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 allotetraploide.

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
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 Mammetje 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 cut-and-dry. 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 fall 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 allopolyploid 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. viscossa. 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.

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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. | BRA1 | CIAT2 | ILRI3 | APG4 | Comments, additional information, collector numbers |
|----------|------|-------|-------|------|-----------------------------------------------------|
| 1        | 12014|       |       | APG 58185* | CSIRO collection, April 1971; RLB B69 |
|          |      | CPI 55802 |       |      |                                                     |
| 2        | 12015|       |       | APG 58187* | CSIRO collection, April 1971; RLB B77 |
|          |      | CPI 55804 |       |      |                                                     |
| 3        | 12019|       |       | APG 58190* | CSIRO collection, April 1971; RLB B97 |
|          |      | CPI 55809 |       |      |                                                     |
| 4        | 12016|       |       | APG 58191* | CSIRO collection, April 1971; RLB C23 |
|          |      | CPI 55810 |       |      |                                                     |
| 5        | 12020|       |       | APG 57821* | CSIRO collection, April 1971; RLB C25 |
|          |      | CPI 55811A |      |      | CPI 55811 = *S. scabra*                             |
| 6        | 12021|       |       | APG 58194* | CSIRO collection, April 1971; RLB C27 |
|          |      | CPI 55813 |       |      |                                                     |
| 7        | 57822 |       |       |       | CSIRO collection, April 1971; RLB C29 |
|          |      | CPI 55871 |       |      |                                                     |
| 8        | 58197* |       |       |       | CSIRO collection, April 1971; RLB C42 |
| 9        | 00145661-5* | 007951 |       | APG 57483* | CSIRO collection, April 1971; RLB B69 |
|          |      | CPI 55816A |       |      |                                                     |
| 10       | 00219732-5* | 007901 | 15767 | APG 57482* | CSIRO collection, April 1971; RLB B77 |
|          |      | CPI 110340 |       |      |                                                     |
| 11       | 00219733-3* | 008095 | 15768 | APG 56718* | CSIRO collection, April 1971; RLB B97 |
|          |      | CPI 92454 |       |      |                                                     |
|          |      | APG 57484* |       |      |                                                     |
| 12       | 00219734-1* | 008206 | 15769 | APG 56723* | CSIRO collection, April 1971; RLB C23 |
|          |      | CPI 110342 |       |      |                                                     |
| 13       | 00219724-2* | 008915 | 2107* | APG 56729* | CSIRO collection, April 1971; RLB C25 |
|          |      | CPI 92463 |       |      |                                                     |
| 14       | 00219725-9* | 009318 | 10517 | 15795 | Cenargen collection, April 1979; LC 1417 |
|          |      | CPI 110372 |       |      |                                                     |
| Ser. no. | BRA¹ | CIAT² | ILRI³ | APG⁴ | Comments, additional information, collector numbers |
|----------|------|-------|-------|------|--------------------------------------------------|
| 15       | 00145502-1 | 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* | 10026* | APG 56942 | CPI 104710 | Joint collection Cenargen-CIAT, August 1981; LC 4335 |
| 18       | 00219727-5* | 10113* | APG 56921 | Joint collection Cenargen-CIAT, August 1981; LC 4351 |
| 19       | 00219728-3* | 10030* | APG 57502 | Joint collection Cenargen-CIAT, August 1981; LC 4402 cv. Unica |
| 20       | 00219729-1* | 10033* | APG 58153 | Joint collection Cenargen-CIAT, August 1981; LC 4447 |
| 21       | 00219730-9* | 10119* | 15793 | CPI 110370 | Joint collection Cenargen-CIAT, August 1981; LC 4447 |
| 22       | 00219735-8* | 10537 | 022811 | 022977 | 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* | 10547 | 15796 | APG 57514 | Joint collection Cenargen-RBG Kew, June 1983; LC 6257 |
| 25       | 00219737-4* | 10471 | APG 58015 | Joint collection Cenargen-RBG Kew, June 1983; LC 6261; species holotype at herbarium CEN |
| 26       | 00145640-9* | 11578 | APG 57579 | Cenargen collection, June 1987; LC 7653 |
| 27       | 00146011-2* | 11583 | APG 57580 | Cenargen collection, June 1987; LC 7661 |
| 28       | 00145653-2* | 11585 | 036625 | 036625 | Cenargen collection, June 1987; LC 7666 |
| 29       | 00219739-0* | 104238 | APG 58052* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 746 |
| 30       | 00145697-9* | 104246 | APG 58069* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 748 |
| 31       | 00145698-7* | 104254 | APG 58068* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 749 |
| 32       | 00145699-5* | 104262 | APG 58067* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 750 |
| 33       | 00145700-1* | 104271 | APG 58066* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 751 |
| 34       | 00145725-8* | 104289 | APG 58065* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 752 |
| 35       | 00145722-5* | 104297 | APG 58064* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 753 |
| 36       | 00145702-7* | 104301 | APG 58063* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 754 |
| 37       | 00145703-5* | 104319 | APG 58062* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 755 |
| 38       | 00145706-8* | 104327 | APG 58061* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 756 |
| 39       | 00145705-0* | 104335 | APG 58060* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 757 |
| 40       | 00145704-3* | 104343 | APG 58059* | Joint collection Cenargen-CSIRO collection, May/June 1996; LAE 758 |

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| Ser. no. | BRA¹ | CIAT² | ILRI³ | APG⁴ | Comments, additional information, collector numbers |
|---------|------|------|------|------|--------------------------------------------------|
| 41      | 00145711-8* | 041351 |  | APG 58051* | Joint Cenagen-CSIRO collection, May/June 1996; LAE 759 |
| 42      | 00145726-6* | 041360 |  | APG 58050* | Joint Cenagen-CSIRO collection, May/June 1996; LAE 760 |
| 43      | 00219740-8* | 041378 |  | APG 58049* | Joint Cenagen-CSIRO collection, May/June 1996; LAE 762 |
| 44      | 00145708-4* | 041394 |  | APG 58047* | Joint Cenagen-CSIRO collection, May/June 1996; LAE 764 |
| 45      | 00145707-6* | 041408 |  | APG 58046* | Joint Cenagen-CSIRO collection, May/June 1996; LAE 765 |
| 46      | 00145710-0* | 041416 |  | APG 58045* | Joint Cenagen-CSIRO collection, May/June 1996; LAE 766 |
| 47      | 00219741-6* | 041513 |  | APG 58036* | Joint Cenagen-CSIRO collection, May/June 1996; LAE 776 |
| 48      | 11957     | 12629  |  | CPI 105546B | IPF xxxx* (accession no. unknown); EPAMIG (Empresa de Pesquisa Agropecuária de Minas Gerais, Brazil) collection |
| 49      | 11945     | 12629  |  | CPI 92838 | cv. Primar |
| 50      | 12630     | 12630  |  | CPI 92838B |  |
| 51      | 00145726-6* | 041360 |  | CPI 110370B | Isolated from CIAT 10119 |
| 52      | 12630     | 12630  |  | CPI 110370C | Isolated from CIAT 10119 |
| 53      | 12630     | 12630  |  | CPI 110370C | No further accession information available |

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).

1BRA: Embrapa Recursos Genéticos e Biotecnologia, Brasília, Brazil ([www.embrapa.br/recursos-geneticos-e-biotecnologia](http://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.
2CIAT: International Center for Tropical Agriculture, Cali, Colombia ([ciat.cgiar.org](http://ciat.cgiar.org)).
3ILRI (formerly ILCA): International Livestock Research Institute, Addis Ababa, Ethiopia ([www.ilri.org](http://www.ilri.org)).
4APG: Australian Pastures Genebank, Adelaide, Australia ([https://pir.sa.gov.au/research/australian_pastures_genebank](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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