Silicophytoliths from a Pampean native tree community (*Celtis ehrenbergiana* community) and their representation in the soil assemblage

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ABSTRACT

Plant phytolith production and their incorporation into soil assemblages has been studied by diverse authors in different regions of the world, mainly in the Northern Hemisphere and Africa. However, these types of studies are scarce in native plant communities from South America, especially in non-grass communities. The comprehension of the relation between plant phytolith production and their incorporation into soils is crucial for the interpretation of past environments and vegetation based on fossil phytolith records. The aim of this work is to describe the silicophytolith production of a Pampean native tree community (*Celtis* ehrenbergiana community) and the silicophytolith assemblages of the soils, in order to understand the relation between silicophytolith production and their incorporation in these natural forests. Silicophytoliths from 19 species of these communities were extracted through a calcination technique; while soil samples were subjected to routine techniques. Soil silicophytoliths were counted and described, and their abundances were referred in relation to total soil mineralogy. Morphologies were similar between species and were mainly derived from the epidermal, vascular and sclerenchymatic tissues. *Celtis* spp. produced abundant diagnostic morphologies, such as cystoliths and platelet echinate silicophytoliths, typical of the genus. Soil assemblages were dominated by grass silicophytoliths and in a lesser proportion by dicotyledons silicophytoliths. However, grasses are scarcely found or absent in actual forests. These results showed that there was not a direct relation between plant silicophytolith production and soil phytolith incorporation in these forests. As it occurs in different environments worldwide, soil silicophytoliths are affected by taphonomical processes (fragmentation, dissolution, mobilization, etc.) and they are not always an exact reflection of phytolith production of local plants. These results indicate that a high silicophytolith production in plants (in this case *Celtis* spp.) is not always reflected in soil assemblages. These aspects should be considered in relation to the interpretation of fossil silicophytolith records.

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1. Introduction

Silicophytoliths are amorphous silica biomineralizations deposited in inter or intracellular spaces of plant tissues of diverse taxa (Lowenstam, 1981; Jahren et al., 1996; Osterrieth, 2004). They have a taxonomic relevance since certain morphotypes are diagnostic at the family, genera or species level (Metcalfe, 1960; Twiss, 1992). Also, due to their high perdurability in soils and sediments, silicophytoliths have been widely applied as indicators of past plant communities in paleoenvironmental, paleontological and archeological studies (e.g. Rovner, 1971; Strömberg, 2004; Piperno, 2006; Osterrieth et al., 2014).

Once the plant or the organ which produces the phytoliths falls to the ground and starts decomposing, silicophytoliths are released and incorporated into the soils. Due to their siliceous composition, they can be preserved in various types of environments, and constitute an important fraction of soils and sediments (Osterrieth et al., 2014). Depending on the environmental and pedological conditions, silicophytoliths, like any mineral particle, are also affected by diverse taphonomical processes (Fredlund and Tieszen, 1994; Albert et al., 2006; Osterrieth, 2008; Iriarte and Paz, 2009; Osterrieth et al., 2009; Fernández Honaine et al., 2009; Madella and Lancelotti, 2012).

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Numerous phytolith studies have shown that the assemblages of the firsts cm of the soil's thickness (0–1, 0–5 cm), allow differentiation among plant communities, showing the relevance of phytoliths as important plant indicators (Piperno, 2006). Plant communities from different regions of the world, such as the Interior Pacific Northwest of USA (Blinnikov, 2005), East and West Africa (Barboni et al., 2007), southeastern Uruguay (Iriarte and Paz, 2009), eastern lowland Bolivia (Dickau et al., 2013), and the Southwestern Amazonian forests (Watling et al., 2016), among others, have been successfully differentiated based on top soil silicophytolith assemblages. Although silicophytoliths produced by plants are mostly deposited and incorporated into the soil below, the top soil assemblages could be modified by different processes. Mobilization and dispersion by wind, water and/or animals, bioturbation, fragmentation or dissolution processes, may modify the original phytolith input (e.g. Twiss, 1983; Fredlund and Tieszen, 1994; Thorn, 2004; Osterrieth et al., 2009; Fernández Honaine et al., 2009; Mercader et al., 2011; Madella and Lancelotti, 2012; Dickau et al., 2013). In addition, and apart from the environmental conditions, the dissolution/fragmentation rate of a pool of phytoliths will depend on their type (size and shape) and consistency (Iriarte and Paz, 2009; Osterrieth et al., 2009). Finally, the phytolith assemblage of a soil or sediment is affected by the previous phytolith content of the parent material (Osterrieth et al., 2009).

For an adequate paleoenvironmental and paleobotanical interpretation of the fossil phytolith record, it is necessary to generate knowledge regarding the phytolith production of actual plants, as well as the taphonomic processes involved during their incorporation into soils and sediments (Osterrieth et al., 2009; Madella and Lancelotti, 2012; Coe et al., 2014). In South America, these types of studies are scarce, and they are mainly related to grass-dominated communities (Alexandre et al., 1999; Fernández Honaine et al., 2009; Montti et al., 2009; Iriarte and Paz, 2009; Del Puerto et al., 2011; Monteiro Dos Reis et al., 2011; Benvenuto et al., 2013), aquatic environments (Dos Santos Pereira et al., 2015; Coe et al., 2017); or to neotropical ecosystems, including many areas of SW Amazonia (Dickau et al., 2013; Watling et al., 2016). Almost no research has been done in temperate woody communities, where phytolith production and incorporation dynamics may be different due to their floristic and environmental conditions.

In the southeastern Pampean region of Argentina, one of the few native arboreal community is represented by "Talar" communities, dominated by *Celtis ehrenbergiana* (Klotzsch) Liebm ex *Celtis tala* (Parodi, 1940; Cabrera, 1976; Romanczuk, 1976). They are located along coastal sectors of Buenos Aires province and grow in diverse environments with variable type of soils, mainly Mollisols types (Cabrera, 1976; Fernández Honaine, 2001; Mérida and Athor, 2006; De Rito, 2015). Due to the location of "talar" communities near ponds or coastal zones, they constituted favorable environments where ancient populations developed. These communities provided protection, floral and faunal resources, fuel, and also food for people, since *Celtis* fruits were eaten by ancient settlers (Aldazabal et al., 2004; Paleo et al., 2002). It has been suggested that the "Talar" community occupied in the past a larger territory than nowadays, The excessive use of wood, the urban development and the expansion of agricultural frontiers have reduced its distribution (Arturi et al., 2006).

Celtis ehrenbergiana belongs to the Cannabaceae family. *Celtis* includes about 70 species, and many of them have been studied in relation to their phytolith production (Bozarth, 1992; Wallis, 2003; Fernández Honaine et al., 2005; Piperno, 2006; Iriarte and Paz, 2009). Previous research showed that *C. ehrenbergiana* produces a high amount of phytoliths (2.07 + 0.92 and 2.93 + 1.13% dry weight, depending on the organ) (Fernández Honaine et al., 2005). Cystoliths, derived from leaves, and tabular echinate or echinate platelets derived from fruits, are the most abundant morphotypes described (Fernández Honaine et al., 2005; Iriarte and Paz, 2009). However, there is no data about the phytolith production of other species of this native community. Considering the ecological and archeological relevance of these communities

at present, it is important to understand their distribution in the past, and phytolith studies could be a useful tool for this purpose, taking into account their high silicophytolith production. On the other hand, the adequate interpretation of fossil and archeological phytolith assemblages relies on the comprehension of the relation between plant phytolith production and their incorporation into the soil. Some previous studies in Brazil and Uruguay, where *Celtis* spp. grow in forests, showed a low presence of fruit *Celtis* phytoliths in soils assemblages, besides the high amount of leaf and fruit phytoliths produced by the plants (Iriarte and Paz, 2009; Dickau et al., 2013). In order to understand the relation between *Celtis* phytolith production and its incorporation into the soils, we studied *Celtis*-dominated communities from SE Buenos Aires province, Argentina. The present study aims to describe the silicophytolith production of the *Celtis* community and also to describe and analyze the silicophytolith assemblages of associated soils of these Pampean forests. The results will contribute to a deeper understanding of phytolith dynamics in natural forests in southeastern South America, where antecedents are very scarce. This understanding is crucial in order to obtain advances in the reconstruction of the paleovegetation and paleoenvironments of the region based on phytolith analyses (Iriarte and Paz, 2009).

2. Study area

The study area is included in the southeast part of the Buenos Aires province, in the Pampean Region, Argentina. This region is characterized by a relief that ranges from undulated to plain. The evolution of the Pampean Plain involves the combination of marine erosion, vegetal cover, eolic action, pedological development and anthropic activity (Schnack et al., 1982). It is one of the most fertile regions of the world and so intense agricultural activities are carried out there which, in turn, have strongly modified the native plant communities, especially grasslands. The area is mesothermic subhumid–humid, with null or little water deficiency (Burgos and Vidal, 1951). The mean annual precipitation is 940.6 mm and the mean annual temperature is 13.8 °C, with a mean of 20 °C during the hottest month (January) and a mean of 7.3 °C during the coolest month (July) (Servicio Meteorológico Nacional, 2010).

Two study sites, where "Talar" communities are developed, were selected: Estancia Nahuel Rucá (37° 37′31,64″ S; 57° 25′17,43″ O, Mar Chiquita district) and Laguna de Los Padres Integral Reserve (57° 52′ 21,96″; 37° 55′ 14,47″ S, General Pueyrredón district) (Fig. 1).

The Estancia Nahuel Rucá is a private field, included in the geomorphological unit of Fluvioeolian Plain and characterized by a silt dune associated with a blowout, now turned into a pond (Martínez, 2001). These geoforms were probably originated by strong winds from the west during the late Pleistocene, associated with preexisting river valleys (Tricart, 1973; Schnack et al., 1982). The representative soils of this area are an association of typical Argiudolls, Natracuolls and typical Hapludolls predominantly, depending on the geomorphological characteristics of each sector (INTA, 1989). From a phytogeographical point of view, it is part of Eastern Pampean distric, Pampean province and is characterized by a grass steppe formed by *Stipa*, now replaced by exotic species (Cabrera, 1976). In particular, the "Talar" community in this site is characterized by an arboreal stratum dominated exclusively by *Celtis ehrenbergiana* and an herbaceous stratum dominated by *Dichondra microcalyx* (36,5%), *Bromus* sp. (14,5%), *Carduus acanthoides* (12%). Other species of Juncaceae, Asteraceae and Poaceae families and *Medicago lupulina*, *Conyza* sp., *Cyperus* sp., *Gamochaeta* sp. are also present in the area (De Rito, 2015). The Estancia Nahuel Ruca has been managed by the present owners since more than 70 years. The main activities in the past were cattle raising, and nowadays the place is also used for tourism (country tourism) and recreation (Urrutia, pers. com.). According to the owner and other studies, the youngest part of the talar community has more than 45 years old (Cicchino, 2006, Urrutia pers. com.).
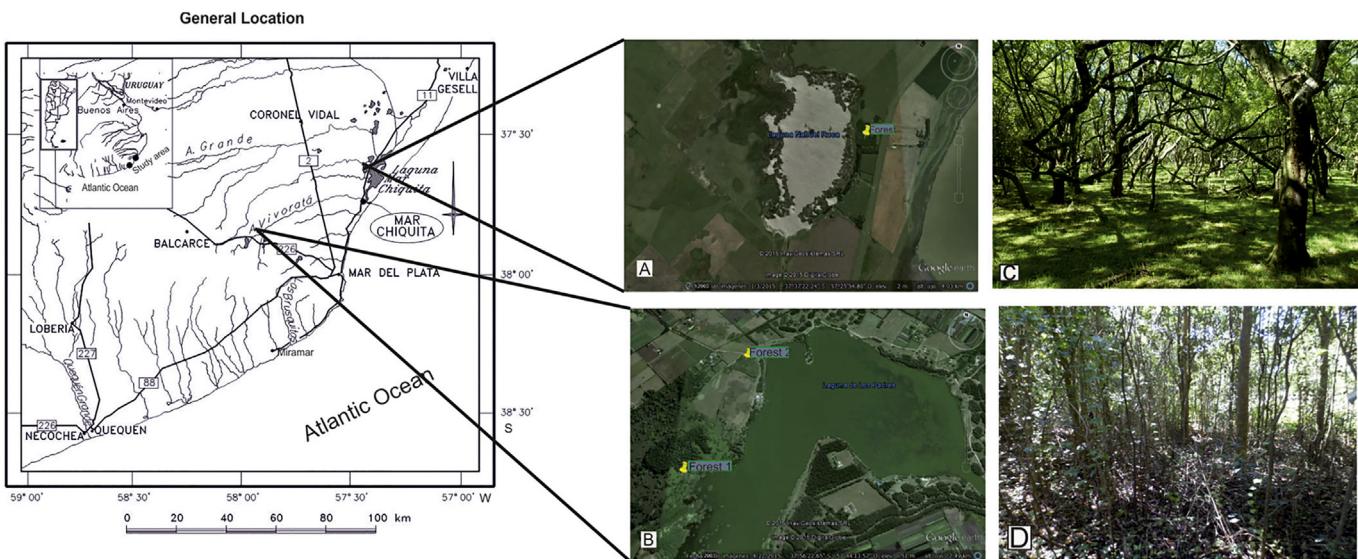
Fig. 1. Location of study area. A) and C) Estancia Nahuel Ruca (forest), B) and D) Laguna de Los Padres Integral Reserve (forests 1 and 2). Study sites are marked in yellow. Image from Google Earth. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Laguna de Los Padres Integral Reserve is a natural area. It belongs to the geomorphological unit known as perirange eolian hills (Martínez, 2001). It comprises a relief of morphologically complex hills, with relative heights of up to 30 m and concave–convex profiles, with intermediate straight patches and slopes between 6 and 8% (Osterrieth et al., 1998). This landscape originated from primary eolian accumulation processes, and was later modified by surface wash (Osterrieth and Martínez, 1993). Subsequently, a cycle of higher humidity and rainfall provided enough water not only to fill the lagoon but also to generate the important aquifer that supplies the region (Cionchi et al., 1982). The representative soils are predominantly Molisolls (Soil Survey Staff, 1996), which have been developed from eolic and fluvioelic sediments deposited during the late Pleistocene-Holocene (Osterrieth and Cionchi, 1985). From the phytogeographical point of view, it is part of Austral Pampean district, Pampean province (Cabrera, 1976). Plant communities associated with wetland are characterized by *Typha* spp., sedges, *Salix* spp. and some grasses, while in the areas of hill and slope there are small forests of "Talar" (*Celtis ehrenbergiana*) and *Colletia paradoxa*, associated with *Ligustrum lucidum* and blackberries (*Rubus ulmifolius*), among other species (Fernández Honaine, 2001). In particular, the studied forests are characterized by *C. ehrenbergiana*, *Celtis*

occidentalis, Ligustrum lucidum, Ligustrum sinense and to a lesser extent by *Eucalyptus* sp. and *Acacia melanoxylon* in the arboreal stratum. No herbaceous stratum was observed in these study sites, except for some plants of *Hedera helix* (De Rito, 2015). In 1957, the area where *Colletia paradoxa*, "curro", developed, which involves the sites where *C. ehrenbergiana* also grew, was declared as a Provincial Reserve (Buenos Aires Provincial Disposition N° 19.322). In 1983, the total area of Laguna de Los Padres became preserved by the Mar del Plata government, and finally in 2010 the whole area was included within the Provincial Protected Areas (Buenos Aires Provincial Disposition N° 469).

3. Materials and methods

3.1. Plant selection and sampling

Based on bibliography and previous vegetation surveys, the dominant plant species present in the two study sites (Nahuel Rucá and Laguna de Los Padres) were collected (Del Río et al., 1992; Fernández Honaine, 2001; Stutz, 2001; De Rito, 2015) (Table 1). Also, two species that are common in "Talar" communities in its northernmost distribution, but they are not currently present in the study area (*Jodina*

Table 1
Species and plant organs used in this study.

Family	Species	Collection place	Leaf	Stem	Flower	Root	Fruit
Adoxaceae	*Sambucus australis* Cham. Et Schltdl	IGCyC herbarium, UNMdP	X	–	–	–	–
Araliaceae	*Hedera helix* L.	Laguna de Los Padres	X	–	–	–	–
Asteraceae	*Baccharis tandiliensis* Speg.	Laguna de Los Padres	X	X	–	–	–
Asteraceae	*Carduus acanthoides* L.	Nahuel Rucá	X	X	X	–	–
Asteraceae	*Conyza* sp. Less.	Nahuel Rucá	X	X	–	X	–
Asteraceae	*Senecio madagascariensis* Poir.	Nahuel Rucá	X	–	X	–	–
Blechnaceae	*Blechnum auriculatum* Cav.	Laguna de Los Padres	X	–	–	–	–
Cannabaceae	*Celtis occidentalis* L.	Laguna de Los Padres	X	X	–	–	X
Cannabaceae	*Celtis ehrenbergiana* (Klotzsch) Liebm (ex *Celtis tala* Gillet ex Planchon)	Laguna de Los Padres/Estancia Nahuel Rucá	X	–	–	–	–
Cervantinaceae	*Jodina rhombifolia* (Hook. &Arn.) Reissek	Uruguay	X	–	–	–	–
Convolvulaceae	*Dichondra microcalyx* Meins	Nahuel Rucá	X	–	–	–	–
Oleaceae	*Ligustrum lucidum* Ait.	Laguna de Los Padres	X	X	–	–	–
Oleaceae	*Ligustrum sinense* Lour.	Laguna de Los Padres	X	X	X	–	X
Rhamnaceae	*Colletia paradoxa* (Spreng) Escal.	Laguna de Los Padres	X	X	–	–	–
Rhamnaceae	*Scutia buxifolia* Reissek.	Uruguay	X	–	–	–	–
Rosaceae	*Rubus ulmifolius* Schott	Laguna de Los Padres	X	–	–	–	–
Solanaceae	*Salpichroa origanifolia* (Lam.) Thell.	Nahuel Rucá	X	–	–	–	–
Solanaceae	*Solanum chenopodioides* Lam. (*S. gracile* Dum.)	Nahuel Rucá	X	–	–	–	–
Solanaceae	*Cestrum parqui* L'Hér.	IGCyC herbarium, UNMdP	X	X	X	–	–

rhombifolia and *Scutia buxifolia)* were included for silicophytolith analyses. In total, 19 species were analyzed.

3.2. Plant silicophytolith extraction and description

Two or three plants of each species were selected for phytolith extraction. Different organs (leaf, stem, and in some cases flower, fruit and/or root) were sampled, weighted and subjected to Labouriau calcination technique (Labouriau, 1983). The material was dried at 56 °C for 24 h, and charred at 200 °C for 2 h. Later, it was boiled in a 5 N HCl solution for 10 min, washed with distilled water and filtered with ashless filter paper, until no more chloride ions were detected. Finally, the material was ignited at 760 °C for 2.5 h, and then weighted. As a result of this technique, ashes mainly composed by silicophytoliths were obtained. The relative content of silica was calculated by the following formula (Fernández Honaine et al., 2005):

$$\text{Silica content } (\%) = (\text{Ash weight}/\text{initial weight previous calcination}) \times 100$$

The ash obtained was mounted in immersion oil. A minimum of 200 silicophytoliths per sample were counted and described under optical microscope (Zeiss Axiostar Plus) at 400× and under scanning electron microscope (JEOL JSM-6460 LV; Japan) at Universidad Nacional de Mar del Plata, Argentina. The photographs were taken with digital camera Cannon Powershot G10. The silicophytolith morphologies used in this study are shown and described in Table 2, and are mainly based on classifications of Twiss (1992), Fredlund and Tieszen (1994) and Madella et al. (2005). The relative frequencies of the phytolith morphotypes of each species were calculated. The species were classified as non-producers, trace producers, common or abundant producers according to Wallis (2003). For this classification, 10 fields of the slide were randomly selected and counted. If the fields of the slide have no phytoliths, the species was classified as non-producer; between 1 and 50 phytoliths as trace producer; between 51 and 150 as common producer, more than 150 as abundant.

3.3. Soil sampling and characterization

In each sampling site (Estancia Nahuel Rucá and forests 1 and 2 of Laguna de Los Padres Integral Reserve), three dominant, large and equidistant trees were selected. In each tree, composite samples (made of three subsamples) from 0 to 1, 0–5 and 5–10 cm depth of A horizon taken at 0.5 m, 1 m and 1.5 m from the trunk, were collected.

In order to characterize the top soils (A horizons), morphological profile descriptions were made according to the standards established

Table 2
List of silicophytoliths used in this work.

Abbreviation	Silicophytolith morphotype	Description	Tissue origin/taxa affinity	References
X	Cylindrical sulcate xylem/Cylindrical sulcate tracheid	Cylindrical shape with silica helically deposit.	Vascular tissue	Madella et al., 2005
CM	Crescent	Trapeziform in side view, crescent moon in surficial view.	Epidermal tissue, short cell/Poaceae	Twiss, 1992
C	Cross	It has four approximately equal lobes.	Epidermal tissue, short cell/Poaceae (mainly Panicoideae)	Mulholland, 1989; Madella et al., 2005
PB	Panicoid bilobate	It is distinguished from the simple lobate by its indented or sculpted ends and well developed lateral plane of symmetry.	Epidermal tissue, short cell/Poaceae (mainly Panicoideae)	Fredlund and Tieszen, 1994
SL	Simple lobate	It is a form with two lobes. It has a more pronounced shank separating the lobes, and the lateral plane of symmetry is better developed.	Epidermal tissue, short cell/Poaceae (mainly Panicoideae, Stipoideae)	Fredlund and Tieszen, 1994
PTE	Polylobate	Morphotypes with more than two lobes linearly arranged.	Epidermal tissue/Poaceae	Madella et al., 2005
TC	Trapeziform crenate	Trapeziform in side view, rectangular crenate in surficial view.	Epidermal tissue, short cell/Poaceae (mainly Pooideae)	Fredlund and Tieszen, 1994; Madella et al., 2005
R	Rondel	Trapeziform in side view, rounded, elliptical or square in surficial view. Equidimensional	Epidermal tissue, short cell/Poaceae (mainly Pooideae)	Mulholland, 1989; Fredlund and Tieszen, 1994; Madella et al., 2005
RE	Rondel elongate	Trapeziform in side view, rounded, elliptical or rectangular in surficial view. Much longer than wide.	Epidermal tissue	Bertoldi de Pomar, 1971
S	Saddle	Body like a barrel. Must exhibit three planes of symmetry: two planes if viewed abaxially or adaxially, and a lateral plane when viewed cross-sectionally.	Epidermal tissue, short cell/Poaceae (mainly Chloridoideae)	Mulholland, 1989; Madella et al., 2005
EC	Elongate crenate	Much longer than wide. Crenate edges.	Epidermal tissue	Madella et al., 2005
EE	Elongate echinate	Much longer than wide. Echinate edges.	Epidermal tissue	Madella et al., 2005
EP	Elongate psilate	Much longer than wide. Smooth edges.	Epidermal tissue	Madella et al., 2005
P	Polyhedral	Diverse polyhedral shapes, with straight sides and big size.	Epidermal tissue/Dicotyledons	Madella et al., 2005
C	Cystolith	Bodies formed by a polyhedral basis, a cylindrical foot and a spherical/ovoid or elliptical body, with smooth to irregular granular surface.	Epidermal tissue/*Celtis* spp. Ulmaceae, Moraceae	Fernández Honaine et al., 2005; Iriarte and Paz, 2009
T	Pointed shaped	Morphologies derived from uni or multicellular hairs.	Epidermal tissue, trichomes	Twiss, 1992
TE	Tabular echinate/Echinate platelets	Tabular with polyhedrical contour and echinate surface	Fruit exo/mesocarp/*Celtis* spp.	Fernández Honaine et al., 2005; Iriarte and Paz, 2009
TEL	Tabular epidermal	Tabular with polyhedrical or rounded contour	Epidermal tissue/Dicotyledons	Madella et al., 2005
SC	Stomatal complex	Small pores traversing the plant epidermis. Two cells that change their pore size, joining together at both ends.	Epidermal tissue	Madella et al., 2005
G	Globular	Spherical or semi spherical morphotype. It includes all type of surfaces	Mesophyll tissue	Madella et al., 2005
F	Fibers	Elongate, straight and narrow, with cuneiform/sharp ends.	Schlerenchyma tissue	This study
SCD	Sclereids	Cylindrical and not straight, sometimes branched, smooth ends.	Schlerenchyma tissue	This study

by the Soil Survey Staff (1996). Also, particle size distribution was determined by sieve and pipette analysis (Ingram, 1971; Galehouse, 1971).

3.4. Soil phytolith extraction and description

Five grams from each soil sample were analyzed. Carbonates (with HCl 10%), organic matter (with heat and H_2O_2 30%), and clays (with Calgon 0.5% and centrifugation at 1000 rpm for 3 min) were eliminated (Álvarez et al., 2008). After cleaning the sample (total sample), about 0.001 g were mounted in immersion oil and at least 400 particles (including phytoliths) were counted under optic microscope (Zeiss Axiostar Plus) at ×400 magnification. Phytolith morphotypes were classified following Table 2. The content of phytoliths and the percentages of the morphotypes in relation to total mineral content was calculated (Álvarez et al., 2008). Also, the number of silicophytoliths per gram of soil was estimated according to Albert and Weiner (2001).

3.5. Data analyses

Differences in silicophytolith content between plant species and between soil samples were analyzed through non parametric tests (Kruskal-Wallis) (Zar, 1984). To establish the phytolith morphotype relevance in the segregation of plant species, principal component analysis (PCA) was performed, on the basis of a variance–covariance matrix. Finally, cluster analysis was carried out with the purpose of analyzing the relationship between the plant communities and soil phytolith assemblages.

4. Results

4.1. Silicophytolith analyses in plants

Mean silica content ranged between 0.07% (*Colletia paradoxa*) and 5.03% (*Celtis occidentalis*) (Fig. 2). No statistically differences were detected between silica content values of the species (KW-H: 31.9837, p = 0.0221, p > 0.01).

Only two out of 19 species did not produce silicophytoliths (*Dichondra mycrocalix* and *Solanum chenopodioides*). Among the 17

producer species, 6 were classified as trace producers and 11 as abundant producers, according to Wallis (2003) classification (Table 3). Phytoliths were observed in all the leaves of the 17 species considered as producers, in all the flowers (4) and fruits (2) analyzed, but in only two stems out of eight.

In general, the silicophytoliths described in all the organs are derived from the silicification of different cell types of epidermis and xylem (Table 3). Phytoliths derived from the silicification of xylem (cylindrical sulcate xylem) were observed in almost all the species analyzed, with abundances between 0.63 and 90% (Plate I. 11 and Table 3). Polyhedrical phytoliths, derived from epidermis tissue, were observed in leaves of Araliaceae, Asteraceae, Oleaceae and Solanaceae species, and also in other organs of some Asteraceae and Solanaeae plants (Plate I. 13 and Table 3). Elongate phytoliths, probably derived from epidermal cells, were described in leaves of Araliaceae and leaves, flowers and stems of Asteraceae (Plate I. 10 and Table 3). Tabular epidermal phytoliths were observed in leaves of Asteraceae, Cannabaceae, Cervantesiaceae, Oleaceae, Rhamnaceae, Rosaceae and Solanaceae species, stems of Cannabaceae and in fruits/flowers of Cannabaceae and Oleaceae species. Point shaped phytoliths (uni and multicellular hairs) were observed in different organs of Araliaceae, Asteraceae, Cannabaceae, Rosaceae, Solanaceae, Oleaceae, Rhamnaceae and Blechnaceae (Plate I. 1, 5, 9 and Table 3). Cystoliths are dominant in leaf and flower phytolith assemblages of Cannabaceae species (Table 3). These morphologies are characterized by a polyhedral base (in some cases, joined by trichomes), a small foot and a globular/spheroid, granular to smooth body. The cystoliths described in this study have a mean length of 20 μm and a width up to 16 μm (Plate I. 4, 6 and 8). Tabular echinate phytoliths, commonly produced by *Celtis* spp., were the dominant morphotypes found in the fruits of *Celtis occidentalis* (Plate I. 7, Table 3). Fibers were found in flowers of *Cestrum parquii*, leaves, flowers and stems of *Carduus acanthoides*, flowers of *Celtis ehrenbergiana* and leaves of *Scutia buxifolia*. Sclereids were the dominant morphotype in leaves of *Scutia buxifolia* (Plate I. 18 and 19 and Table 3). Finally, leaves of *Blechnum auriculatum* were characterized by fragments composed by internal and lobate silicified walls (Plate I. 14, 15 and Table 3).

The three first axes of principal component analyses (PCA) accounted for 65% of total variance (29% axis 1, 21.57% axis 2 and
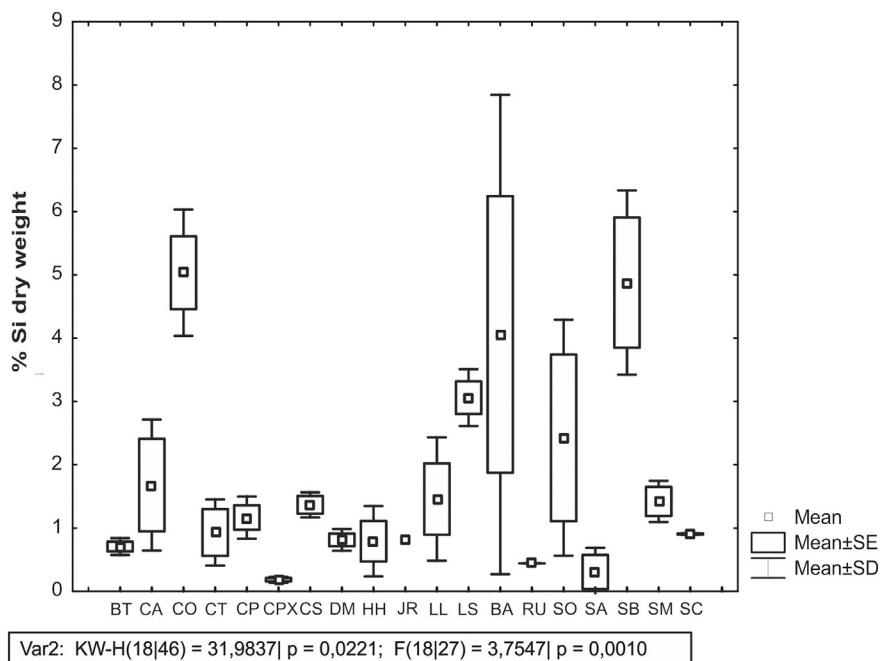
Fig. 2. Box-plot of silica content of plant species. BT: *Baccharis tandiliensis*. BA: *Blechnum auriculatum*. CA: *Carduus acanthoides*. CO: *Celtis occidentalis*. CT: *Celtis ehrenbergiana*.CP: *Cestrum parqui*. CPX: *Colletia paradoxa*. CS: *Conyza* sp. DM: *Dichondra microcalyx*. HH: *Hedera helix*. JR: *Jodina rhombifolia*. LL: *Ligustrum lucidum*. LS: *Ligustrum sinense*. RU: *Rubus ulmifolium*. SO: *Salpichroa origanifolia*. SA: *Sambucus australis*. SB: *Scutia buxifolia*. SM: *Senecio madagascariensis*. SC: *Solanum chenopodioides*.

Table 3
Description of the plant phytolith assemblages and type of producer.

| Species	Organ (L: leaf; R: root; FL: flower; FR: fruit; S: stem)	Cylindrical sulcate xylem	Fragments of silicified cell walls	Elongate	Polyhedrical	Cystoliths	Point shaped (uni-cellular hairs)	Pointed shaped (multi-cellular hairs)	Fragments composed by internal and lobate silicified walls	Tabular epidermal	Tabular echinate/Echinate platelets	Fibers	Sclereids	Stomatal complex	Type of producer
Sambucus australis	L	7.69	92.31	–	–	–	–	–	–	–	–	–	–	–	Trace
Hedera helix	L	19.61	–	30.39	17.65	–	29.41	–	–	–	–	–	–	2.94	Trace
Baccharis tandiliensis	L	40.29	–	–	51.37	–	–	0.13	–	–	–	–	–	8.21	Abundant
	S	–	–	–	–	–	–	–	–	–	–	–	–	–	Non producer
Carduus acanthoides	L	31.74	–	31.99	23.19	–	12.18	–	–	–	–	0.39	–	0.51	Abundant
	S	23.39	–	–	42.26	–	18.71	–	–	–	–	15.64	–	–	Abundant
	Fl	18.84	–	68.15	2.74	–	2.39	–	–	–	–	7.88	–	–	Trace
Conyza sp.	L	3.67	–	–	25.95	–	–	70.38	–	–	–	–	–	–	Abundant
	S	–	–	–	–	–	–	–	–	–	–	–	–	–	Non producer
	R	43.10	–	51.72	–	–	–	–	–	–	–	–	–	5.18	Trace
Senecio madagascariensis	L	34.91	–	–	–	–	4.14	–	–	36.09	–	–	–	24.85	Trace
Blechnum auriculatum	L	2.89	–	–	–	–	0.89	–	91.13	1.12	–	–	–	3.98	Abundant
Celtis ehrenbergiana	L	0.89	–	–	–	85.08	13.14	–	–	0.89	–	–	–	–	Abundant
	Fl	1.79	–	–	–	79.02	2.23	–	–	15.63	–	1.33	–	–	Abundant
Celtis occidentalis	L	–	–	–	–	42.95	38.93	–	–	18.12	–	–	–	–	Abundant
	S	25.30	–	–	–	–	–	–	–	74.70	–	–	–	–	Abundant
	Fr	0.63	–	–	–	–	–	–	–	18.72	80.53	–	–	0.12	Abundant
Jodina rhombifolia	L	39.64	–	–	–	–	1.63	–	–	54.44	–	–	–	4.29	Abundant
Dichondra microcalyx	L	–	–	–	–	–	–	–	–	–	–	–	–	–	Non producer
Ligustrum lucidum	L	52.16	–	–	29.25	–	4.03	–	–	9.08	–	–	–	5.48	Abundant
	S	–	–	–	–	–	–	–	–	–	–	–	–	–	Non producer
Ligustrum sinense	L	53.65	–	–	20.22	–	2.33	–	–	17.88	–	–	–	5.92	Abundant
	S	–	–	–	–	–	–	–	–	–	–	–	–	–	Non producer
	Fl	74.47	–	–	–	–	–	–	–	23.56	–	–	–	1.97	Common
	Fr	75.98	–	–	–	–	–	–	–	24.02	–	–	–	–	Common
Colletia paradoxa	L	90.20	–	–	–	–	9.80	–	–	–	–	–	–	–	Trace
	S	–	–	–	–	–	–	–	–	–	–	–	–	–	Non producer
Scutia buxifolia	L	8.87	–	–	–	–	–	–	–	3.99	–	12.98	73.83	0.33	Abundant
Rubus ulmifolius	L	80.30	–	–	–	–	9.09	–	–	10.61	–	–	–	–	Trace
Salpichroa origanifolia	L	50.00	–	–	–	–	13.64	–	–	36.36	–	–	–	–	Trace
Solanum chenopodioides	L	–	–	–	–	–	–	–	–	–	–	–	–	–	Non producer
Cestrum parqui	L	45.90	–	–	46.20	–	–	–	–	–	–	–	–	7.90	Abundant
	Fl	31.42	–	–	49.08	–	–	–	–	–	–	17.86	–	1.64	Common
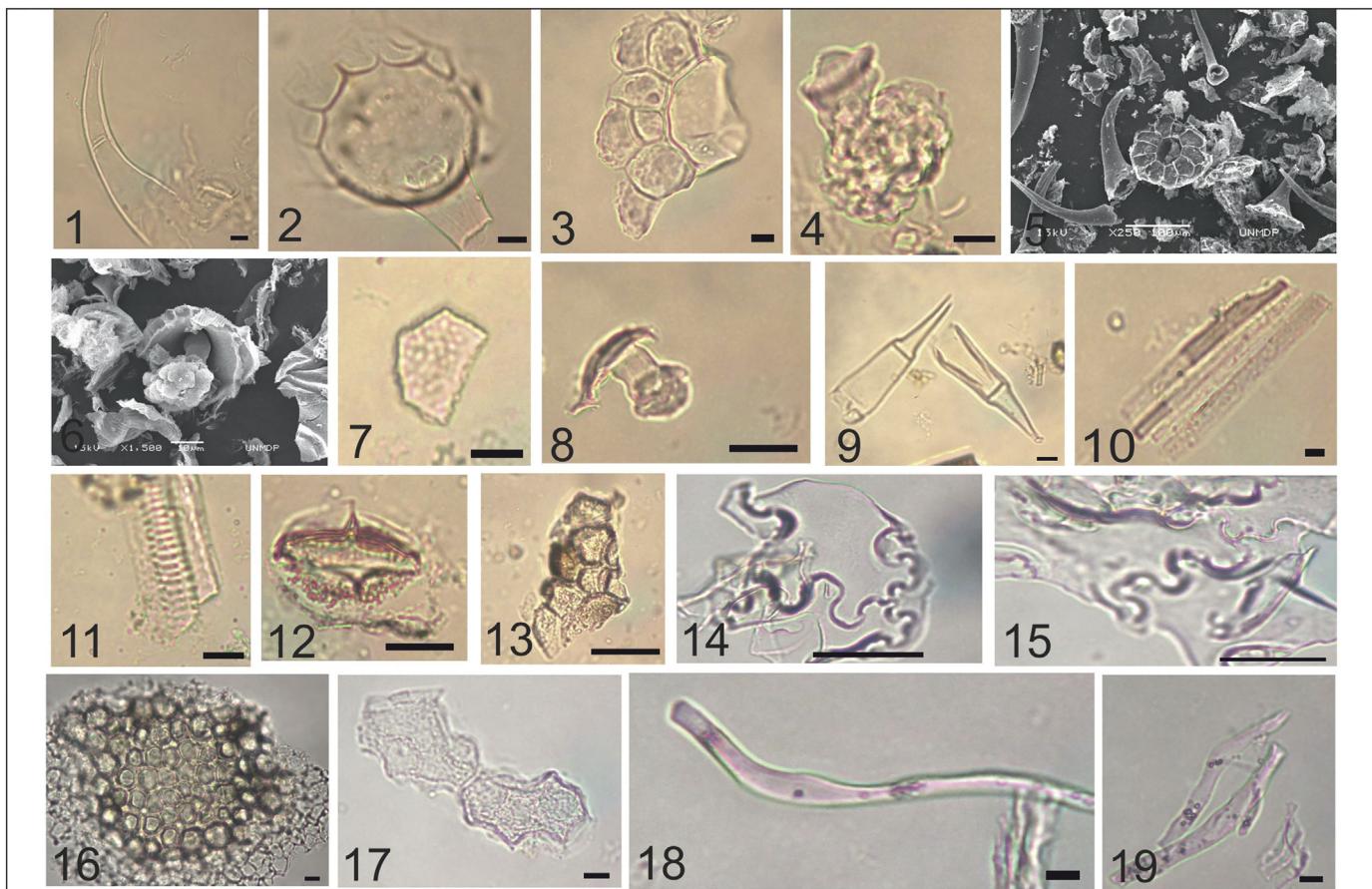
Plate I. Photographs taken under SEM (5, 6) and light microscope of the silicophytoliths of the species studied (1–4, 7–19). 1–2) *Celtis occidentalis,* silicified hair base (leaf), 3) *Celtis occidentalis,* epidermal phytoliths (leaf), 4) *Celtis occidentalis,* cystolith (leaf), 5) *Celtis occidentalis,* silicified hair (leaf), 6) *Celtis occidentalis,* cystolith (leaf), 7) *Celtis occidentalis,* tabular echinate phytolith (fruit), 8) Cystolith of *Celtis ehrenbergiana* (leaf), 9) *Conyza* sp., Silicified hair (leaf), 10) *Carduus acanthoides,* elongate and articulated phytoliths (leaf), 11) *Colletia paradoxa,* xylem (leaf), 12) *Baccharis tandiliensis,* stomatal complexes (leaf), 13) *Baccharis tandiliensis,* polyhedral cells (leaf), 14–15) *Blechnum auriculatum,* fragments composed by internal and lobate silicified walls (frond), 16) *Ligustrum sinense,* epidermal tissue associated with mesophyll cells (leaf), 17) *Ligustrum lucidum,* polyhedral phytoliths (leaf), 18–19) *Scutia buxifolia,* Sclereid (leaf), Scale bar = 10 μm.

13.64% axis 3) (Fig. 3). Cystoliths and cylindrical sulcate xylem mainly contributed to axis 1, and allowed the separation of *Celtis* spp. (CO and CT in the figure) from *Ligustrum* spp., *Colletia paradoxa* (CPX) and *Rubus ulmifolius*. Tabular epidermal, polyhedrical phytoliths, pointed shaped and stomatal complexes contributed to axis 2, and allowed the separation of Asteraceae species and *Hedera helix* from, for example, *Sambucus australis* (SA). However, as a consequence of redundancy and multiplicity in the phytolith morphotypes found in species assemblages, it was not possible to differentiate clear groups of taxa in concordance to systematic affinity.

4.2. Morphological and phytolith analyses of soils

All soils corresponded to typical Argiudolls (Soil Survey Staff, 1996). For Nahuel Rucá site, the upper sector of the mollic epipedons was described as black (10 YR2/1, in wet condition) and dark gray (10 YR3/1, in dry condition), while in Laguna de Los Padres sites the color ranged between dark brown/black (10 YR3/2-2/1, in wet condition) and very dark brown/gray (10 YR3/2, in dry condition). In general, they have a slightly plastic and slightly adhesive consistence and the predominant textural fraction were silts, and within them, coarse silts (phi = 4.5). The soils in Nahuel Rucá site have a medium to coarse granular structure, while in Laguna de Los Padres site they have a medium to coarse/very coarse granular structure.

The percentage of silicophytoliths in relation to total mineral composition in all soil samples ranged between 37 and 64% (Table 4). No statistically differences were detected between forests (F = 1.63; p =

0.44); however, Kruskal-Wallis and non-parametric multiple comparison tests showed that 5–10 cm level had the lowest percentage, between 37 and 52% (F = 15.506173; p < 0.01) (Table 5). In concordance with these results, the number of silicophytoliths per gram of soil decreased with depth (from 29 to 13 million per gram of soil). Also, the number of silicophytoliths per gram of soil was statistically lower in forest 1 from Laguna de Los Padres (F = 17.37; p < 0.01) (Table 5).

Phytolith analyses of soil assemblages showed that rondels (8–22%) (Plate II. 4, Fig. 4, Table 4), commonly assigned to Poaceae (Pooideae and Stipoideae subfamilies) and elongate phytoliths (6–20%) (Plate II. 1 and 2, Fig. 4, Table 4), produced either by monocotyledons or dicotyledons, were the most abundant morphologies. Nahuel Rucá profile presented phytoliths produced by grasses (such as bilobates and saddles), but in low percentages (<5%) (Plate II. 8 and Fig. 4). Instead, in Laguna de Los Padres site, the grass silicophytoliths were more abundant, especially trapeziform crenates (4–7%) (Plate II. 7 and Fig. 4), typical of Pooideae subfamily, and crescent moon phytoliths (<3%). It is worth mentioning the almost null presence of silicophytolith characteristic of *Celtis* spp. (cystoliths or tabular echinate) in all the soil samples (Fig. 4). They were found in only three samples (NR 0–1 cm and two LDP 0–5 cm), with percentages lower than 1% (only one *Celtis* phytolith within 350 total particles).

Cluster analysis based on phytolith assemblages of plant species and soil samples showed two different groups (Fig. 5). The first group is composed by all the soil samples from both sites (Nahuel Rucá and Laguna de Los Padres), while the second group is composed by plant
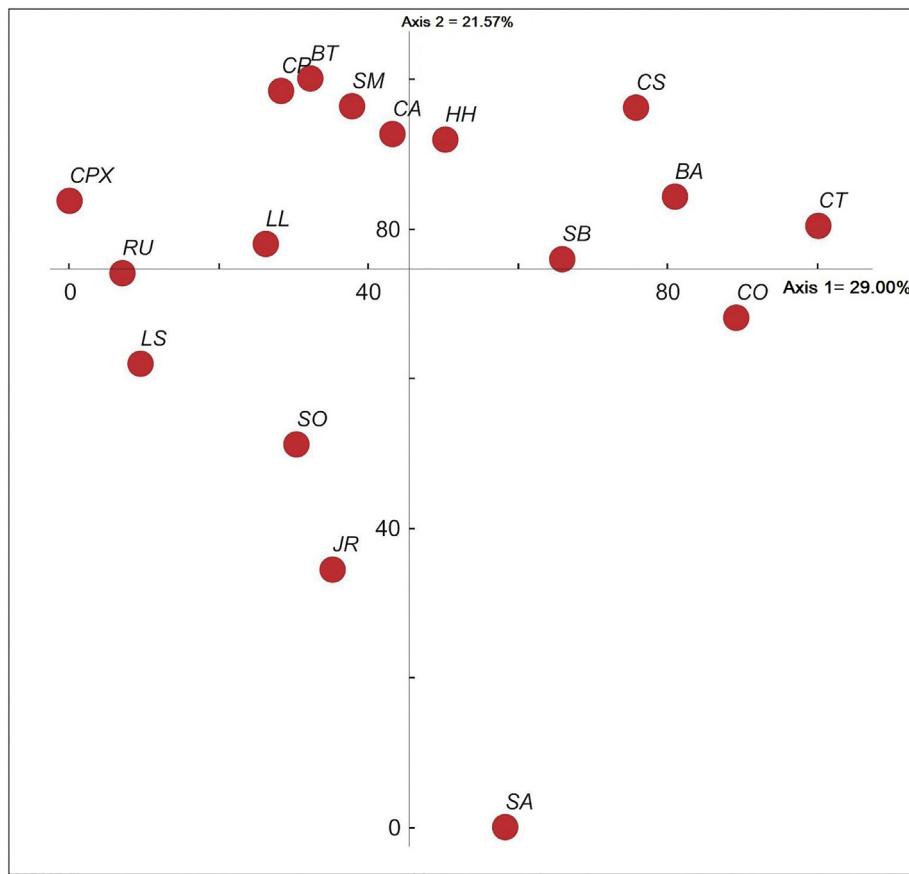
Fig. 3. Principal component analysis of plant species based on phytolith assemblages. Only axes 1 and 2 are shown. The abbreviations are the same as those used in Fig. 2.

species. The species more closely associated with soil samples were *Colletia paradoxa*, *Jodina rhombifolia*, *Ligustrum lucidum*, *Rubus ulmifolius* and *Salpichroa origanifolia*. These species share some phytolith morphotypes with soil samples; in this specific case the trichomes.

5. Discussion

5.1. Plant silicophytolith analysis

The values of silica content presented in this study constitute the first data for some genera of the Adoxaceae, the Araliaceae, the Blechnaceae, the Convolvulaceae, the Oleaceae and the Rhamnaceae families. There are scarce studies that quantify the silicophytolith content in plants and/or which use the same methodology. However, the data obtained in this study mainly coincides with previous research. Within the Asteraceae, the values are similar to those reported by Borrelli et al. (2011) (between 0.67 and 2.27%), but they are lower than those reported by Piperno (2006) (3.4%). Rosaceae species have also been studied by Benvenuto (2011) and Thorn (2004), and the values are similar to those described in the present study. *Celtis occidentalis* has shown higher values than the ones obtained by Fernández Honaine et al. (2005) for *Celtis ehrenbergiana* (2.93 + 1.13%). Finally, the values of silica content in Solanaceae species were similar to those obtained by Borrelli et al. (2011) (0.13–4.7%). Differences between species or between individuals of the same species may be attributed to other factors which also affect silicification, such as environmental conditions (Si availability, soil type, climate, etc.) and/or internal factors (such as phenology, age of plants and organs, etc.) (Jones and Handreck, 1967; Hodson et al., 2005). Silicophytolith content may be variable during the life cycle of an individual plant, and/or between plants which belong to the same taxa but have grown in different environments. As a result, the silica content in plants is

not considered to have a taxonomic value. However, the knowledge of the content of amorphous silica in plants is relevant for the comprehension of silicon dynamics (Si cycle) in different environments and the role of plants in that cycle (Borrelli et al., 2010; Schoelynck et al., 2014).

Phytolith assemblages of some species/genera of the Adoxaceae, the Araliaceae, the Blechnaceae, the Convolvulaceae and the Rhamnaceae families have been described for the first time in the present study. According to Piperno (2006), the Araliaceae family is included within families with null or scarce phytolith production, in coincidence with the results obtained in this study. Ge et al. (2011) found elongate psilate and polyhedrical phytolith in *Acanthopanax senticosus* (Araliaceae), as well as it was found in the species here studied (*Hedera helix*). Silicification in Asteraceae is very variable, and it has been studied by diverse authors (Pearsall, 2000; Wallis, 2003; Thorn, 2004; Blinnikov, 2005; Fernández Honaine et al., 2006; Piperno, 2006; Iriarte and Paz, 2009; Morris et al., 2009; Borrelli et al., 2011). Typical morphotypes of this group are derived from epidermal tissue, such as tabular epidermal, tabular lobate phytoliths/puzzle and point shaped (hairs). *Celtis* spp. (Cannabaceae) have also been studied by diverse authors and typical cystoliths have been described by all of them in leaf assemblages (Kealhofer and Piperno, 1998; Wallis, 2003; Fernández Honaine et al., 2005; Piperno, 2006; Tsartsidou et al., 2007; Iriarte and Paz, 2009). The fruit of *Celtis* spp. has been described by Fernández Honaine et al. (2005) and Iriarte and Paz (2009), and platelets echinate phytoliths, here described as tabular echinate phytoliths, were dominant in the phytolith assemblages. *Dichondra microcalyx* (Convolvulaceae), as well as other species of the same family described by Wallis (2003) and Piperno (2006), did not produce phytoliths. The Oleaceae family, represented by *Ligustrum lucidum* and *Ligustrum sinense*, produced abundant phytoliths, contrary to descriptions made by Piperno (2006) who included this family within the non-producers group. However, Kealhofer and Piperno (1998) found in *Ligustrum* spp. an unusual

Table 4

Percentage of silicophytoliths and morphotypes in soils. See Table 2 for abbreviations of morphotypes. FB: fragments of bilobates, O: others phytoliths; U: unidentified phytoliths; % Si: % of silicophytoliths. A) Nahuel Ruca samples, B) Laguna de Los Padres Forest 1 samples, C) Laguna de los Padres forest 2 samples.

A

	NR1 0–1 cm	NR2 0–5 cm	NR3 5–10 cm	NR4 0–1 cm	NR5 0–5 cm	NR6 5–10 cm	NR7 0–1 cm	NR8 0–5 cm	NR9 5–10 cm
SL	1,4522821	2,0325203	3,2258064	2,4038461	1,4861995	3,0042918	2,0833333	2,2167487	3,6876355
FB	1,037344	1,4227642	1,9354838	2,8846153	2,3354564	1,2875536	1,6203703	2,4630541	1,5184381
R	17,634854	17,073170	17,204301	14,423076	18,046709	11,158798	15,972222	15,024630	9,9783080
RE	1,2448132	1,8292682	1,5053763	1,2019230	0,2123142	0,858369	1,3888888	2,2167487	1,084598
S	1,2448132	0,8130081	1,7204301	0,7211538	1,2738853	1,0729613	1,1574074	0,7389162	0,6507592
TC	0,8298755	2,2357723	0,4301075	5,2884615	7,4309798	0,6437768	5,5555555	1,2315270	0,2169197
EP	20,331950	14,227642	12,043010	9,1346153	7,2186836	17,381974	11,574074	15,763546	17,787418
EE	0,2074688	0,4065040	1,2903225	2,8846153	1,9108280	1,5021459	2,7777777	0,4926108	0,4338394
T	1,037344	2,0325203	1,7204301	2,1634615	1,4861995	0,4291845	3,9351851	3,6945812	3,0368763
C	0	0	0	0	0,2123142	0	0	0	0
TE	0	0	0	0,2403846	0	0	0	0	0
O	1,4522821	2,8455284	2,365591	4,0865384	6,3694267	1,9313304	2,7777777	0,9852216	1,5184381
U	4,3568464	5,4878048	4,0860215	6,7307692	9,341825	5,1502145	5,5555555	6,4039408	4,1214750
% SI	50,829875	50,406504	47,526881	51,923076	57,112526	44,420600	54,398148	51,231527	44,034707

B

	LDP1 0–1 cm	LDP2 0–5 cm	LDP3 5–10 cm	LDP4 0–1 cm	LDP5 0–5 cm	LDP6 5–10 cm	LDP7 0–1 cm	LDP8 0–5 cm	LDP9 5–10 cm
SL	2,2573363	3,5714285	2,6960784	1,5981735	3,016241	1,1904761	3,4403669	1,8306636	0,7092198
PB	0,45146727	0,89285714	0	1,36986301	0,69605568	1,19047619	0	1,37299771	0,70921986
FB	2,7088036	1,3392857	2,6960784	0,9132420	1,6241299	1,4285714	0,6880733	2,0594965	0,9456264
R	17,832957	17,633928	8,5784313	20,776255	16,009280	13,809523	16,513761	18,764302	15,839243
RE	1,3544018	1,5625000	0,7352941	1,1415525	1,3921113	1,4285714	3,2110091	0,9153318	2,1276595
S	1,58013544	1,5625	0,98039216	0,68493151	2,32018561	1,66666667	2,06422018	2,05949657	0
TC	2,25733634	2,00892857	0	7,76255708	4,87238979	4,52380952	0,91743119	2,05949657	4,01891253
EP	10,158013	7,5892857	12,25490	9,1324200	10,672853	6,904761	13,073394	8,9244851	8,510638
EE	3,1602708	0,669642	0,2450980	2,9680365	1,6241299	1,4285714	0,229357	1,3729977	0,9456264
CM	0,677200	1,7857142	0	1,5981735	1,1600928	0,7142857	0,6880733	1,3729977	1,8912529
T	1,3544018	1,7857142	1,47058824	1,82648402	2,08816705	0,71428571	2,06422018	1,83066362	1,6548463
C	0	0	0	0	0	0	0	0	0,2364066
TE	0	0,2232142	0	0	0,2320185	0,2380952	0	0	0
O	1,80586907	0,44642857	1,96078431	4,10958904	1,39211137	0,95238095	2,29357798	3,43249428	4,0189125
U	9,70654628	8,25892857	6,61764706	10,2739726	7,42459397	9,0476190	5,9633027	10,297482	8,510638
% SI	55,304740	50,669642	38,235294	64,155251	54,292343	45	51,14678	56,292906	49,881796

C

	LDP10 0–1 cm	LDP11 0–5 cm	LDP12 5–10 cm	LDP13 0–1 cm	LDP14 0–5 cm	LDP15 5–10 cm	LDP16 0–1 cm	LDP17 0–5 cm	LDP18 5–10 cm
SL	1,89125296	1,2195122	0,67873303	1,39211137	1,21654501	1,18764846	1,13636364	1,21654501	0,46948357
PB	0,70921986	0,97560976	0,67873303	0,92807425	1,21654501	2,13776722	0,68181818	1,45985401	1,17370892
FB	2,60047281	0,48780488	1,35746606	2,08816705	0,243309	1,42517815	0,45454545	0,243309	2,11267606
R	22,4586288	16,3414634	16,0633484	20,1856148	21,8978102	14,9643705	20,9090909	15,8150852	13,8497653
RE	0,70921986	1,95121951	1,58371041	1,16009281	0,72992701	1,42517815	0,68181818	0,486618	0
S	1,1820331	0,73170732	0,67873303	0,46403712	0,243309	0,71258907	0,90909091	1,21654501	0
TC	3,78250591	5,12195122	4,52488688	5,56844548	5,10948905	0	6,13633664	3,89294404	5,16431925
EP	12,2931442	9,26829268	6,56108597	12,9930394	8,51581509	10,9263658	8,86363636	8,75912409	6,33802817
EE	0,94562648	0,73170732	0,22624434	1,16009281	1,21654501	2,6128266	1,13636364	1,45985401	1,17370892
CM	2,12765957	0,97560976	2,0361991	2,08816705	0	2,6128266	1,81818182	0,72992701	0
X	1,89125296	2,19512195	0,90497738	0,69605568	0,97323601	0,47505938	1,13636364	0,72992701	0
T	2,36406619	0,97560976	1,13122172	1,62412993	0,72992701	2,13776722	1,36363636	0,97323601	0
C	0,2364066	0	0	0	0	0	0	0	0
TE	0	0	0	0	0	0,9501187	0	0	0
O	0,23640662	0,73170732	0	0	1,70316302	1,18764846	0,68181818	1,21654501	1,17370892
U	6,85579196	10,2439024	9,04977376	8,81670534	10,9489051	6,65083135	16,5909091	12,1654501	5,8685446
% Si	61,465721	52,9268293	46,8325792	60,324826	55,7177616	52,0190024	64,0909091	50,8515815	37,7934272

hemispherical clump of subepidermal cells which, according to them, could be diagnostic. In the present study, the dominant morphotypes were derived from xylem and epidermis, but they were not considered as diagnostic. Piperno (2006) and Parr and Sullivan (2005) considered the Rhamnaceae family as non-producer, however, in the present study the species analyzed (*Colletia paradoxa* and *Scutia buxifolia*) showed a production between trace and abundant. Particularly, *Scutia buxifolia* produced a high amount of phytoliths probably derived from sclereids, which could be considered as diagnostic. However, those species of the area which were not included should be studied, in order to support this last idea. *Rubus ulmifolius* (Rosaceae) was characterized as a trace producer, in coincidence with Piperno's (2006) findings, and most of the phytoliths produced derived from xylem silicification.

However, Thorn (2004) and Benvenuto et al. (2013) found abundant silicified hairs and epidermal cells in different species of the same family, indicating, as well as in the Asteraceae, differences in phytolith production within the family. The Solanaceae family has been studied by diverse authors and has been described as non-producer but also as abundant producer (Wallis, 2003; Piperno, 2006; Mercader et al., 2009; Borrelli et al., 2011). The present study coincides with these previous findings, since the three species analyzed showed very different behavior: *Cestrum parqui* is an abundant producer, whereas *Salpichroa origanifolia* is a trace producer and *Solanum chenopodioides* does not produce phytoliths. It is also interesting that within the same genera (*Solanum*) different silica accumulation behavior has been observed. For example, Borrelli et al. (2011) found that *Solanum glaucophyllum*

Table 5

Kruskal Wallis and non-parametric multiple comparisons tests. A) Test of differences of Si content between plant species. B) Test of differences in the percentage of phytoliths in soil samples taken in different forests (NR: Nahuel Ruca, LDP: Laguna de Los Padres 1, LP: Laguna de Los Padres 2). C) Test of differences in the percentage of phytoliths in soil samples taken at different depths (0–1, 0–5 and 5–10 cm). D) Non parametric multiple comparisons of C. E) Test of differences in the number of phytoliths/gr soil, in soil samples taken in different forests (NR: Nahuel Ruca, LDP: Laguna de Los Padres 1, LP: Laguna de Los Padres 2). F) Non-parametric multiple comparisons of E.

A. Kruskal-Wallis ANOVA by Ranks; Var2 (Spreadsheet1) Independent (grouping) variable: Var1 Kruskal-Wallis Test: H (18, N = 46) = 31,98372 p = ,0221

	Code	Valid	Sum of ranks
BT	101	3	41
CA	102	2	57
CO	103	3	128
CT	104	2	39
CP	105	3	73,5
CPX	106	3	10
CS	107	2	58
DM	108	3	50
HH	109	3	51,5
JR	110	1	17
LL	111	3	73
LS	112	3	111
BA	113	3	94
RU	114	2	17
SO	115	2	63
SA	116	2	13
SB	117	2	85
SM	118	2	59
SC	119	2	41

B. Kruskal-Wallis Test

X1:NR (sorted)	Rank(X1)	X2:LPD (sorted)	Rank(X2)	X3:LP (sorted)	Rank(X3)
44,0347072	3	38,2352941	2	37,7934272	1
44,4206009	4	45	5	46,8325792	6
47,5268817	7	49,8817967	8	50,8515815	12
50,4065041	9	50,6696429	10	52,0190024	16
50,8298755	11	51,146789	13	52,9268293	17
51,2315271	14	54,2923434	18	55,7177616	21
51,9230769	15	55,3047404	20	60,324826	24
54,3981482	19	56,2929062	22	61,465721	25
57,1125265	23	64,1552511	27	64,0909091	26
	X1:NR	X2:LPD	X3:LP	Total	
N	9	9	9	27	
Mean	50,2093165	51,6643071	53,5580708	51,8105648	
Var	18,5546214	53,3491057	65,9716701	44,3752177	
Median	50,8298755	51,146789	52,9268293	51,2315271	
Rank sum	105	125	148	378	
Rank mean	11,6666667	13,8888889	16,4444444	14	

Kruskal-Wallis Statistic

Chi^2	1,63315697	N.S. (p > 0.05)
Df	2	
Probability	0,44194118	

C. Kruskal-Wallis Test

X1:0–1 cm (sorted)	Rank(X1)	X2:0–5 cm (sorted)	Rank(X2)	X3:5–10 cm (sorted)	Rank(X3)
50,8298755	11	50,4065041	9	37,7934272	1
51,146789	13	50,6696429	10	38,2352941	2
51,9230769	15	50,8515815	12	44,0347072	3
54,3981482	19	51,2315271	14	44,4206009	4
55,3047404	20	52,9268293	17	45	5
60,324826	24	54,2923434	18	46,8325792	6
61,465721	25	55,7177616	21	47,5268817	7
64,0909091	26	56,2929062	22	49,8817967	8
64,1552511	27	57,1125265	23	52,0190024	16
	X1:0–1 cm	X2:0–5 cm	X3:5–10 cm	Total	
N	9	9	9	27	
Mean	57,0710375	53,2779581	45,0826988	51,8105648	
Var	30,0224409	7,0028096	22,7179612	44,3752177	
Median	55,3047404	52,9268293	45	51,2315271	
Rank sum	180	146	52	378	
Rank mean	20	16,2222222	5,77777778	14	

Kruskal-Wallis Statistic

Chi^2	15,5061728	*** (p ≤ 0.001)
Df	2	
Probability	0,00042942	

D. Steel-Dwass Test: pairwise comparisons for one-way layout design

X1:0–1 cm (sorted)	Rank(X1)	X2:0–5 cm (sorted)	Rank(X2)	X3:5–10 cm (sorted)	Rank(X3)
50,8298755	11	50,4065041	9	37,7934272	1
51,146789	13	50,6696429	10	38,2352941	2
51,9230769	15	50,8515815	12	44,0347072	3
54,3981482	19	51,2315271	14	44,4206009	4
55,3047404	20	52,9268293	17	45	5
60,324826	24	54,2923434	18	46,8325792	6
61,465721	25	55,7177616	21	47,5268817	7
64,0909091	26	56,2929062	22	49,8817967	8
64,1552511	27	57,1125265	23	52,0190024	16

	X1:0–1 cm	X2:0–5 cm	X3:5–10 cm	Total
N	9	9	9	27
Mean	57,0710375	53,2779581	45,0826988	51,8105648
Var	30,0224409	7,0028096	22,7179612	44,3752177
Median	55,3047404	52,9268293	45	51,2315271
Rank sum	180	146	52	378
Rank mean	20	16,2222222	5,77777778	14

t-Table   Upper Right: tij; lower left: upper probability (studentized range distribution)

	X1:0–1 cm		X2:0–5 cm		X3:5–10 cm	
X1:0–1 cm			1,45698559	N.S. (p > 0.05)	3,31133089	** (p ≤ 0.01)
X2:0–5 cm	0,3118436				3,22302874	** (p ≤ 0.01)
X3:5–10 cm	0,00267183		0,00363099			

E. Kruskal-Wallis Test

X1:NR (sorted)	Rank(X1)	X2:LDP (sorted)	Rank(X2)	X3:LP (sorted)	Rank(X3)
12189157,9	7	8302902,05	1	15168027,6	14
13609894,4	9	11073976,9	2	17007267,2	17
13659244,6	10	11144281,5	3	17317907,2	18
14064926,1	12	11459910	4	20975073,4	21
15221606,4	15	12020926,5	5	21395704	22
15511923,4	16	12168833,8	6	21437912,2	23
18567014,4	19	12751449,1	8	29705280	25
19388878,7	20	13663868,5	11	29876352	26
22152708,6	24	14605103,3	13	30048358,2	27

	X1:NR	X2:LDP	X3:LP	Total
N	9	9	9	27
Mean	16040595	11910139,1	22547986,9	16832907
Var	1,08E + 13	3,20E + 12	3,48E + 13	3,49E + 13
Median	15221606,4	12020926,5	21395704	15168027,6
Rank sum	132	53	193	378
Rank mean	14,6666667	5,88888889	21,4444444	14

Kruskal-Wallis Statistic

Chi^2	17,3791887	*** (p ≤ 0.001)
Df	2	
Probability	0,00016833	

F. Steel-Dwass Test: pairwise comparisons for one-way layout design

X1:NR (sorted)	Rank(X1)	X2:LDP (sorted)	Rank(X2)	X3:LP (sorted)	Rank(X3)
12189157,9	7	8302902,05	1	15168027,6	14
13609894,4	9	11073976,9	2	17007267,2	17
13659244,6	10	11144281,5	3	17317907,2	18
14064926,1	12	11459910	4	20975073,4	21
15221606,4	15	12020926,5	5	21395704	22
15511923,4	16	12168833,8	6	21437912,2	23
18567014,4	19	12751449,1	8	29705280	25
19388878,7	20	13663868,5	11	29876352	26
22152708,6	24	14605103,3	13	30048358,2	27

	X1:NR	X2:LDP	X3:LP	Total
N	9	9	9	27
Mean	16040595	11910139,1	22547986,9	16832907
Var	1,08E + 13	3,20E + 12	3,48E + 13	3,49E + 13
Median	15221606,4	12020926,5	21395704	15168027,6
Rank sum	132	53	193	378
Rank mean	14,6666667	5,88888889	21,4444444	14

t-Table   Upper right: tij; lower left: upper probability (studentized range distribution)

|	X1:NR		X2:LDP		X3:LP	
X1:NR			2,86982011	* (p ≤ 0.05)	−2,34000716	
X2:LDP	0,01144702				−3,57623736	** (p ≤0.01)
X3:LP	0,05046938		0,00101594			
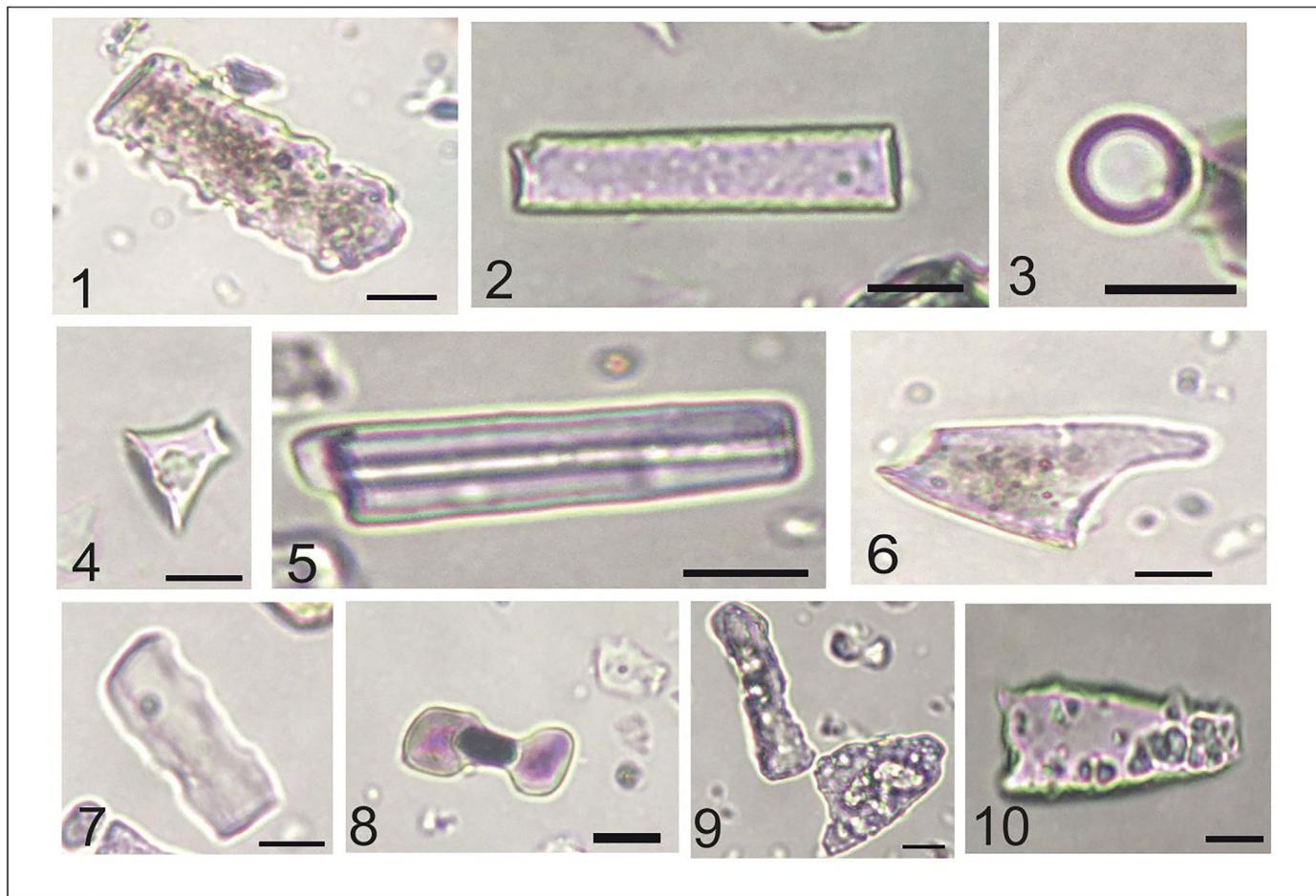
Plate II. Photographs of the silicophytoliths and other amorphous silica components in soil samples. 1) Elongate echinate, 2) Elongate psilate, 3) Cyst of Crysophyceae, 4) Rondel, 5) Sponge spicule, 6) Trichome, 7) Trapeziform crenate, 8) Bilobate, 9–10) Weathered phytoliths. Scale bar = 10 μm.

produces abundant cylindrical sulcate tracheids and tabular epidermal (polyhedrical and lobate) phytoliths, while in the present study *S. chenopodioides* did not produce phytoliths. Pterydophyte phytoliths have been described by Parr and Sullivan (2005), Sundue (2009) and Mazumdar (2011). Mazumdar (2011) has analyzed *Blechnum orientale* and has found that elongated epidermal plates with smooth surface and lobed margins are common and has considered them as a diagnostic feature. Parr and Sullivan (2005) studied a species of *Blechnum*, and the results were coincident with the ones described in the present report.

5.2. Plant phytolith assemblages and systematics

The relation between phytolith morphologies, anatomy and systematics has been highlighted by numerous authors, being the most clear and strongest relation present in the Poaceae family (e.g. Metcalfe, 1960; Twiss, 1992; Gallego and Distel, 2004; Hodson et al., 2005; Fernández Honaine et al., 2006). However, in the present study, where no grass species were included, the multivariate analyses showed a poor discrimination between the families studied due to redundancy and multiplicity (Rovner, 1971). Redundancy means that different taxa can produce the same morphotypes (in the present study elongates, cylindrical sulcate xylem, polyhedrical, etc.), while multiplicity is related to the fact that one taxon can produce different morphotypes in the same organ (Rovner, 1971). The only families which could be differentiated from the rest were Cannabaceae and Asteraceae. *Celtis* spp.

(Cannabaceae) were clearly distinguished from other species by the presence of cystoliths; and Asteraceae species were differentiated by the presence and abundance of phytoliths derived from xylem and epidermal cells.

5.3. Silicophytolith content in soils

The silicophytolith component represents an important fraction of the analyzed soils, reaching values up to more than 50% of the total mineralogy. Depending on the soil type and the methodology applied, different silicophytolith contents have been obtained from the soils of the region (Osterrieth, 2000). The content for typical Argiudolls of the Pampean Region ranged between 15 and 70% (Gonzales and Osterrieth, 1996; Osterrieth, 2000; Osterrieth, 2006; Fernández Honaine, 2007; Borrelli et al., 2010; Osterrieth et al., 2014). Typical Hapludolls of the region have contents ranging between 34 and 68% (Osterrieth, 2000; Álvarez and Osterrieth, 2004; Osterrieth, 2006; Osterrieth et al., 2014). Instead, silicophytolith content in Entisolls, commonly developed in coastal areas, ranged between 10 and 30% (Osterrieth, 2006; Osterrieth et al., 2014). The number of silicophytoliths per gram of soil decreases with depth, and the values coincide with the ones obtained by Borrelli (2008), who found a decrease in silicophytoliths from 6 to 8 million silicophytoliths/g. in the A horizon to 1 million silicophytoliths/g soil in the B horizon, depending on the plant community analyzed. This reduction of the content of silicophytoliths is a consequence of the different taphonomical processes which affect the phytolith pool, such as
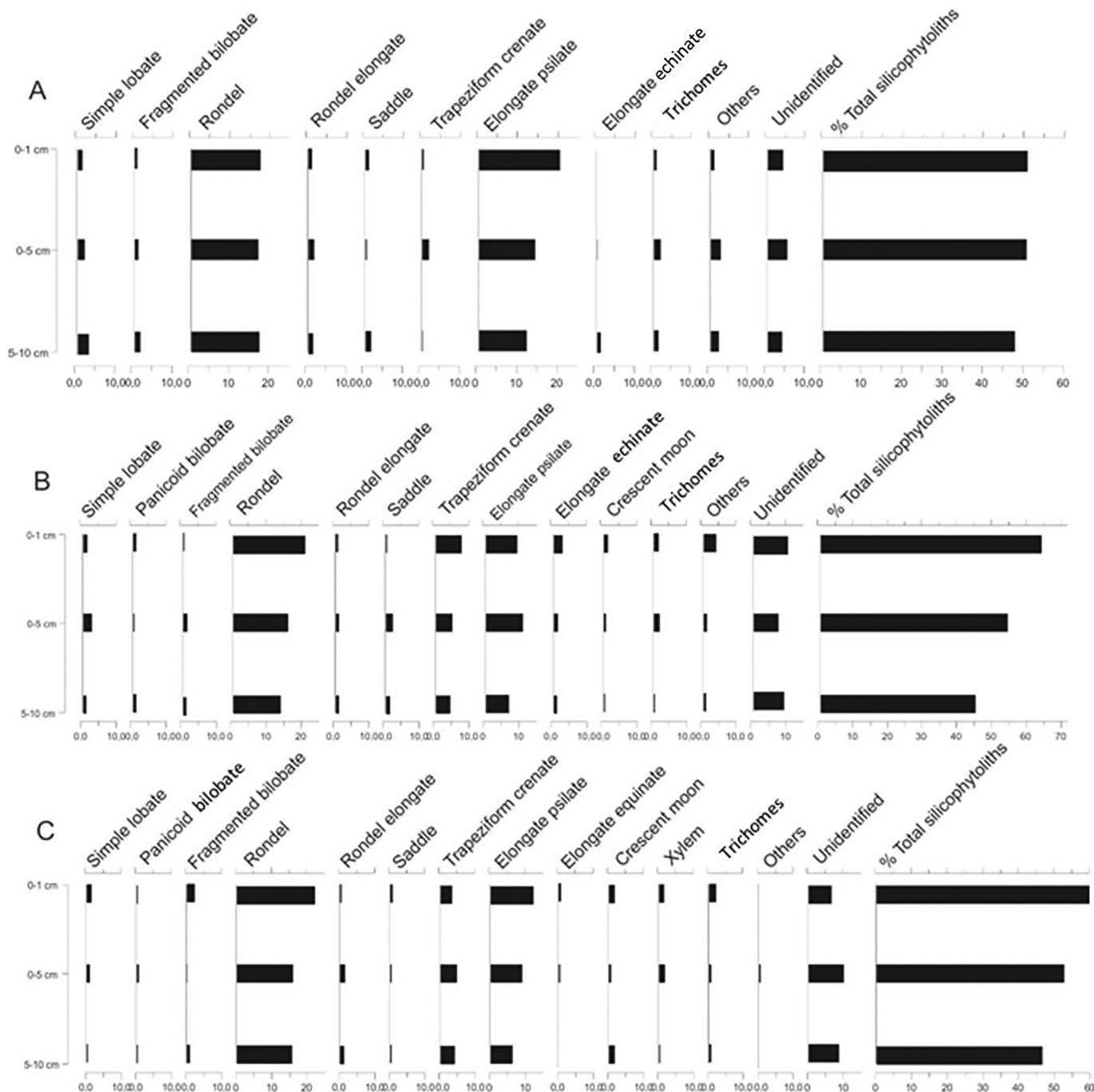
Fig. 4. Percentages of phytolith morphologies and total content of silicophytoliths in the soil samples in (A) Nahuel Rucá site, (B) Laguna de Los Padres site, forest 1, (C) Laguna de Los Padres site, forest 2. Only one profile from each sampling site is shown.

fragmentation and chemical dissolution (Osterrieth et al., 2009; Osterrieth et al., 2014). It is well known that silicophytoliths constitute one of the Si sources in soils, and different dissolution processes affect them (e.g. Sommer et al., 2006; Borrelli et al., 2010; Schoelynck et al., 2014).

The high content of silicophytoliths in Arguidolls and Hapludolls of this region are probably the consequence of the predominance of grass-dominated communities during the Holocene (Soriano et al., 1991). Due to the high phytolith productivity of the Poaceae family, the input of biogenic amorphous silica may have also been high. Finally, the parental material of these soils (loess) has also got a high content of silicophytoliths (Osterrieth et al., 2009).

5.4. Relation between plant phytolith production and soil phytolith assemblages

By analyzing the assemblages found in soils in relation to the assemblages produced by local modern-day plants, differences between these two groups have been detected. Some morphotypes present in soils were not produced by the plants developed on them and some morphotypes produced by these plants were not included in soil assemblages. Except for phytoliths derived from xylem, some trichomes (pointed shaped phytoliths) and elongates, the rest of the phytolith morphotypes produced by the plants (including cystoliths and tabular echinate of *Celtis* spp.) were not incorporated or were degraded. On
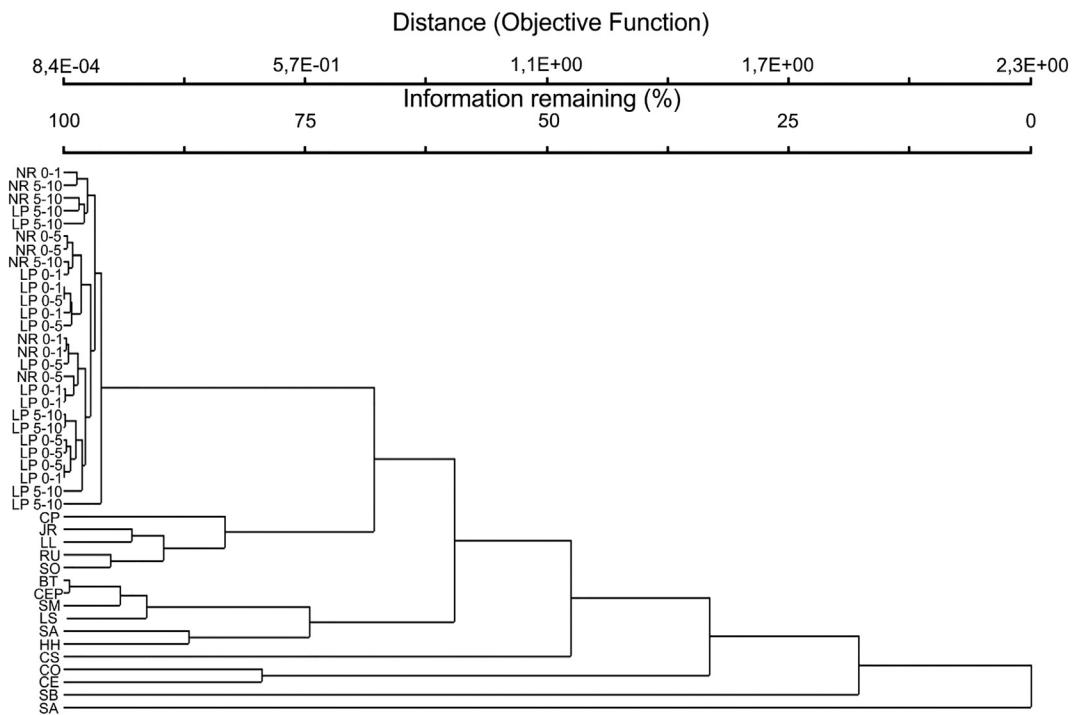
Fig. 5. Dendrogram showing grouping of plant species and soil samples based on their phytolith assemblages. NR: Estancia Nahuel Rucá. LDP: Laguna de Los Padres Integral Reserve. CP: *Colletia paradoxa*, JR: *Jodina rhombifolia*, LL: *Ligustrum lucidum*, RU: *Rubus ulmifolius*, SO: *Salpichroa origanifolia*, BT: *Baccharis tandiliensis*, CEP: *Cestrum parqui*, SM: *Senecio madagascariensis*, LS: *Ligustrum sinense*, CA: *Carduus acanthoides*, HH: *Hedera helix*, CS: *Conyza* sp., CO: *Celtis occidentalis*, CE: *Celtis ehrenbergiana*, SB: *Scutia buxifolia*, SA: *Sambucus australis*.

the contrary, grass phytoliths were abundant in soils, but grasses are hardly found in these forests. In concordance with these observations, cluster analyses showed that there was scarce relation between plant and soil phytolith assemblages. Diverse authors have shown that soil phytolith pool is not an exact replica of local plant production, and multiple factors such as dissolution/fragmentation, eolian, water or animal movement, and specific features of plant production can account for plant and soil differences (e.g. Fredlund and Tieszen, 1994; Wallis, 2003; Fernández Honaine et al., 2009; Iriarte and Paz, 2009; Mercader et al., 2011; Benvenuto et al., 2013).

The low proportions of local plant phytoliths (non-grass and arboreal species) in soils may be related to a higher susceptibility to dissolution of the morphologies in relation to, for example, grass phytoliths (Thorn, 2004; Fernández Honaine et al., 2009). Variable levels of chemical degradation and fragmentation have been observed in diverse phytolith morphologies of the soil assemblages studied. According to Osterrieth et al. (2009), chemical dissolution is in direct relation to soil and environment biogeochemistry. Also, the surface/volume ratio of the morphotypes, the level of impurities in amorphous silica matrix and the level of silicification play an important role (Osterrieth et al., 2009). The amount of phytoliths produced by different taxa can also account for differences in the soil assemblages. For example, phytolith production by grasses is superior to other species, and so the non-grass phytolith incorporation may be masked by the first one (Thorn, 2004; Fernández Honaine et al., 2009). Finally, the presence in the soil assemblage of morphotypes which were not produced by local vegetation may be the consequence of the transport and dispersion processes that affect phytoliths. Wind, water and animals are the main agents responsible for the mobilization and transport of phytoliths from the site where they were produced to different distances (Romero et al., 1999; Fredlund and Tieszen, 1994; Fernández Honaine et al., 2009; Osterrieth et al., 2009; 2014). Some previous works in the region showed the presence of phytoliths within aerial particles, indicating the possible transport of these biomineralizations over long distances (Latorre et al., 2012).

Although, in the present study, the presence of silicophytoliths produced by *Celtis* species were almost null in soil samples, and in relation to the total of mineral particles (including others silicophytoliths), they have been reported in archeological or soil samples by other researchers in the region. Osterrieth et al. (2008) have shown the presence of cystoliths related to *Celtis* spp. at a level of archeological occupation (9400–10,400 A.P.) in the Archaeological Site Paso Otero 5, in the southeastern region of Buenos Aires province, Argentina. Due to the presence of these morphotypes in this archeological level, it was suggested that these autochthonous trees (talas) might have been used as firewood by the inhabitants of the region. Iriarte and Paz (2009) and Dickau et al. (2013) observed echinate irregular platelets produced in the fruit of *Celtis* spp. in soils associated with riparian forest environments in southeastern Uruguay and in areas near the Amazon. However, in all these studies, the abundance of these morphotypes in samples was very low, taking into account that the percentages were referred to the total of phytoliths and not to the total of mineral particles of the soils. These results may explain the fact that *Celtis* phytoliths were absent in the soil samples analyzed here, indicating that their incorporation is scarce or their dissolution is high. The high production of a type of morphotype in some taxa does not always imply a good representation in soils. This also happens with cone sedges, which presence in soils is very low or null (Iriarte and Paz, 2009; Novello et al., 2012).

Besides the poor representation of *Celtis* phytoliths in soil assemblages, they can be diferentiated from soil phytolith records of other plant communities of the Pampean region, such as native grasslands. Previous work in pampean grasslands showed a higher diversity of grass phytolith morphotypes and a higher percentage of total phytoliths in their soils than in *Celtis* soils (Fernández Honaine et al., 2009). Different type of grasslands (*Paspalum quadrifarium* grassland or "flechillar", dominated by *Stipa* and *Piptochaetium* spp.) were characterized by different grass morphologies. Trapeziform crenate and *Stipa* type bilobates were dominant in "flechillar", while crosses, panicoid bilobates and simple lobate were common in *P. quadrifarium* grassland (Fernández Honaine, 2007; Fernández Honaine et al., 2009). These differences in

the abundance and diversity of grass phytoliths may allow the differentiation of plant communities based on soil phytolith assemblages.

6. Conclusions

Seventeen out of nineteen species analyzed produced silicophytoliths and some descriptions represent the first data in some taxa. The highest and more diverse silicophytolith content was found in leaves or culms. Due to redundancy and multiplicity, plant species, commonly developed in tala forests in SE Pampean Plains, were hardly distinguishable. The only exceptions were *Celtis* spp. (due to the presence of cystoliths and echinate platelets) and Asteraceae species. Soil phytolith assemblages were mainly dominated by grass phytoliths (mainly belonging to Stipoideae and Pooideae subfamilies). This plant group was not actually present in the forests, however, it conforms, along with Panicoideae species, the typical elements of native grasslands from Pampean Plains. Almost no cystoliths were observed in superficial soil levels (0–1 cm). These results showed that there was not a direct relation between plant phytolith production and phytolith soil incorporation in these forests. As it occurs in different environments of different regions of the world, the phytolith assemblages incorporated to soils are affected by diverse taphonomical processes (such as fragmentation, dissolution, mobilization, etc.) and they are not always an exact reflection of phytolith production of local plants. Also, these results showed that a high phytolith production in plants is not always reflected on soil assemblages. However, *Celtis* soil phytolith assemblages can be differentiated from other typical pampean plant community, such as grasslands. These aspects should be considered in any study in relation to the interpretation of fossil phytolith records.

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