

Genetic Resources Communication

Clearing confusion in *Stylosanthes* taxonomy. 3. *S. hamata* sensu stricto vs. *S. hamata* sensu lato

Aclarando confusiones en la taxonomía de Stylosanthes. 3. S. hamata sensu stricto vs. S. hamata sensu lato

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Abstract

Stylosanthes hamata (L.) Taub., a suffruticose leguminous species with spreading prostrate or ascending stems, is widely distributed in the Caribbean region. It was originally described as *Hedysarum hamatum* by Linnaeus and later transferred to *Stylosanthes* by Taubert. To date, chromosome analysis of accessions of *S. hamata* originating from the Caribbean islands has revealed all to be diploids ($2n=20$). An accession of a morphologically similar *Stylosanthes* species, collected near Maracaibo in Venezuela in 1965 and subsequently misidentified as *S. hamata*, has found application as sown forage on low fertility soils in the subhumid to dry tropics since its registration as cultivar Verano in Australia in 1975. This morphotype has been shown to be tetraploid, and has been referred to in the literature as “tetraploid *S. hamata*” or “*S. hamata* sensu lato”. More recent work has demonstrated that the tetraploid is in fact an allotetraploid with *S. hamata* sensu stricto and *S. humilis* Kunth as the putative diploid progenitors. Various authors have recommended that the allotetraploid be treated as a separate species. We support this recommendation and suggest that, based on the information provided in this paper, the new species be described and validly published following examination of a more exhaustive range of specimens.

Keywords: Cytology, Fabaceae, molecular markers, morphology, phylogeny.

Resumen

Stylosanthes hamata (L.) Taub. es una leguminosa subarborescente con tallos postrados a ascendentes. Es ampliamente distribuida en la región del Caribe y fue originalmente descrita por Linnaeus como *Hedysarum hamatum* y después transferida por Taubert a *Stylosanthes*. Con base en análisis de cromosomas quedó evidente que todas las accesiones de *S. hamata* originarias de las islas del Caribe son diploides ($2n=20$). Una accesión de una especie de *Stylosanthes* morfológicamente similar, colectada en 1965 cerca de Maracaibo, Venezuela y erróneamente identificada como *S. hamata*, llegó a ser ampliamente usada como forraje sembrado en suelos de baja fertilidad en regiones tropicales secas a subhúmedas, después de su registro como cultivar Verano en Australia en 1975. Se estableció que este morfotipo es tetraploide y en la literatura se le encuentra denominado “*S. hamata* tetraploide” o “*S. hamata* sensu lato”. En un estudio más reciente se demostró que el tetraploide es en realidad un alotetraploide con *S. hamata* sensu stricto y *S. humilis* Kunth como supuestos progenitores diploides. Varios autores han recomendado que el alotetraploide sea tratado como una especie separada. Apoyamos esta recomendación y sugerimos que, con base en la información recopilada en este documento, la nueva especie sea descrita y válidamente publicada.

Palabras clave: Citología, Fabaceae, filogenética, marcadores moleculares, morfología.

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Introduction

As with previous papers in this series ([Cook and Schultze-Kraft 2019](#); [Schultze-Kraft et al. 2020](#)), we draw attention to an issue involving two related chromosomal races of *Stylosanthes*, one diploid and one tetraploid. In this case the two broad karyotypic groups are mostly referred to under the same species epithet, *hamata*. The taxonomic confusion arose following the decline of large areas of naturalized stands of *S. humilis* Kunth in northern Australia in the early 1970s due to the spread of anthracnose, a serious disease caused by the fungus, *Colletotrichum gloeosporioides*. Research identified an accession of *Stylosanthes* originating from near Maracaibo in Venezuela as having potential to replace *S. humilis*. This accession, catalogued as *S. hamata* CPI 38842, was released as cultivar ‘Verano’ in Australia ([McKay 1975](#)), with a similar accession, CPI 55822, from the same Maracaibo region, released as ‘Amiga’ ([Edye 1997](#)), both appearing in the registration statement as *Stylosanthes hamata* (L.) Taub., with a tetraploid chromosome complement of $2n=40$. Previous work had shown *S. hamata* to be diploid, $2n=20$ ([Cameron 1967](#)). Although plants of ‘Verano’ and ‘Amiga’ are similar to diploid morphotypes, there is now strong evidence that the cultivars more correctly belong to a new tetraploid species.

The recommendation to revise *S. hamata*, providing clear taxonomic distinction between the diploid and tetraploid types, is not novel, having already been raised over a number of years by Stace and Cameron ([1987](#)), Maass and Sawkins ([2004](#)), and Calles and Schultze-Kraft ([2016](#)). This paper serves to reiterate the urgency for taxonomic revision of *S. hamata sensu lato* by presenting current cytological evidence supported by morphological, geographical, genetic, and rhizobiological evidence that *S. hamata sensu lato* actually comprises two distinct species.

Taxonomy

Stylosanthes hamata was described by Linnaeus ([1758](#)) as *Hedysarum hamatum* based on Sloane’s illustration of a specimen from Jamaica and Burman’s illustration of a specimen from Sri Lanka. Taubert ([1891](#)) provided a more detailed description in a monograph of *Stylosanthes* and transferred the species to *Stylosanthes*.

The Maracaibo tetraploid has been referred to in the literature as “tetraploid *Stylosanthes hamata*” or “*Stylosanthes hamata sensu lato*”, neither being

strictly appropriate. The former is incorrect because there is published scientific evidence showing it to be an allotetraploid with *S. hamata* as one of the putative genome donors, and an allopolyploid should not be assigned to the taxon of one of the putative parents (pers. comm. M. Schori, USDA ARS). The latter term should not be used because it is imprecise, implicitly embracing both types. Stace and Cameron ([1984](#)) addressed the issue by referring to the tetraploid as *Stylosanthes* sp. nov. ($2n=40$), which also lacks specificity. Stace (pers. comm. to R. Schultze-Kraft, June 1984) suggested the allotetraploid be called “*Stylosanthes maracaibensis*” in reference to the geographical origin of the species, or “*S. hemihamata*” in reference to its allopolyploid origin. However, neither of the proposed epithets has been validly published as prescribed by the International Code of Nomenclature for algae, fungi, and plants ([Turland et al. 2018](#)). We will therefore refer to the Maracaibo allotetraploid as *Stylosanthes* sp. nov. throughout the remainder of this paper.

The genus *Stylosanthes* can be divided into two taxonomic sections on the basis of presence or absence of a small feathery appendage at the base of the flower and loment, possibly a small rudimentary secondary floral axis often referred to as the axis rudiment. *Stylosanthes hamata* possesses the axis rudiment and is accordingly placed in section *Stylosanthes*, while the other genome donor of *Stylosanthes* sp. nov., *S. humilis*, which lacks the axis rudiment, is assigned to section *Astyposanthes* (Hert.) Mohl. *Stylosanthes* sp. nov., which possesses the axis rudiment in the lower flowers only, may best remain unassigned by virtue of its intersectional origins.

Cytology and morphology

The existence of both diploid ([Cameron 1967](#)) and tetraploid ([Brolmann 1979](#); [Stace and Cameron 1984, 1987](#)) accessions assigned to *S. hamata* in various genetic resource collections has been long recognized. In his pioneer chromosome work, Cameron ([1967](#)) showed two Caribbean island accessions, CPI 33205 from Guadeloupe and CPI 33231 from Puerto Rico, to be diploid ($2n=20$). The Jamaican specimen from which the lectotype Sloane illustration was prepared was most probably also diploid since current understanding suggests that the diploid race only is native in Jamaica and other Caribbean islands. Recognition of a tetraploid race within the northern South American populations of *S. hamata* was first mentioned by Stace and Cameron ([1984](#)). During 1986, the collection of *Stylosanthes* sp. nov. was substantially increased, following collecting expeditions, primarily to Venezuela

but also to Colombia (Edye 1986), targeting collection of “tetraploid *S. hamata*”.

S. hamata has been described by a number of authors since Taubert (1891): Mohlenbrock (1957); Costa (2006); Costa et al. (2008); Calles and Schultze-Kraft (2010); and Vanni (2017). However, none of these provides any morphological distinction between diploids and tetraploids, even though several may unknowingly have included tetraploid specimens from within the possible geographic distributional range of *Stylosanthes* sp. nov. Similarly, Burt’s (1983) observation that there was considerable variability among the many accessions held as *S. hamata* in the Australian tropical forages collection may also be confounded, since by 1983 there were already more than 20 tetraploid accessions in the CSIRO collection. It is therefore conceivable that some characters or dimensional range extremes may be attributable to tetraploid specimens in those descriptions, but any morphological differences were considered to fall within the species circumscription.

The only published description of *Stylosanthes* sp. nov.

(Edye and Topark-Ngarm 1992) nominates a number of features that could separate this species from *S. hamata* (L.) Taub., but does not identify the specimens observed in compiling the description. A similar description prepared by Stace (unpublished 1987) was based on the examination of only two specimens of *Stylosanthes* sp. nov. from each of Venezuela and Colombia. While both nominate a number of relative morphological differences between the two species, the most consistent field differences in both descriptions are the presence in *Stylosanthes* sp. nov. of the axis rudiment in the lower part of the inflorescence only and of a long terminal bristle on the tips of the stipules and bracts. We believe that these differences need to be confirmed through examination of a wider range of identified herbarium specimens for a comprehensive description of a new species.

Table 1 below highlights some of the currently recognized key differences and similarities among the three species, drawing on information from Edye and Topark-Ngarm (1992) and various sources relating to *S. hamata* and *S. humilis*.

Table 1. Comparison of key features of *Stylosanthes* sp. nov. and its putative parent species.

Feature	<i>S. hamata</i>	<i>Stylosanthes</i> sp. nov.	<i>S. humilis</i>
Ploidy	$2n=20$	$2n=40$	$2n=20$
Life cycle	Short-lived perennial	Short-lived perennial	Obligate annual
Stem hairs	Line of fine hairs along alternating sides of internodes	Line of fine hairs along alternating sides of internodes	Line of fine hairs along alternating sides of internodes
Stem bristles	Absent	Absent	Abundant
Stipule bristles	Absent	On tips of teeth	On sheath and teeth
Bract bristles	Absent	On tips of teeth	Abundant
Axis rudiment	Present	In lower flowers only	Absent
Loment beak	Uncinate; beak \leq upper articulation	Uncinate, slightly coiled; beak \geq upper articulation	Uncinate to coiled; longer than other two spp., beak \geq upper articulation
Seed color	Mostly cream, yellow to light brown	Frequently tan to dark maroon, \pm mottled	Mostly brown to black

Geographic distribution

The diploids are geographically more widespread than the tetraploids, being found from about 28° N in Florida, USA, through much of the Caribbean island region to about 8° N in Venezuela, with adventive populations between about 3° and 9° S in the north-eastern Brazilian states of Ceará and Pernambuco (Edye and Maass 1997).

Three distinct tetraploid populations have been identified (Edye and Maass 1997):

- Venezuela-Colombia population occurring between 9° N and 11°30' N found sympatrically with diploid

S. hamata. This is the group that has been the target of forage collection expeditions and provided two forage cultivars. It is also the group that has contributed to taxonomic confusion.

- Guatemala population represented in the Australian Pastures Genebank by two accessions, APG 57426 (=CPI 46587) and APG 57837 (=CPI 46588), occurring around 16° N.
- USA population at four separate sites along the southeast coast of Florida between about 26° N and 27° N; distinguished by short curved beak on the upper articulation; possibly a separate species; sympatric with the more widespread diploids (Brolmann 1979).

A disjunct population of a species identified as *S. hamata* but of undetermined ploidy occurs at about 21° S in the landlocked state of Mato Grosso do Sul, Brazil (Costa et al. 2008).

Reference to tabulated collection data for a large range of diploid and tetraploid accessions held in the Australian forage germplasm collection as *S. hamata* (Date 2010), shows that average annual rainfall was (300–)500–1,000(–1,600) mm in areas where diploid accessions were collected and (250–)500–800(–2,200) mm for tetraploids. Soil pH at collection sites was mostly in the range of (6.2–)6.5–7.5(–8.5) for diploid and (5.4–)6.0–7.5 for tetraploid accessions. Both diploids and tetraploids are commonly found at lower elevations, but collections of both have been made at elevations >1,000 masl. Lists of diploid and tetraploid accessions with the Australian CPI and CIAT equivalent accession numbers are shown in the Appendix. Stace and Cameron (1987) also included genomic structure along with ploidy in the list of CPI accessions held as *S. hamata* by CSIRO in 1981. This work revealed that the two Guatemalan tetraploids have different genomic structure from that of *Stylosanthes* sp. nov. that they refer to as the “Maracaibo tetraploid”.

Rhizobiology

Date (2010) noted that with few exceptions, *S. hamata* and *Stylosanthes* sp. nov. fell into different pairs of groups produced from analysis of extensive accession × *Bradyrhizobium* effectiveness experiments. The former showed a high level of specificity in respect to effectiveness of nodulation by bradyrhizobia, and the latter showed the typical rhizobial response patterns of promiscuity for tetraploid accessions. In this screening, *Bradyrhizobium* strains CB2126 and CB3050 were selected as suitable for *S. hamata* and the wide-spectrum strains CB756 and CB1650 for *Stylosanthes* sp. nov. CB2126 and/or CB3050 were also effective on many of the more promiscuous *Stylosanthes* sp. nov. accessions (Eagles and Date 1999).

Molecular biology and phylogeny

The dearth of stable morphological characters means that classification of *Stylosanthes* at the species level is extremely difficult. However, various cytological and molecular-level procedures have facilitated phylogenetic analysis that irrefutably separates *Stylosanthes* sp. nov. from *S. hamata*. Stace and Cameron (1984, 1987), using

alcohol dehydrogenase (ADH) isozyme analysis, first demonstrated that *Stylosanthes* sp. nov. ($2n=40$) comprises *S. hamata* ($2n=20$) and *S. humilis* ($2n=20$) genomes, implying that *Stylosanthes* sp. nov. is an allotetraploid product of the two diploid species. They also noted that *Stylosanthes* sp. nov. should not be confused with another taxon known at the time as *Stylosanthes* sp. aff. *hamata* that has since been identified as *S. scabra* Vogel. Curtis et al. (1995), using restriction fragment length polymorphism (RFLP) analysis of genomic DNA from representative accessions of *S. humilis*, *S. hamata* and *Stylosanthes* sp. nov. (‘Verano’), presented molecular evidence that the two diploids are progenitors of ‘Verano’. Gillies and Abbott (1996) undertook detailed analysis of chloroplast DNA restriction fragment length variation to reconstruct the maternal phylogeny of a range of *Stylosanthes* species. They concluded that *S. humilis* is the likely maternal parent of *Stylosanthes* sp. nov., and *S. hamata*, by inference from previously published findings, the likely paternal progenitor. Further evidence on the origin and individuality of *Stylosanthes* sp. nov. is provided by Vander Stappen et al. (1999a, 1999b, 2002).

Conclusion

This paper presents clear evidence that the tetraploid taxon to which the widely used forage cultivars ‘Verano’ and ‘Amiga’ belong is not only cytologically and to some extent morphologically different from the diploid *S. hamata sensu stricto*, but can conclusively be separated from that species on the basis of its phylogeny as determined from molecular studies. It is clearly not an autotetraploid derived solely from *S. hamata* (L.) Taub., but an allotetraploid derived from *S. hamata* (L.) Taub. and *S. humilis* Kunth. We strongly and respectfully suggest that future authors desist from using taxon names such as “tetraploid *S. hamata*” and “*S. hamata sensu lato*” in reference to the above cultivars and conspecific accessions, but in the absence of a validly published name, the allotetraploid be referred to in the first instance as *Stylosanthes* sp. nov. (Maracaibo allotetraploid).

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Appendix: Range of *Stylosanthes hamata* and related tetraploid species germplasm, as far as ploidy levels have been assessed, with Australian (CPI) and CIAT forage genebank identifiers.

A: Diploid accessions [<i>Stylosanthes hamata</i> (L.) Taub.]				Source ^{2,3}
CPI No.	CIAT No.	Country ¹	State/Department	
33205	1010	GLP	Port Louis	1, 2, 3, 4(*)
33231	12299	PRI	San Juan	1, 2, 3, 4(*)
36046	12316	USA	Florida	2, 3, 4(*)
37037	12318	DOM		2, 3
37038	12319	DOM		2, 3, 4
38843	12322	USA	Florida	2, 3
40264	12339	BRA	Pernambuco	2, 3, 4
40268	12332	BRA	Ceará	2, 3
40275	12333	BRA	Ceará	2, 3
49080	12346	COL	Atlántico	2, 3
50997	12356	VEN		2, 3, 4
50998	not reg.	VEN		4
56211	not reg.	GLP		2, 3
57247	12389	VEN	Falcón	2
57248	12390	VEN	Falcón	2, 3
61623	12404	VEN	Nueva Esparta	2
61624	not reg.	VEN	Nueva Esparta	2
61669	not reg.	VEN		2, 3
61670	12406	VEN		2, 3, 4
61671	12407	VEN		2, 3
61672A	12408	VEN		3
62160	87	COL	Atlántico	2
62162	not reg.	VEN	Nueva Esparta	4
65361	58	COL	Atlántico	2
65363	87	COL	Atlántico	2, 4
65364	88	COL	Atlántico	4
65369	141	COL	Atlántico	2
65370	142	COL	Atlántico	2
70358	not reg.	ATG	St. George	2
70359	12426	ATG	St. John	2
70360	12427	ATG	St. John	2, 4(*)
70361	12428	ATG	St. John	2
70362	12429	ATG	St. John	2
70363	not reg.	LCA		2
70364	12430	ATG	St. George	2
70365	12431	ATG	St. Phillip	2
70366	12432	ATG	St. George	2, 4(*)
70367	12433	ATG	St. George	2
70368	not reg.	ATG	St. George	2
70369	12434	CUB	Matanzas	2
70370	12435	ATG	St. George	2, 4(*)
70371	12436	ATG		2, 4(*)
70372	not reg.	ATG		2, 4(*)
70373	not reg.	ATG		2
70374	12437	ATG		2, 4(*)
70375	not reg.	ATG		2
70376	12438	ATG	St. George	2
70377	not reg.	ATG		2
70520	12439	USA	Florida	2
70523	12440	USA	Florida	4(*)

Continued

A: Diploid accessions [<i>Stylosanthes hamata</i> (L.) Taub.]				Source ^{2,3}
CPI No.	CIAT No.	Country ¹	State/Department	
70524	12441	USA	Florida	4
70525	12442	USA	Florida	2, 4
70526	12443	USA	Florida	2
70527	12444	USA	Florida	2
72850	12446	USA	Florida	4
72852	12447	USA	Florida	4
72854	12448	USA	Florida	4
72959	12449	USA	Florida	2, 4
73484	12450	ATG	St. George	4(*)
73485	12451	ATG	St. George	2
73486	12452	ATG	St. George	4(*)
73487	12453	ATG	St. George	4(*)
73488	12454	ATG	St. John	4(*)
73490	not reg.	ATG	St. Phillip	2
73491	not reg.	ATG	St. George	4(*)
73497	not reg.	KNA	St. Kitts	4(*)
73498	not reg.	ATG	St. Paul	4(*)
73499	not reg.	ATG	St. Paul	4(*)
73501	12457	ATG	St. George	4(*)
73505	not reg.	ATG		4(*)
73506	not reg.	ANT	Curaçao	4(*)
73507	not reg.	ANT	Curaçao	4(*)
73509	not reg.	ANT	Curaçao	4(*)
73511	1475	CUB	Matanzas	4
73513	12459	KNA	Nevis	4(*)
73514	12460	KNA	Nevis	4(*)
73515	12461	KNA	Nevis	4(*)
73517	1465	KNA	Nevis	4(*)
73519	1466	KNA	Nevis	4(*)
73523	12462	ANT	Curaçao	4(*)
82313	not reg.	CUB	Santiago de Cuba	2
94130	12666	USA		4
94443	12674	USA		4
99670	12680	USA	Florida	4
99675	12685	PRI	Corozal	4
105678	not reg.	BRA	Bahia	4(*)
109305	11194	COL	Atlántico	4
109307	11196	COL	Atlántico	4
109308	11197	COL	Atlántico	4
109310	11199	COL	Atlántico	4
109312	11201	COL	Atlántico	4
109314	11203	COL	Atlántico	4
109315	11204	COL	Atlántico	4
109316	11205	COL	Magdalena	4
109346	11237	COL	Guajira	4
110066	12534	VEN	Zulia	4
110067	12535	VEN	Zulia	4
110077	12539	VEN	Falcón	4
110083	12542	VEN	Falcón	4
110084	12543	VEN	Falcón	4
110087	12544	VEN	Falcón	4
110090	12547	VEN	Falcón	4

Continued

A: Diploid accessions [<i>Stylosanthes hamata</i> (L.) Taub.]				Source ^{2,3}
CPI No.	CIAT No.	Country ¹	State/Department	
110099	12553	VEN	Lara	4
110108	12558	VEN	Lara	4
110110	11779	VEN	Cojedes	4
110114	11781	VEN	Nueva Esparta	4
110119	not reg.	VEN	Sucre	4
110125	not reg.	VEN	Aragua	4
110171	not reg.	VEN	Lara	4
110173	12586	VEN	Lara	4
110174	11793	VEN	Lara	4
110176	12587	VEN	Lara	4
110179	12588	VEN	Trujillo	4
110181	11795	VEN	Trujillo	4
110185	11796	VEN	Lara	4
110186	12590	VEN	Lara	4
110190	12593	VEN	Mérida	4
110207	not reg.	VEN	Distrito Capital	4
110311	124	COL	Atlántico	4
B: Tetraploid accessions [<i>Stylosanthes</i> sp. nov. (Maracaibo allotetraploid)]				Source ^{2,3}
CPI No.	CIAT No.	Country ¹	State/Department	
38842	1	VEN	Zulia	2, 3
38842	1953	VEN	Zulia	2
55812	12371	VEN	Zulia	2, 3
55820	12372	VEN	Zulia	2, 3
55821	12373	VEN	Zulia	2, 3, 4
55822	12374	VEN	Zulia	2, 3, 4
55823	12375	VEN	Zulia	2, 3
55824	12376	VEN	Zulia	2, 3
55825	12377	VEN	Zulia	2
55826	12378	VEN	Zulia	2, 3, 4
55827	12379	VEN	Zulia	2, 3
55828	12380	VEN	Zulia	2, 3
55830	12381	VEN	Zulia	2, 3
55831	12382	VEN	Zulia	2, 3
61672B	12408	VEN		2, 3
61672BB	12408	VEN		4
65365	114	VEN	Zulia	2, 4
65367	120	VEN	Zulia	2
65368	122	VEN	Zulia	2, 4
65371	147	VEN	Guárico	2, 4
65962	12412	COL	Magdalena	4
65965	12415	COL	Magdalena	2, 4
68837	167	COL	Guajira	2, 4
68838	174	COL	Magdalena	2, 4
68840	1039	COL	Magdalena	2, 4
109320	11209	COL	Magdalena	4
109325	11214	COL	Magdalena	4
109326	11215	COL	Magdalena	4
109331	11221	COL	Magdalena	4
109332	11222	COL	Magdalena	4
109344	11235	COL	Guajira	4
109347	11238	COL	Guajira	4

Continued

B: Tetraploid accessions [<i>Stylosanthes</i> sp. nov. (Maracaibo allotetraploid)]				Source ^{2,3}
CPI No.	CIAT No.	Country ¹	State/Department	
109349	11240	COL	Cesar	4
109350	11241	COL	Cesar	4
110024	12409	VEN	Zulia	4
110025	12509	VEN	Zulia	4
110026	12510	VEN	Zulia	4
110027	12511	VEN	Zulia	4
110028	12512	VEN	Zulia	4
110029	12513	VEN	Zulia	4
110030	12514	VEN	Zulia	4
110033	12515	VEN	Zulia	4
110035	12516	VEN	Zulia	4
110036	11761	VEN	Zulia	4
110037	11762	VEN	Zulia	4
110038	12517	VEN	Zulia	4
110039	12518	VEN	Zulia	4
110040	12519	VEN	Zulia	4
110041	12520	VEN	Zulia	4
110042	12521	VEN	Zulia	4
110043	11763	VEN	Zulia	4
110044	12522	VEN	Zulia	4
110045	12523	VEN	Zulia	4
110046	11764	VEN	Zulia	4
110048	12525	VEN	Zulia	4
110049	12526	VEN	Zulia	4
110050	11765	VEN	Zulia	4
110051	11766	VEN	Lara	4
110057	12529	VEN	Zulia	4
110068	12536	VEN	Zulia	4
110069	12537	VEN	Zulia	4
110070	11770	VEN	Zulia	4
110095	11778	VEN	Lara	4
110098	12552	VEN	Lara	4
110104	12555	VEN	Trujillo	4
110109	12559	VEN	Lara	4
110116	11782	VEN	Táchira	4
110134	12568	VEN	Zulia	4
110135	12569	VEN	Zulia	4
110138	11787	VEN	Zulia	4
110162	12580	VEN	Zulia	4
110166	12582	VEN	Aragua	4
110168	12584	VEN	Yaracuy	4
110205	12596	VEN	Miranda	4
110206	12597	VEN	Distrito Capital	4
110209	12598	VEN	Aragua	4
110316	179	COL	Magdalena	4
110317	182	VEN	Zulia	4

C: Tetraploid accessions (Guatemala and Florida)				Source ^{2,3}
CPI No.	CIAT No.	Country ¹	State/Department	
46587	12343	GTM	Alta Verapaz	2, 3, 4
46588	12344	GTM		2, 3
94444	12675	USA	Florida	4

¹Country abbreviations: ANT = Netherlands Antilles; ATG = Antigua and Barbuda; BRA = Brazil; BHS = Bahamas; CUB = Cuba; COL = Colombia; DOM = Dominican Republic; GLP = Guadeloupe; GTM = Guatemala; LCA = Saint Lucia; KNA = Saint Kitts and Nevis; PRI = Puerto Rico; USA = United States of America; VEN = Venezuela.

²Sources: 1 - Cameron ([1967](#)); 2 - H. Stace pers. comm. (1984); 3 - Stace and Cameron ([1987](#)); 4 - Date ([2010](#)).

³Source with (*): accession is mentioned as “presumed diploid”.