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REGULAR PAPER

Flowering cycles of woody bamboos native to southern South America

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Abstract Neotropical woody bamboos range from northern Mexico to southern Argentina and Chile. The most interesting aspect of bamboo biology is their flowering habit. The species that are the most intriguing are those that manifest a cyclic pattern of gregarious flowering after long vegetative periods. The flowering cycle has been described in very few species. The goal was to identify mass flowering events of woody bamboo species native to Argentina and neighboring areas, and to estimate the flowering cycle of each species. Sixteen species were surveyed: *Chusquea culeou*, *C. deficiens*, *C. lorentziana*, *C. montana*, *C. quila*, *C. ramosissima*, *C. tenella*, *C. valdiviensis*; *Colanthelia rhizantha*; *Guadua chacoensis*, *G. paraguayana*, *G. trinii*; *Merostachys clausenii*, *M. multiramea*, *Rhipidocladum neumannii* and *R. racemiflorum*. To reconstruct flowering dates, information from literature and herbarium collections was consulted and more than 990 records were gathered. Flowering cycles were estimated by recording the intervals between reported flowering events. Evidence of regular flowering cycles of ca. 30 years was found for most of the species considered. There is a remarkable concentration of flowering cycles about multiples of 15–16 years. Flowering synchrony among different species of woody bamboos was recorded for the first time in South America.

Keywords Bambuseae · Flowering cycles · Flowering synchrony · Herbarium data · Mass flowering events

Introduction

Bamboos have an extremely wide range of global distribution that occurs in the tropical, sub-tropical and temperate regions of all continents except Europe and Antarctica, from lowland to 4,000 m altitude (Alam 2008; Judziewicz et al. 1999). Neotropical woody bamboos (Poaceae, Bambusoideae, Bambuseae) range from northern Mexico to southern Argentina and Chile. In the fast disappearing Andean montane forest, bamboo is usually found along forest edges or in gaps. Also, in cool temperate southern South America, woody bamboos are well known as understory dominants in beech forests (Judziewicz et al. 1999). Wherever bamboos constitute an important component of the forest, they have profound effects on the dynamics and structure of plant communities (Caccia et al. 2009; Campanello et al. 2007; Holz and Veblen 2006), and also on the population dynamics of animal species that rely on bamboos for refuge or feeding (Areta et al. 2009; Gallardo et al. 2008; Piudo et al. 2005).

The most interesting aspect of bamboo biology seems to be the flowering habit. The species that are the most intriguing are those that fall between a state of constant vegetative growth and constant flowering to manifest a cyclic pattern of flowering after long periods of vegetative growth that last even up to 120 years (Janzen 1976). All individuals growing over vast expanses of land flower and die in synchrony along with individuals growing elsewhere even far away. The phenomenon of mass flowering is the synchronized flowering at long intervals by a large population (Ramanayake 2006).

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The period between two mass flowerings is generally regarded as the flowering cycle (Alam 2008). A more or less fixed, species-specific periodicity to the phenomenon has been described over at least two generations in very few species (Carvalho et al. 2013; Isagi et al. 2004; Janzen 1976; Kawamura 1927; Parodi 1955; Seifriz 1950). The most outstanding example of periodicity is the seven documented mass flowering events since 813 AD of a Japanese bamboo which flowers at intervals of 120 years approximately (Kawamura 1927).

Little is known about the intervals between successive mass flowering events of native American bamboos. Seifriz (1920, 1950) reported mass flowering events of *Chusquea abietifolia* Griseb. in Jamaica. The author's records showed that it flowered in 1880–1886, 1918–1919 and 1948–1949, indicating a 32-year flowering period. Parodi (1955) recorded two consecutive mass flowering events of *Guadua trinii* from Argentina, establishing a 30-year flowering cycle. More recent reports are those of Liebsch and Reginato (2009) establishing a 30–34-year cycle for *Merostachys skvortzovii* Sendulsky and Carvalho et al. (2013) of a 27–28-year flowering period for *Guadua weberbaueri* Pilg. and *G. sarcocarpa* Londoño & P. M. Peterson.

It is not possible to observe the cyclic nature of bamboo flowering due to their long life spans, necessitating dependence on past records of flowering. The lack of long-term phenological direct observations can be filled by herbarium specimens (Lavoie and Lachance 2006; Pohl 1991). These could be used to reconstruct flowering dates and then estimate flowering cycles. However, herbarium specimens often lack information about the extent of the flowering event. Thus, it cannot be assumed that every flowering date represents a mass flowering episode. Species are regarded as flowering gregariously only if repeated collections from the same populations were made and definite information on the nature of flowering was available (Clark 1989).

In Argentina and neighboring areas, five native genera occur: *Chusquea* Kunth, *Guadua* Kunth, *Colanthelia* McClure & E. W. Sm., *Merostachys* Spreng. and *Rhipidocladum* McClure, with 16 species approximately (Morrone et al. 2008; Zuloaga et al. 2012). Woody bamboo species native to Argentina occur in three distinct areas. Firstly, Atlantic rain forest of northeastern Argentina (also found in southern Brazil, Paraguay and Uruguay) is a tropical area with the highest bamboo diversity in Argentina. In this area, the following native species occur: *Chusquea ramosissima* Lindm., *C. tenella* Nees; *Colanthelia rhizantha* (Hack.) McClure; *G. chacoensis* (Rojas) Londoño & P. M. Peterson, *G. paraguayana* Döll, *G. trinii* (Nees) Nees ex Rupr.; *M. clausenii* Munro and *M. multiramea* Hack. (Guerreiro and Rúgolo de Agrasar 2012; Lizarazu 2012; Lizarazu and Vega 2012). Secondly, high montane forest of northwestern Argentina (also found in southern Bolivia) is a wet and humid area with altitudes reaching up to 3,000 m. *Chusquea deficiens* Parodi, *C. lorentziana* Griseb. and *R. neumannii* Sulekic, Rúgolo & L. G. Clark are endemic to this area. *R. racemiflorum* (Steud.) McClure is also found here (Guerreiro and Rúgolo de Agrasar 2012; Rúgolo and Vega 2012). Thirdly, Andean–Patagonian beech forest of southern Argentina and Chile is an evergreen temperate rainforest and the only genus present here is *Chusquea* with three species: *C. culeou* E. Desv., *C. montana* Phil. and *C. valdiviensis* Phil. (Guerreiro and Rúgolo de Agrasar 2012).

In this study, I have conducted a comprehensive survey of the mass flowering profiles of Argentina woody bamboos. This survey includes *Chusquea quila* Kunth, although its presence in Argentina is not clear (Clark 2000; Guerreiro and Rúgolo de Agrasar 2012; Morrone et al. 2008; Zuloaga et al. 1994). The goal of this work is to identify mass flowering events of woody bamboo species native to Argentina and neighboring areas and, with this information, estimate the flowering cycle of each species.

Materials and methods

Records of mass flowering events of woody bamboos species in Argentina and neighboring areas were gathered from the following herbarium collections: BA, BAA, BAB, BM, CORD, CTES, JUA, K, LIL, MCNS, MERL, MVM, NY, P, SI, US and W (Thiers 2013). More than 860 flowering records were gathered. These, along with the 129 records found in historical and current literature, made a total of more than 990 records of flowering events of woody bamboo species native to southern South America (Table 1; Text S1).

The flowering cycle of each species was determined following the methodology proposed by Kawamura (1927) which consists of calculating the intervals between the

Table 1 Number of mass flowering records gathered for each bamboo genus

Genus	The number of species studied	The number of records		
		Herbarium	Literature[a]	Total
Chusquea	8	464	67	531
Colanthelia	1	9	1	10
Guadua	3	126	15	141
Merostachys	2	230	38	268
Rhipidocladum	2	35	8	43
Total	16	864	129	993

[a] Text S1

recorded flowering events of a given species in a given geographical location and finding a repeated interval. When working with historical data, lack of complete chronological records is usually found. So, when this is the case and different intervals are found, these are reduced to a repeated multiple by assuming there were other flowering events which were not properly recorded (Guerreiro and Lizarazu 2010; Kawamura 1927; Pohl 1991).

Results

A total of 993 records of woody bamboo flowering events in southern South America were gathered from herbarium collections and literature review. In Fig. 1 (and Fig. S1), flowering records of the species studied here are presented, using the methodology proposed by Kawamura (1927) to estimate the flowering cycle of a given bamboo species in a given geographic location. With the information gathered, the approximate length of the flowering cycle of woody bamboo species native to southern South America was estimated (Table 2). This was not possible when only one mass flowering event was recorded, such as in *Chusquea deficiens*, *C. valdiviensis*, *Colanthelia rhizantha* and *R. racemiflorum.* It is important to note that the information presented on Table 2 is not definitive. The study of bamboo flowering is currently bedeviled by the problem that flowering is so rare that adequate verification is not possible.

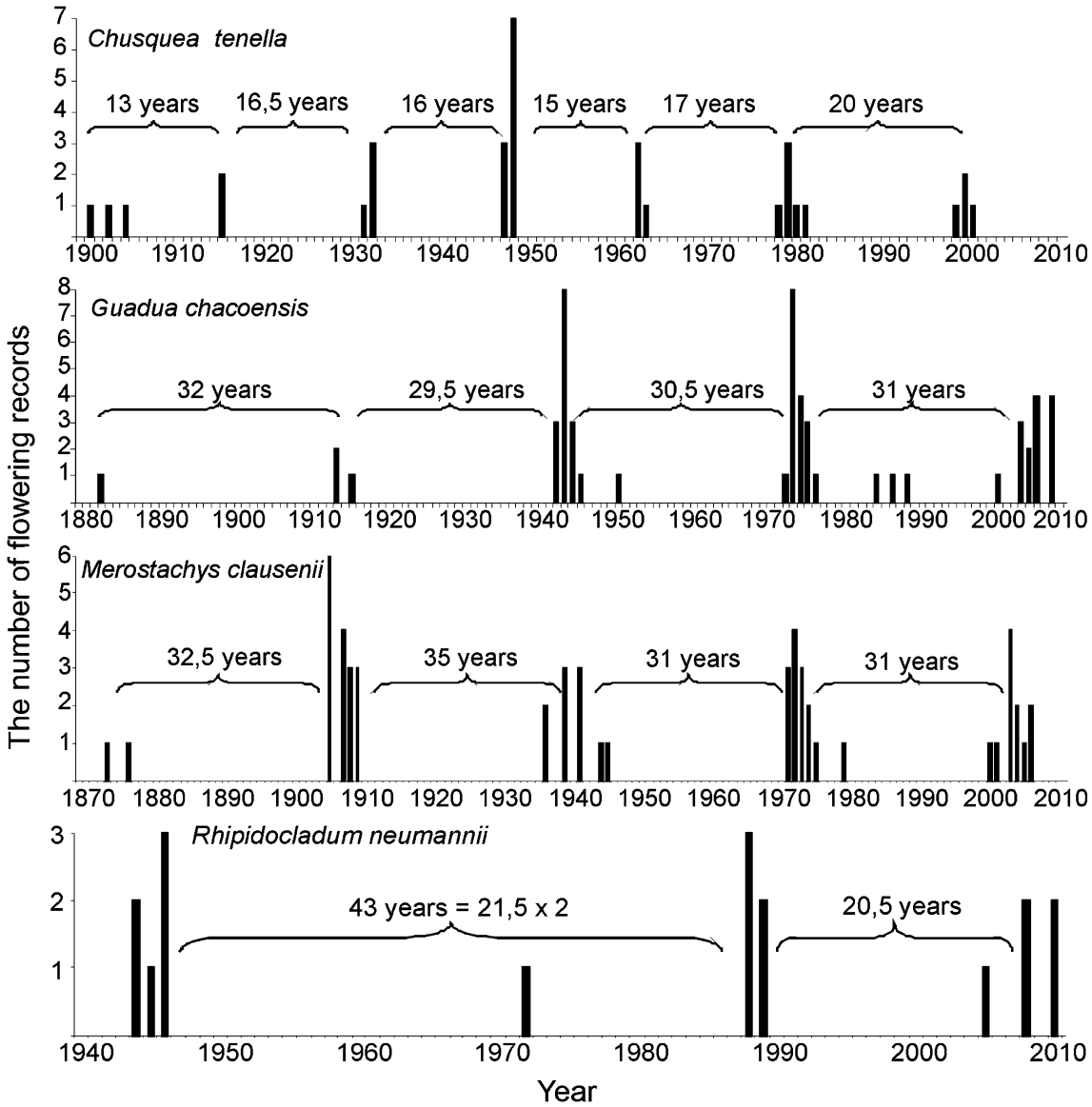

Fig. 1 Number of flowering records per year for one species of each bamboo genera considered here, showing flowering intervals used to estimate the flowering cycle

Table 2 Recorded mass flowering events and estimated flowering cycle of bamboo species native to southern South America

Species	Duration of mass flowering events	Flowering cycle (years)
Chusquea culeou	1938–1939, 2000–2001	62
C. deficiens	1939	–
C. lorentziana	1874, 1941–1942, 1971–1974, 2003–2005	32
C. montana	1858–1862, 1944–1945, 1985	41
C. quila	1795, 1886–1888, 1947, 1992	45
C. ramosissima	1916–1919, 1945–1949, 1977–1981, 2003–2005	29
C. tenella	1901–1905, 1916, 1932–1933, 1948–1949, 1963–1964, 1979–1982, 2000–2001	16
C. valdiviensis	1992	–
Colanthelia rhizantha	1992–1996	–
Guadua chacoensis	1883, 1914–1916, 1943–1946, 1974–1977, 2004–2008	31
G. paraguayana	1936–1939, 1974–1976	38
G. trinii	1920–1923, 1952–1953, 1984	31
Merostachys clausenii	1874–1877, 1906–1910, 1940–1946, 1974–1976, 2004–2006	32
M. multiramea	1875, 1906–1909, 1937–1943, 1971–1975, 2003–2007	32
Rhipidocladum neumannii	1944–1946, 1988–1989, 2008–2010	21
R. racemiflorum	2001	–

Several mass flowering events were identified in *Chusquea culeou* and *C. ramosissima* but there were also many sporadic flowering events recorded for both species during the intermast periods. At the same time, during this study sporadic flowering of a clump of *C. culeou* was recorded by the author, but unlike what has been previously recorded (Clark 1989; Pearson et al. 1994), this particular clump did not die after flowering and, instead, resumed vegetative growth, developing new shoots and branches. The same situation was recorded in a clump of *G. chacoensis* which flowered during the last mass flowering event of 2004–2008 but, unlike every other clump in the population, it did not die afterwards. This particular clump is currently part of the new generation of *G. chacoensis* which established from seed after the mass flowering event of 2004–2008 (author's personal observation).

When reconstructing the history of mass flowering events of woody bamboos in Argentina and neighboring areas, from the late 19th century to the present, it is clear that there is a regular flowering cycle in most of the species considered here. Also, the life cycles of some of these species seems to be synchronized. Mass flowering events of different species occurred simultaneously on several occasions over the last century. For example, in 1945, mass flowering events of *Chusquea montana*, *C. ramosissima*, *Guadua chacoensis*, *Merostachys clausenii* and *Rhipidocladum neumannii* were recorded. Then, in 1974, there were mass flowering events of *C. lorentziana*, *G. chacoensis*, *G. paraguayana*, *M. clausenii* and *M. multiramea*. And again in 2004–2005, *C. lorentziana*, *C. ramosissima*, *G. chacoensis*, *M. clausenii* and *M. multiramea* flowered massively in their respective ranges. Most of these species show flowering cycles of 30 years or so. This simultaneity of flowering events of different species, i.e. synchronous life cycles, has not been previously recorded in southern South America (Fig. 2).

Discussion

Few studies have described bamboo flowering to date. In this paper, information on flowering cycles and lifespan of woody bamboos native to southern South America have been provided. Studying data from herbarium specimens is a recent development in phenological studies. They provide useful information to examine long-term trends in phenological events. Herbarium specimens are far more abundant than field observations, thus these records could dramatically increase the amount of reliable data available for phenological studies (Miller-Rushing et al. 2006).

Campbell (1985) reviewed flowering cycles of 20 taxa, most of them from southeastern Asia, but he also included data from *Chusquea tenella* (Dutra 1938) and *G. trinii* (Parodi 1955). Among those species with some evidence of regularity, the author found a remarkable concentration of mean periods with multiples of 15–16 years. In the present study, this curious pattern was also detected. In 9 out of 13 species with evidence of regular mass flowering events, mean flowering cycles are multiples of 15–16: one species had a mean cycle of 16 years, 6 species of 29–32 years

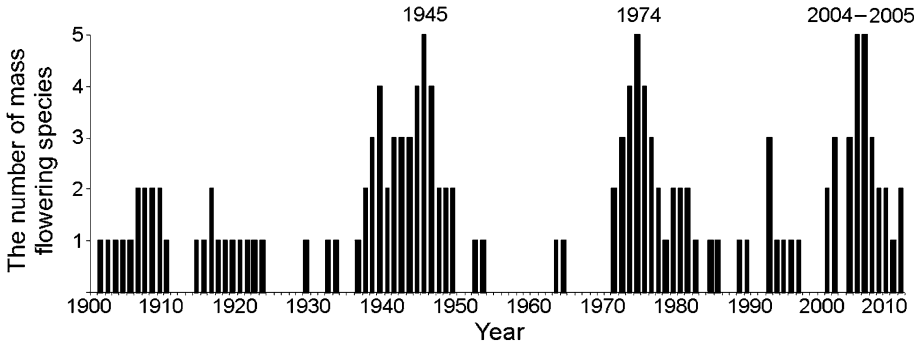

Fig. 2 Number of species that mass flowered annually in the last 110 years, noticing the years when five different species of woody bamboos mass flowered simultaneously

(15–16 × 2), one species of 45 years (15 × 3) and one species of 62 years (15–16 × 4) (Table 2).

In this study, only mass flowering events recorded in southern South America were considered. *R. racemiflorum* is a widespread and somewhat polymorphic species that ranges from central Mexico down to northwestern Argentina (Rúgolo and Vega 2012). Mass flowering events of this species have been recorded in Ecuador, Colombia and Costa Rica, but they have not been considered in this study since plants of a given species may show diverse flowering behavior under different environmental conditions (McClure 1966), also geographical or intraspecific variation may play a role. Anyway, Pohl (1991) reports for this species a flowering cycle of 16 years, considering two consecutive mass flowering events in Costa Rica. All other species considered here have distributions restricted to southern South America.

Some species of bamboos are facultatively monocarpic, i.e., they may or may not die after flowering (Judziewicz et al. 1999). Also, polycarpy has been reported in some bamboos (Miyazaki et al. 2009). Regarding *Chusquea ramosissima*, Montti et al. (2011) reported that some clumps did not die after flowering. Here, the same situation was recorded in *C. culeou* and *G. chacoensis*. Sometimes a species may also show sporadic flowering in some clumps within populations during the intermast period. In these species, there are almost always some clumps in flower. The percentage of flowering clumps is usually low and may vary from year to year, but flowering plants are usually to be found (Clark 1989; McClure 1966). According to the records gathered in this work, this is the case for *Chusquea culeou* and *C. ramosissima*. In other examples, during a mass flowering event, a few clumps may remain in a state of vegetative growth for no known reason (Ramanayake 2006). This was documented by Seifriz (1920) during the mass flowering of *Chusquea abietifolia* in Jamaica in 1918 and by Montti et al. (2011) in *C. ramosissima*. Clearly, flowering behavior may vary greatly even between relatively closely related species (Judziewicz et al. 1999).

Wherever bamboo is found, there are similar accounts of mass flowering events. This led to conjectures on the evolutionary forces that drove bamboo to flower, set seed and die in synchrony at intervals measured in decades. There are several different evolutionary hypotheses to explain bamboo life cycles, monocarpy and synchronism within flowering population. To date, the most generally accepted hypothesis is the consumer satiation or predator-escape hypothesis. Janzen (1976) proposed that flowering synchrony is the product of stabilizing selection, in which intense predation of seeds during non-gregarious flowering and predator satiation with gregarious flowering, strongly favors synchrony. Predator satiation also has been invoked to explain masting in many other species and to explain intraseasonal and interannual reproductive synchrony in both plants and animals (Ims 1990). In mass flowering plants and especially those that are wind-pollinated, as most bamboos appear to be (Judziewicz et al. 1999), synchrony may also be advantageous in improving outcross pollination rates (Koenig and Ashley 2003).

Synchronous reproduction among conspecifics has several demonstrated fitness benefits, including enhanced rates of pollination, increased attraction of seed dispersers and reduced seed predation (Crone et al. 2011). Mass flowering at long, regular intervals seen in some species of woody bamboos represents an extreme example of such intraspecific synchrony.

Flowering synchrony among different species of woody bamboos has also been reported. Campbell (1985) noted 'some synchrony between species, with a general periodicity of about 30 years in east Asia'. In this work, the same situation was recorded. Several species of woody bamboos native to southern South America show synchronous flowering cycles: *Chusquea lorentziana*, *C. ramosissima*, *G. chacoensis*, *M. clausenii* and *M. multiramea*, all of them with flowering cycles of approximately 30 years (Fig. 2). Moreover, 12 of the 16 species considered in this work had mass flowering episodes in the decades 1940s, 1970s and/or 2000s. This may be, as stated by Campbell (1985), 'evidence of a general synchronous tendency over large continental regions'.

Studies on bamboo flowering are hindered by the infrequency and unpredictability of the phenomenon. This

study provided new information for an important number of woody bamboo species native to southern South America and has led to several predictions (Table S1) that only time will corroborate.

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Appendix

Representative material examined

Chusquea culeou E. Desv.: Argentina, Neuquén, Los Lagos, Villa La Angostura, 23 April 2009, Rúgolo 2332 (SI).

Chusquea deficiens Parodi: Argentina, Salta, Anta, Maíz Gordo mountain range, 10 January 1939, Devoto 1010 (BAA).

Chusquea lorentziana Griseb.: Argentina, Salta, Guachipas, Pampa Grande, 2 May 1942, Hunziker 1548 (SI).

Chusquea montana Phil.: Argentina, Neuquén, Los Lagos, Villa La Angostura, Bayo Mountain, 8 January 2010, Rúgolo 2343 (SI).

Chusquea quila Kunth: Chile, XI Región, Aisén, Palena river valley, 28 January 1994, Rúgolo 1980 (SI).

Chusquea ramosissima Lindm.: Argentina, Misiones, Iguazú, Iguazú National Park, 24 July 2010, Lizarazu and Guerreiro 27 (SI).

Chusquea tenella Nees: Argentina, Misiones, San Pedro, Piñalito Park, 6 March 2000, Deginani et al. 1746 (SI).

Chusquea valdiviensis E. Desv: Argentina, Neuquén, Los Lagos, Nahuel Huapi National Park, Victoria Island, February 1946, Peréz Moreau 58 (SI).

Colanthelia rhizantha (Hack.) McClure: Argentina, Misiones, Belgrano, Andresito falls, 1 March 1995, Zuloaga et al. 5137 (SI).

Guadua chacoensis (Rojas) Londoño & P. M. Peterson: Argentina, Corrientes, General Paz, Santa Isabel stream, 13 November 2004, Quarín 4291 (SI).

Guadua paraguayana Döll: Argentina, Santa Fe, Obligado, Villa Ocampo, 20 January 1974, Quarín 1917 (CTES - LIL).

Guadua trinii (Nees) Nees ex. Rupr.: Argentina, Misiones, Iguazú, Iguazú National Park, sendero Macuco, 21 July 2010, Lizarazu and Guerreiro 6 (SI).

Merostachys clausenii Munro: Argentina, Misiones, Iguazú, Iguazú National Park, sendero Macuco, 24 July 2010, Lizarazu and Guerreiro 28 (SI).

Merostachys multiramea Hack.: Argentina, Misiones, Cainguas, Cuña Pirú camping site, 24 November 2004, Zuloaga and Belgrano 8147 (SI).

Rhipidocladum neumannii Sulekic, Rúgolo & L. G. Clark: Argentina, Salta, José de San Martín, Pescado river, 2 May 2003, Morrone et al. 4555 (SI).

Rhipidocladum racemiflorum (Steud.) McClure: Argentina, Salta, Santa Victoria, Baritú National Park, 22 June 1999, Hilgert and Hill 2367 (SI).

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