 –Siberian cedar pine forests, 9 – Alpine meadows, 10 – Alpine tundras, 11 – Floodplain meadows, 12 – Birch forests, 13 – Shrublands, 14 – Fir Forests, 15 – Petrophytic Steppes.

Our communities are dominated by almost exclusively C3 Pooid morphotypes (almost no saddles, crosses, or other types typical of C4 grass-dominated communities in the subtropics or tropics where other subfamilies are much more common).

Wavy plates indicate petrophytic steppes of the Northern Altay, they are 2-3 times more common in these communities than elsewhere. They are also common in steppe meadows and meadow steppes, many of which are also petrophytic (develop on rocky substrates). Polylobate trapezoidal forms are most common (up to 25%) in dry upland meadows and subalpine meadows. Most forests have them in intermediate amounts, while steppes and subalpine and alpine communities have very few of them. Wet floodplain meadows have intermediate values.

Pseudo-bilobate forms are most common in the soils under pine and fir forests, and are evidently contributed by the same species as the producers of polylobate forms. They are virtually absent from the swamp spruce forest. Low trapezoidal rondel is present at 5% in most communities, however, alpine meadows and tundras have slightly higher values, as well as in fir forests (especially as compared to other forests). Floodplain meadows have the lowest proportions of this morphotype. Low conical rondel is the most common of all rondel types. True steppes and meadow steppes have the most of it, followed by pine and fir forests, petrophytic steppe and alpine meadows and tundras. It is uncommon in dry upland meadows, Siberian cedar pine or birch forests, shrublands. It is rare in larch and spruce forests, subalpine and floodplain meadows.

Lanceolate phytoliths with a long awn are the most common in pine and fir forests, slightly less – in larch and birch forests, and in upland and floodplain meadows. True and meadow steppes and shrublands have intermediate proportions, while subalpine and alpine meadows, alpine tundras, Cedar pine forests, petrophytic steppes, and spruce swamps have the smallest values.

Long oval particles are most common in spruce and Siberian cedar pine forests and subalpine meadows. They have intermediate values in larch and birch forests, upland and floodplain meadows, and tundras. They are the least common in steppes, steppe meadows, pine and fir forests, alpine meadows and shrublands. Long ribbed particles are the most common type of long cells. They are most common in birch and fir forests, moderately common in larch and Siberian pine forests, alpine, subalpine and floodplain meadows, shrublands. They are less common in meadow steppes and petrophytic steppes and in alpine tundras. Finally, they are virtually absent in spruce swamp and true steppes. Thus, they can be used for distinguishing different kinds of dark coniferous forests (fir vs. spruce), birch vs. larch forests, and finally true steppes from other graminoid- dominated communities. Irregular plates, which are in all likelihood not produced by grasses, are dominant in spruce swamp. They are also common in true and petrophytic steppes and in floodplain meadow. Thus, they are most common in the driest and the wettest communities.

When sums of different morphotypes are used, the differences among the assemblages are amplified (Figure 3). Bulliforms are overall rarely found in the analyzed samples, but they are the highest in the floodplain meadows. The rondel sum is the highest in steppes and alpine communities. The pine and fir forests have them at moderately high values. Shrublands, upland meadows, Siberian pine forests have lower proportion of rondels. Finally, they are rare in subalpine and floodplain meadows, larch and birch forests, and spruce swamp. The highest proportions of lanceolate phytoliths are found in all forests, except spruce swamp and Siberian cedar pine forest, but also in floodplain and upland meadows, which commonly replace forests after timber harvesting in the study area. Conversely, the lowest proportions of lanceolates are observed in steppes, steppe meadows, subalpine and alpine meadows, alpine tundras and Siberian cedar pine forests. Therefore, this sum of morphotypes allows to discriminate steppe from forest, and also Cedar pine and spruce swamp forests from other forests. Long cells are very common in all assemblages. Still, their highest values are observed in Siberian cedar pine forests, subalpine and floodplain meadows, and shrublands. They are lower in other communities, especially <25% in steppes, alpine meadows and pine forests. Thus, the sum of all long cells may help distinguish pine forests from other forests, alpine tundras from alpine meadows, and shrublands from most forests or all graminoid-dominated communities. Plates of diverse, especially irregular, shapes may form in many different taxa, ranging from ferns and horsetails, to some conifers, to sedges and even some dicot plants. However, they are not common in grasses, where plates if present are more or less rectangular. Plates are very common in the spruce swamp, and are common in steppes, floodplain meadow and shrublands. All forests and meadows that formed in place of forests at lower elevations, in contrast, have <10% of these. PCA revealed that assemblages of phytoliths in our study area are relatively similar to each other, with the first two axes accounting for only 21% of all information. The first axis (Table 1) is greatly influenced by lanceolate and long ribbed cells in the positive direction and irregular plates and long triangular cells in the negative direction. The second axis is greatly influenced by long oval cells in the positive direction and low conical rondel in the negative direction.

Table 1. Loadings for the first two axes of PCA using all morphotypes (only the most important ones shown).

Morphotypes/Variables	PC1	PC2
Low conical rondel	-0.146947	-0.780279
Lanceolate with massive base	0.526757	0.411984
Lanceolate with a long awn	0.623389	0.351003
Lanceolate triangular	-0.416280	0.503892
Long oval regular cells	-0.399075	0.670702
Long oval asymmetric cells	-0.240232	0.560030
Long ribbed cells	0.566487	0.085938
Long ribbed asymmetric cells	0.550321	-0.178580
Long triangular cells	-0.515753	0.273533
Irregular plates	-0.584087	-0.101637

The PCA ordination 1 plot of the first two axes (Figure 3) reveals the following plant communities as broadly similar:
true and petrophytic steppes, and alpine meadows and tundras. All of these have relatively high proportion of rondels, and for the alpine meadows many are grouped especially because of the high proportion of low conical rondels. We can also see that Siberian cedar pine assemblages are intermediate between tundras on the one hand and subalpine meadows and larch forests on the other. This makes sense, because Cedar pine and larch forests develop near the treeline and some subalpine meadows at the same latitudes may be their early successional communities developing after timber cuts.

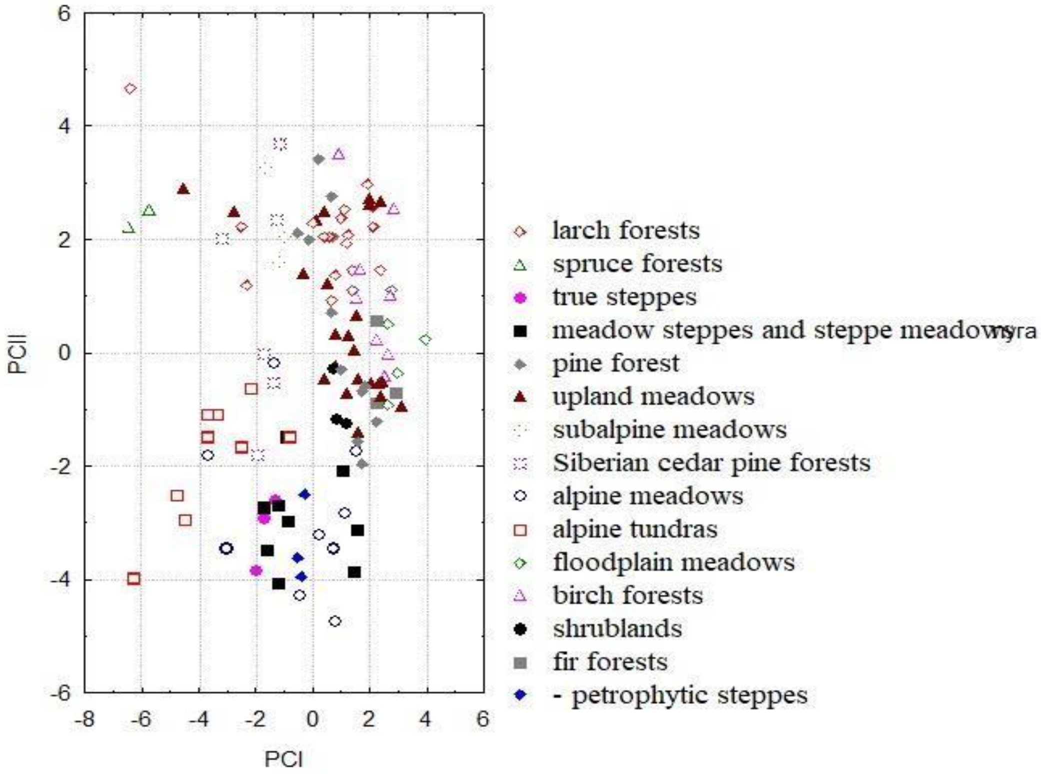


Figure 3. PCA ordination 1 plot of the first two axes when using individual morphotype percentages as inputs

Shrubland assemblages resemble those of fir forests and upland meadows, but also with some pine and birch forests, and floodplain meadows. However, they are different from forests by the axis 1. Larch forests have the most distinct assemblages from the grass-dominated assemblages (steppes and meadows) and are somewhat similar to other forests, except fir and birch. Spruce swamp has a very distinct assemblage along the first axis, but is similar to other forests along the second. Overall, the forests are different from non-forested communities. We ran another PCA ordination (#2), in which five most common morphotypes were combined as sums (lanceolates, bulliform, rondels, plates and long cells). This approach actually revealed a stronger information trend (30% were captured by the first two axes, Table 2). Axis 1 was mainly influenced by the long cell sum proportion, while axis 2 – by bulliform sum.

Table 2. Loadings for the first two axes of PCA using sums (only more important categories shown).

Morphotypes/Variabls	PC1	PC2
Bulliform sum	0.255159	0.729305
Polylobate trapezoids	-0.539073	0.296900
Low saddles	0.586174	-0.207710
True bilobates	-0.083600	0.508971
Conical particles (sedges)	-0.628214	0.401365
Phytoliths of conifers	-0.011745	-0.483295
Lanceolate sum	-0.080344	-0.515640
Long cell sum	0.727448	-0.100060
Plates sum	0.524068	-0.330565
Globular particles	-0.678400	-0.069513

Using sums in the second PCA allows to even better group alpine tundras with true and meadow steppes. This is similar to what Blinnikov (2005) found for the steppe and alpine communities of NE Oregon and SE Washington states. Basically, the lack of tree components emphasizes similarity based on graminoid-produced forms both at low and high elevations. Along the first axis of PCA ordination 2 tundras and steppes are different from other communities in having more polylobate trapezoids, saddles, conical phytoliths and plates. Along the second axis of PCA ordination 2 alpine meadows and petrophytic steppes are grouped close to each other and are distinct from alpine tundras, other steppes, and steppe meadows in having more bulliform cells, true bilobates, and lanceolates (Figure 4).

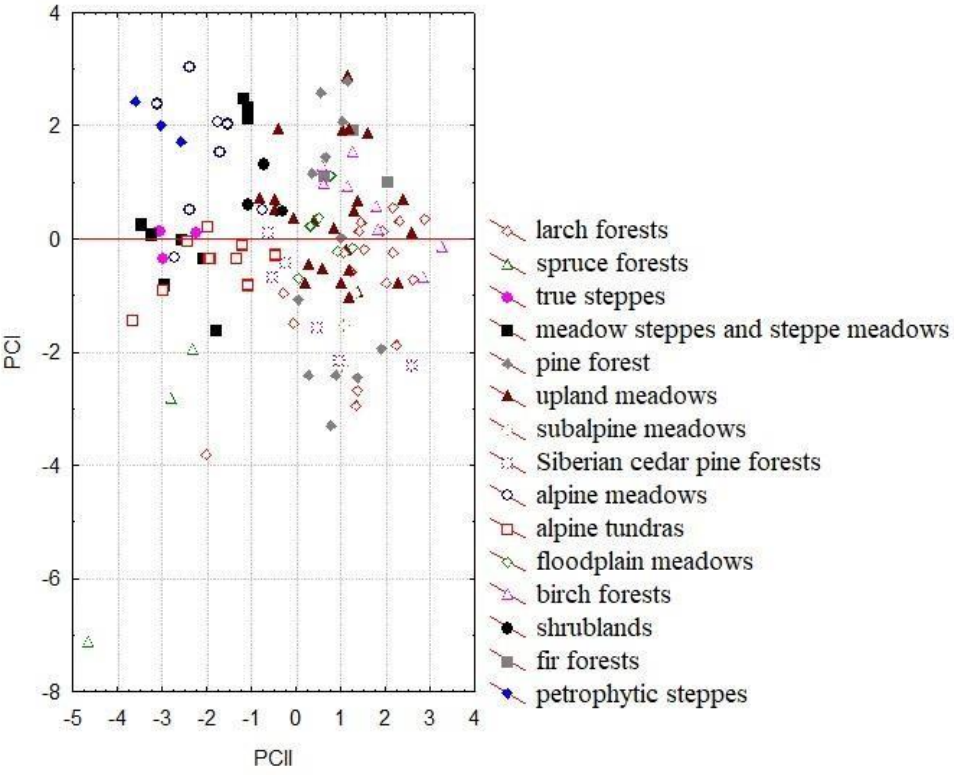


Figure 4. PCA ordination 2 plot of the first two axes when using morphotype sums percentages as inputs

Siberian cedar pine forests have assemblages intermediate between tundras and larch/pine forests, but differ from fir and birch forests along the first axis. Most forests are actually similar to each other and to upland and subalpine meadows (which are components of successional mosaics at lower and higher elevations respectively).

Comparing our new results with previously published, broader geographical scope and larger number of different plant community types allowed to refine our understanding of the phytolith diversity (Solomonova et al., 2019). The assemblage sets in this study correspond to the previously obtained data from the Northern Altay. We confirm our earlier findings from 2018 that low-elevation steppes and high-elevation grasslands produce broadly similar assemblages. The main indicator morphotype sum for them is rondels. Rondels are especially well represented in the lowland communities, but are also high in the alpine zone (Silantyeva et al., 2018). Blinnikov (1994) found the same relationship in his study of phytoliths in modern soils in the alpine zone of Teberda Reserve of NW Causasus in Russia. In a study from NE China, rondels were found to predominate in any non- forested communities, even in those that develop after a forest (Li et al., 2018). However, their main indicator morphotype is bilobates, given the presence of Panicoids in much greater proportion in the regional flora of China. In our area, bilobates that are found are primarily of Pooid type (e.g., pseudo-bilobate trapezoids cf. Stipa) and other lobate forms probably from Calamagrostis or Brachypodium in pine and fir forests. In an earlier study, it was shown that some regionally important forest types can be distinguished based on phytoliths (Solomnonova et al., 2019). The new data in this study allow to distiniguish fir-dominated forests for the first time, and also suggest that both subalpine and upland meadows have assemblages similar to many forest communities (especially Siberian cedar pine), which is not surprising given the mosaic nature of these transient successional communities near ecotones (lower and upper treelines). An important group of morphotypes are lanceolate forms (trichomes in the broad sense). They are prevalent in the forests and meadows formed in place of former forests, but also in floodplain meadows, where many grasses and sedges may produce them. They are likewise common in the plains of Altaysky Kray away from the mountains (Silantyeva et al., 2018). The most common lanceolate morphotype are the ones with a long awn and relatively compact base, so called "meadow trichomes" of A. Golyeva (Golyeva, 2007), who considers them a diagnostic form for meadows in general. We confirm this relationship for many low-elevation meadows in our studies, as well as for pine and fir forests. When our data are compared to those from NE China, a region of broadly similar topography, our study area contains more diagnostic morphotypes of forest assemblages. In China, many of such are dominated by phytoliths of sedges, mainly of conical papillae type (Li et al., 2018), which are poorly preserved in soils as compared to grass phytoliths and which are largely absent from our study area (Gao et al., 2018).

Conclusion

Our results reveal a few distinct groups of phytolith assemblages in the study area: 1) high-elevation communities; 2) steppe and meadow-steppe communities at lower elevations, 3) forests and meadows at intermediate elevations. The first and second group are similar in the high proportion of rondels, including low conical rondels as the most common type. Within second group, petrophytic steppes are the most distinct. Shurblands are broadly similar to petrophytic steppes and some forests. Within forests, conifer-dominated ones are different from broadleaf. Birch forests are similar to larch forests, probably based on the phytoliths produced in the ground layer of vegetation. Neither birch nor larch produce very significant amounts of distinct phytoliths. Subalpine meadows and nearby Cedar pine forests have similar assemblages probably due to an inheritance of former phytoliths of forest under meadows at the location near treeline, where mosaics of forest and meadow are dynamic. Similarly, at lower elevations, upland meadows produce assemblages resembling larch and birch forests, although there are a few morphotypes that are distinct to the meadows (more rondels and long cells and some plates).

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