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Genetic Resources Communication

Clearing confusion in *Stylosanthes* taxonomy: 1. *S. seabrana* B.L. Maass & 't Mannetje

Aclarando confusiones en la taxonomía de Stylosanthes: *1.* S. seabrana *B.L. Maass & 't Mannetje*

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Abstract

Stylosanthes seabrana was first formally described as a new species in 2002 following extensive morphological and agronomic characterization, accompanied by genetic and molecular studies. Since then it has been proposed as a synonym of *Stylosanthes scabra* Vogel. This paper refutes this synonymization and indicates the indisputable evidence that *S. seabrana*, a diploid, is a likely putative progenitor of the allotetraploid *S. scabra*.

Keywords: Agronomy, cytology, morphology, phylogeny, rhizobiology, *Stylosanthes scabra*.

Resumen

Stylosanthes seabrana fue formalmente descrita como una especie nueva en 2002, como resultado de extensivas caracterizaciones morfológicas y agronómicas, junto con estudios genéticos y moleculares. En 2011 se propuso que se trata de un sinónimo de *Stylosanthes scabra* Vogel. En este trabajo se refuta esta sinonimización y se muestra que existen múltiples estudios para indicar que *S. seabrana*, una especie diploide, es probablemente un progenitor putativo de *S. scabra*, una especie alotetraploide.

Palabras clave: Agronomía, citología, filogenética, morfología, rizobiología, *Stylosanthes scabra*.

Introduction

Since recognition in Australia of the forage value of the adventive species, *Stylosanthes humilis* Kunth, in the early 20th century, there has been continuing focus on the genus, *Stylosanthes*, to determine the commercial pasture potential of other species within the genus. Of the 40 species of *Stylosanthes* currently accepted by the US National Plant Germplasm System (GRIN), 7 have been demonstrated to have commercial agricultural merit. Large collections of a number of species were assembled by CIAT in Colombia and CSIRO in Australia, including shrubby stylo (*Stylosanthes scabra*) that was found to have potential in the acid, infertile soils of subhumid and semi-arid northern Australia. The most recent addition to the list of commercial species in the genus, *S. seabrana* B.L. Maass & 't Mannetje, has proven well-adapted to the slightly acid to alkaline, more fertile clay and clay-loam soils in the same region, but extending into the subtropics.

Taxonomy of *Stylosanthes seabrana*

While characterizing the *S. scabra* collection held by CIAT in Colombia, Maass (1989) identified a group of plants from Bahia state in Brazil that shared a number of morphological characteristics with *S. scabra* but were morphologically and agronomically different from *S. scabra* and other known species of *Stylosanthes*. Following the provisional name given to this form by plant collectors, she referred to the group in her classification as "cf. *scabra*-Type". This

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promising phenotypic group was subsequently referred to as *S.* sp. aff. *scabra* by Jansen and Edye (1996), and eventually as "*Stylosanthes seabrana*" by Edye et al. (1998), accepting that *S.* sp. aff. *scabra* was indeed a different species from *S. scabra*. The name was selected in reference to the town of Seabra in the region of Bahia state, where the earliest accessions of the species were collected. The scientific name, *Stylosanthes seabrana*, was formalized by Maass and Mannetje (2002). The common name, Caatinga stylo, was adopted in Australia, referring to the xerophytic Caatinga vegetation type in northeastern Brazil on the medium- to heavy-textured soils on which the species is largely found. Vanni and Fernandez (2011) disputed the conclusion of Maass and Mannetje (2002), claiming instead that *S. seabrana* is a synonym of *S. scabra*, a claim that is hereby rejected based on a comprehensive assessment of all relevant information/evidence.

Morphology

To help direct future plant evaluation in the sub-humid/semi-arid tropics of Australia, and to obtain a clearer picture of the taxonomic and agronomic boundaries of a number of promising *Stylosanthes* species, morphological and agronomic classificatory experiments involving large numbers of entries of *S. scabra*, *S. hamata* (L.) Taub. and *S.* sp. aff. *scabra* (= *S. seabrana*) were conducted at CSIRO Lansdown Research Station, north Queensland (Jansen and Edye 1996; Date et al. 2010). Each used a numerical classification program, PATN (Belbin 1995) that, at the 5 group level, separated entries largely into homogeneous groups, with *S.* sp. aff. *scabra* separated from *S. scabra*. Shapes of the terminal leaflet and the terminal leaflet apex, the presence or absence of leaflet and stem hairs, the presence or absence of inflorescence bristles, the presence or absence of stipule horn lateral bristles and stipule horn terminal bristles were the most useful attributes defining groups. Maass and Mannetje (2002) used the most consistent of these and other observations to develop a key to distinguish the 3 species morphologically.

Key to *Stylosanthes seabrana*, *S. hamata* and *S. scabra*:

1a. Beak equal to or exceeding the upper article, leaflets without bristles……..…………..……………………… *S. hamata*
1b. Beak shorter than the upper article, leaflets with bristles
    2a. Leaflets narrowly elliptical, glabrous except for long bristles on the margins and midrib and prominently raised veins on the lower surface…………... *S. seabrana*
    2b. Leaflets elliptical to obovate, pubescent with bristles at least underneath or on the margins without prominently raised veins on the lower surface... *S. scabra*

Many collections and studies of *Stylosanthes scabra* have been conducted since Vogel (1838) described the specimen from Serra da Moeda, Minas Gerais, Brazil and Mohlenbrock (1957) reviewed the genus, *Stylosanthes*. On this basis, it can be presumed that the Edye and Topark-Ngarm (1992) description based on research experience and the description of Costa and Ferreira (1984) might be more comprehensive than earlier keys. Vanni and Fernandez (2011) provide what they call a "standard description" of *S. scabra*, which differs from those of Vogel (1838), Mohlenbrock (1957) and Costa and Ferreira (1984)/Edye and Topark-Ngarm (1992), all varying somewhat in their choice of descriptors. However, some characteristics provided in the various keys help to further distinguish *S. seabrana* from *S. scabra* morphologically. A characteristic not used in the Maass and Mannetje (2002) key is the length of the axis rudiment, 7–8 mm in their description of *S. seabrana* and 4–5 mm in *S. scabra* (Mohlenbrock 1957; Edye and Topark-Ngarm 1992).

Agronomy

There are clear agronomic differences between *S. seabrana* and *S. scabra*. Early research in the 1960s and 1970s to identify other *Stylosanthes* species to extend the range of *S. humilis* identified the potential of *S. scabra* and the tetraploid form of *S. hamata* (= *S. hemihamata* nom. nud.), resulting in the release of cultivars of each. However, while these were very effective in the light, acid infertile soils of northern Australia, they were not adapted to the heavier, more fertile clay soils in the region. Attention was then turned to the group of *Stylosanthes* sp. aff. *S. scabra* that were collected on broadly similar soils in Brazil (Edye and Maass 1997). These proved well-adapted to heavy- and medium-textured alkaline soils in Australia, and unlike *S. scabra*, were also adapted to the more frost-prone environment of southern Queensland (Edye and Hall 1993; Jansen and Edye 1996). CSIRO applied for Plant Breeders Rights for the 2 most promising lines in 1996 (granted in 1997) as "Caatinga Stylo (*Stylosanthes* sp. nov. aff. *S. scabra*) cvv. Primar and Unica" to provide a legume base for forage systems on neutral to alkaline soils of central and southern Queensland.

Early evaluation highlighted another important difference between the 2 species. While *S. scabra* is promiscuous in its root nodule bacterial requirements, nodulating effectively on native strains of *Bradyrhizobium* in Australia or the broad spectrum CB 756 commercial strain (Date 1997), this was not the case for Caatinga stylo. During field evaluation at a range of sites in Queensland in the 1990s, Caatinga stylo accessions nodulated poorly and ineffectively and frequently failed to nodulate at all (Edye 1994; Edye et al. 1998). Most accessions grew well for 1 or 2 years, before beginning to show classical signs of nitrogen deficiency. Success of the new cultivars was contingent on discovery of an effective and persistent strain of inoculum. Accordingly, nodules were collected during germplasm collections in Brazil, and strains of *Bradyrhizobium* were isolated, tested and released prior to release of cvv. Primar and Unica (Date 2010; 2016).

Ploidy

A major part of the argument advanced by Vanni and Fernandez (2011) revolves around their finding both diploid and tetraploid specimens in the roots of seedlings grown from a sample of commercial seed of *S. seabrana* cv. Unica from Australia. In their Introduction, they make the following confusing statement: "In addition, they (referring to Maass and Mannetje 2002) reported different levels of ploidy in *S. scabra*, $2n = 40$ chromosomes and *S. seabrana*, $2n = 20$ chromosomes." The ploidy cited for the 2 species is correct; however it in no way supports their contention of dual ploidy in *S. scabra*. Rather, Vanni and Fernandez (2011) use this confusing statement to support their claim that: "ploidy levels are not valid criteria for species distinction in the genus *Stylosanthes*, as *S. scabra* has been reported to be one of the few species with diploid ($2n = 20$) and tetraploid ($2n = 40$) genotypes (Cameron 1967)." This is not the case. In fact, Cameron (1967) determined the chromosome number for a single accession of *S. tuberculata* (presumably *Stylosanthes tuberculata* S.F. Blake syn. *S. scabra* Vogel), which he found to be tetraploid ($2n = 40$) only. Since then a number of workers (Battistin and Martins 1987; Liu et al. 1999; Lira 2015) have reported tetraploidy in *S. scabra*. No report of diploidy in the species exists in the published literature.

'Unica' was derived from CPI 110361, which has been shown to be diploid (Liu and Musial 1997), so the question arises: how could there have been the 2 ploidy levels in the sample tested by Vanni and Fernandez (2011)? The answer lies in the fact that the seed lot on which Vanni and Fernandez (2011) based their taxonomic revision was a commercial sample. Since seed crops of both *S. scabra* and *S. seabrana* are grown in the same general area in north Queensland, it is probable that a commercial sample of seed may contain both species, either from contamination in the crop (*S. scabra* is now naturalized in the region), in the harvester from a previously harvested crop of *S. scabra* or during post-harvest handling. There is no seed certification scheme for this cultivar in Australia and post-harvest cleaning procedures for harvesting machinery are not as stringent for standard commercial crops as for certified crops.

Phylogeny

Until relatively recently, morphological characters were the only means of describing species, but they have not always provided the level of resolution required to categorically define interspecific and intraspecific differences. Vanni and Fernandez (2011) consider that the form of leaflets, the absence or presence of bristles and hairs on stipules and leaflets and their venation are not sufficient to separate species. Whether or not this is valid is debatable. However, the evidence provided from genetic and molecular studies is indisputable. As discriminatory methodologies improved with the development of molecular technologies, so did the evidence to more clearly define relationships within and between taxonomic groups.

It has been shown that *S. scabra* is an allotetraploid with *S. viscosa* Sw. as one of the putative diploid progenitors (Stace and Cameron 1984; Vander Stappen et al. 2002). The identity of the other diploid progenitor is not so clear-cut. Stace and Cameron (1984) postulated that, since *S. scabra* bears an axis rudiment on the loment, a characteristic governed by a dominant gene, and *S. viscosa* lacks an axis rudiment (section *Stylosanthes*), the other parent must bear an axis rudiment (section *Styposanthes*). Working with chloroplast DNA, Gillies and Abbott (1996) proposed *S. hamata* sensu stricto as the section *Styposanthes* progenitor, while Liu and Musial (1997) provided evidence that the other putative progenitor was *Stylosanthes* sp. aff. *S. scabra* (= *S. seabrana*). These 2 species fell into the same basal genome group A, determined by restriction fragment length polymorphisms (RFLP) and sequence-tagged-sites (STS) analyses by Liu et al. (1999). In the same study, *S. viscosa* fell into basal genome group B and *S. scabra* into group AB. More recent work (Tewari and Chandra 2008; Chandra and Kaushal 2009; Marques et al. 2018) confirms the proposition of allotetraploid origins of *S. scabra* with *S. hamata* or *S. seabrana* as the maternal donor and *S. viscosa* as the paternal donor. However, Marques et al. (2018) point out the difficulty in precise identification of the maternal donor since both the diploid and the polyploid species have diverged since the allopolyploidy event some 0.63 to 0.52 million years ago.

Conclusion

Stylosanthes seabrana is clearly morphologically, agronomically, rhizobially, cytologically and phylogenetically different from *S. scabra* (Appendix I), and taxonomic logic dictates that it must be treated as a separate species. It is no more conspecific with *S. scabra* than is its other putative progenitor, *S. viscosa*. Similar confusion is faced by practitioners in relation to 2 other *Stylosanthes* diploid-allotetraploid derivative pairs, *S. hamata* - *S. hemihamata* nom. nud. and *S. macrocephala* - *S. capitata*, that will be dealt with in subsequent papers in this series.

Taxonomists at the US Germplasm Resources Information Network (GRIN; https://npgsweb.ars-grin.gov/gringlobal/taxon/abouttaxonomy.aspx) have reviewed their earlier decision to accept the Vanni and Fernandez (2011) thesis of synonymy between *S. seabrana* and *S. scabra* and have now listed *S. seabrana* as a valid species. A list of all *S. seabrana* germplasm accessions registered in the major *Stylosanthes* genebanks is presented as Appendix II. All accessions with known origin have been collected in Bahia State, except for ser. nos. 15 and 16 which are from Minas Gerais, Brazil.

Acknowledgment

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(Note of the editors: All hyperlinks were verified 17 January 2020.)

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Appendix I. Differences in brief between *Stylosanthes seabrana* and *S. scabra*.

Characteristic/trait	*S. seabrana*	*S. scabra*
Leaflet shape	Narrowly elliptical	Elliptical to obovate
Leaflet indumentum	Glabrous except for long bristles on the margins and midrib	Pubescent with bristles at least underneath or on the margins
Leaflet venation	Prominently raised veins on the lower surface	Without prominently raised veins on the lower surface
Length of axis rudiment	7–8 mm	4–5 mm
Ploidy	Diploid ($2n = 20$)	Tetraploid ($2n = 40$)
Genome	A	AB
Soil pH	Neutral to alkaline	Acid
Soil texture	Medium-heavy	Light
Soil fertility	Moderate to high	Low
Rhizobial specificity	Very specific	Promiscuous

Appendix II: *Stylosanthes seabrana* germplasm accessions registered in the major tropical forages genebanks (January 2020).

Ser. no.	BRA[1]	CIAT[2]	ILRI[3]	APG[4]	Comments, additional information, collector numbers
1		12014		**APG 58185*** CPI 55802	CSIRO collection, April 1971; RLB B69
2		12015		**APG 58187*** CPI 55804	CSIRO collection, April 1971; RLB B77
3		12019		**APG 58190*** CPI 55809	CSIRO collection, April 1971; RLB B97
4		12016		**APG 58191*** CPI 55810	CSIRO collection, April 1971; RLB C23
5		12020		**APG 57821*** CPI 55811A	CSIRO collection, April 1971; RLB C25 CPI 55811 = *S. scabra*
6		12021		**APG 58194*** CPI 55813	CSIRO collection, April 1971; RLB C27
7				**APG 58232*** CPI 55871	CSIRO collection, April 1971; RLB C29
8				**APG 58197*** **APG 57822** CPI 55816A	CSIRO collection, April 1971; RLB C42 CPI 55816 = *S. seabrana*
9	**00145661-5*** 007951	2050*		**APG 57483** CPI 110341	Joint collection Cenargen-CIAT, September 1978; LC 1172
10	**00219732-5*** 007901	2043*	15767	**APG 57482** CPI 110340	Joint collection Cenargen-CIAT, September 1978; LC 5186
11	**00219733-3*** 008095	2070	15768	**APG 56718** CPI 92454 **APG 57484** CPI 110342	Joint collection Cenargen-CIAT, September 1978; LC 5208
12	**00219734-1*** 008206	2085*	15769	**APG 56723** **AGP 57485** CPI 110343 CPI 92463	Joint collection Cenargen-CIAT, September 1978; LC 5221
13	**00219724-2*** 008915	2107*		**APG 56729** CPI 92476 CPI 110344	Joint collection Cenargen-CIAT, October 1978; LC 1234
14	**00219725-9*** 009318	10517	15795	CPI 110372	Cenargen collection, April 1979; LC 1417

Continued

Ser. no.	BRA[1]	CIAT[2]	ILRI[3]	APG[4]	Comments, additional information, collector numbers
15	**00145502-1** 030058			**APG 57165** CPI 105729	IPF 1038* (NSC 933a); an EPAMIG (Empresa de Pesquisa Agropecuária de Minas Gerais, Brazil) collection (“*S. scabra*”) from Itamarandiba, Minas Gerais (June 1979)
16				**APG 56854*** CPI 93099	CSIRO collection, May 1981; DFC 562; accession collected at Mato Verde, Minas Gerais (May 1981)
17	**00219726-7*** 022462	10026*		**APG 56942** CPI 104710	Joint collection Cenargen-CIAT, August 1981; LC 4335
18	**00219727-5*** 022594	10113*			Joint collection Cenargen-CIAT, August 1981; LC 4351
19	**00219728-3*** 022608	10030*			Joint collection Cenargen-CIAT, August 1981; LC 4353
20	**00219729-1*** 022811	10033*		**APG 57502** **APG 58153** CPI 110361	Joint collection Cenargen-CIAT, August 1981; LC 4402 cv. Unica
21	**00219730-9*** 022977	10119*	15793	CPI 110370	Joint collection Cenargen-CIAT, August 1981; LC 4447
22	**00219735-8*** 029220	10537			Joint collection Cenargen-RBG Kew, June 1983; LC 5782a
23	**00219738-2***				MSB 48767 from the RBG Kew Millenium Seed Bank Project; joint collection Cenargen-RBG Kew, June 1983; LC 6171a; LC 6171 (= BRA 00145997-3, former BRA 029335) is *S. macrocephala*
24	**00219736-6*** 029327	10547	15796	**APG 57514** CPI 110373	Joint collection Cenargen-RBG Kew, June 1983; LC 6257
25	**00219737-4*** 028961	10471		**APG 58015** ATF 2350	Joint collection Cenargen-RBG Kew, June 1983; LC 6261; species holotype at herbarium CEN
26	**00145640-9*** 036609	11578		**APG 57579** CPI 115993	Cenargen collection, June 1987; LC 7653
27	**00146011-2*** 036617	11583		**APG 57580** CPI 115994	Cenargen collection, June 1987; LC 7661
28	**00145653-2*** 036625	11585		**APG 57581** CPI 115995	Cenargen collection, June 1987; LC 7666
29	**00219739-0*** 041238			**APG 58052*** ATF 2523	Joint Cenargen-CSIRO collection, May/June 1996; LAE 746
30	**00145697-9*** 041246			**APG 58069*** ATF 2540	Joint Cenargen-CSIRO collection, May/June 1996; LAE 748
31	**00145698-7*** 041254			**APG 58068*** ATF 2539	Joint Cenargen-CSIRO collection, May/June 1996; LAE 749
32	**00145699-5*** 041262			**APG 58067*** ATF 2538	Joint Cenargen-CSIRO collection, May/June 1996; LAE 750
33	**00145700-1*** 041271			**APG 58066*** ATF 2537	Joint Cenargen-CSIRO collection, May/June 1996; LAE 751
34	**00145725-8*** 041289			**APG 58065*** ATF 2536	Joint Cenargen-CSIRO collection, May/June 1996; LAE 752
35	**00145722-5*** 041297			**APG 58064*** ATF 2535	Joint Cenargen-CSIRO collection, May/June 1996; LAE 753
36	**00145702-7*** 041301			**APG 58063*** ATF 2534	Joint Cenargen-CSIRO collection, May/June 1996; LAE 754
37	**00145703-5*** 041319			**APG 58062*** ATF 2533	Joint Cenargen-CSIRO collection, May/June 1996; LAE 755
38	**00145706-8*** 041327			**APG 58061*** ATF 2532	Joint Cenargen-CSIRO collection, May/June 1996; LAE 756
39	**00145705-0*** 041335			**APG 58060*** ATF 2531	Joint Cenargen-CSIRO collection, May/June 1996; LAE 757
40	**00145704-3*** 041343			**APG 58059*** ATF 2530	Joint Cenargen-CSIRO collection, May/June 1996; LAE 758

Continued

Ser. no.	BRA[1]	CIAT[2]	ILRI[3]	APG[4]	Comments, additional information, collector numbers
41	**00145711-8*** 041351			**APG 58051*** ATF 2522	Joint Cenargen-CSIRO collection, May/June 1996; LAE 759
42	**00145726-6*** 041360			**APG 58050*** ATF 2521	Joint Cenargen-CSIRO collection, May/June 1996; LAE 760
43	**00219740-8*** 041378			**APG 58049*** ATF 2520	Joint Cenargen-CSIRO collection, May/June 1996; LAE 762
44	**00145708-4*** 041394			**APG 58047*** ATF 2518	Joint Cenargen-CSIRO collection, May/June 1996; LAE 764
45	**00145707-6*** 041408			**APG 58046*** ATF 2517	Joint Cenargen-CSIRO collection, May/June 1996; LAE 765
46	**00145710-0*** 041416			**APG 58045*** ATF 2516	Joint Cenargen-CSIRO collection, May/June 1996; LAE 766
47	**00219741-6*** 041513			**APG 58036*** ATF 2507B	Joint Cenargen-CSIRO collection, May/June 1996; LAE 776 ATF 2507 = *S. macrocephala*
48		11957		**APG 57614** CPI 105546B	IPF xxxx* (accession no. unknown); EPAMIG (Empresa de Pesquisa Agropecuária de Minas Gerais, Brazil) collection CPI 105546 = *S. scabra* HMS 6 41
49		**11945** 12629		**APG 56763** APG 58152 CPI 92838B TQ 100	cv. Primar CPI 92838 = *S. tomentosa* DFC 008
50				**APG 57629** CPI 110370B	Isolated from CIAT 10119
51				**APG 57630** CPI 110370C	Isolated from CIAT 10119
52				**APG 58173** TQ 102	No further accession information available
53		12630			Probably a donation from the former CSIRO collection, but no further information available in the CIAT Genetic Resources database

Notes:

a) Some accessions are still registered under species names other than *S. seabrana*.

b) Accession numbers in **bold** are those to be preferably used.

c) Asterisk (*) indicates the most original accession number, i.e. the one assigned by the institution(s) that conducted the respective original collecting mission. This information is useful for eventual enquiries on passport data information, genetic purity and the like.

d) Sources: Databases of the former CSIRO Australian Tropical Forages Genetic Resources Centre (ATFGRC); Embrapa Recursos Genéticos e Biotecnologia; and CIAT; Maass and Mannetje (2002).

[1] BRA: Embrapa Recursos Genéticos e Biotecnologia, Brasília, Brazil (www.embrapa.br/recursos-geneticos-e-biotecnologia); the first BRA number (in bold) corresponds to the new Alelo code; former BRA numbers (second line) are still in use.

[2] CIAT: International Center for Tropical Agriculture, Cali, Colombia (ciat.cgiar.org).

[3] ILRI (formerly ILCA): International Livestock Research Institute, Addis Ababa, Ethiopia (www.ilri.org).

[4] APG: Australian Pastures Genebank, Adelaide, Australia (https://pir.sa.gov.au/research/australian_pastures_genebank); former Australian plant introduction numbers with CPI and ATF prefixes, also TQ, are still in use.

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