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Saccharum species as horticultural classes

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Abstract Sugarcane, commonly referred to as *Saccharum officinarum*, is currently divided into six species, two of them are wild and four exist only in cultivation. The two wild species and three of the cultivated ones are interfertile and have produced the interspecific hybrids that constitute the sugarcane of commerce. All species are represented by wide ranges of intergrades preserved as clones through vegetative propagation. Species are separated by variable floral characters, sugar content, chromosome numbers and epidermal hair groups. Floral characteristics are sometimes useful with clones that flower, sugar is present in widely overlapping ranges and is highly influenced by environment, chromosome numbers range from 36 to 170 in the genus and range widely within species, and some epidermal hair groups are more quantitative than qualitative. Molecular techniques show that *Saccharum spontaneum* is distinctly different from the other species in cytoplasmic DNA, and cluster analyses of nuclear DNA support the difference. Not only are the species interfertile but chromosomal pairing and recombination have been demonstrated, as has the possibility that some *Saccharum* species are hybrids of others. Taken together, these observations suggest that there is little basis for the present separation and that the six species should more properly consist of two: one being *S. spontaneum*, based on molecular data, and the other *S. officinarum* including the other four species and all interspecific hybrids.

Key words Chromosomes · Molecular analyses · Sugarcane · Taxonomy

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The status of *Saccharum* species

Many sugarcane technologists recognize six species as the constituents of the genus *Saccharum* (Naidu and Sreenivasan 1987; Roach and Daniels 1987). Two, *S. spontaneum* and *S. robustum*, are found growing wild in Asia and Indonesia and four are cultivated. These four include *S. officinarum*, the garden cane of Indonesia which supported the world's commercial production for over a century, *S. barberi* and *S. sinense*, which are ancient land races in Asia, and *S. edule*, which has an aborted inflorescence that is served as a vegetable. The variety of forms included in these groups is the focus of this new perspective for *Saccharum officinarum.*

Described by Linnaeus as *S. officinarum*, cultivated sugarcane has been classified by that name ever since, but the classification has been accepted with dissent. Earle (1928) reviewed the changes in the classification of sugarcane beginning with Linnaeus' listing of two species, *S. officinarum* and *S. spicatum*, in the first (1753) edition of his "Species Plantarum". By the 3rd edition (1797), *Saccharum* had grown to include 11 species, reached 22 species in "*Enumeratio Plantarum*" (1893) and fell back to 12 species in the 1897 edition of Engler and Prantl's taxonomy. In 1927, Jeswiet (1927) listed three accepted species, *S. officinarum*, *S. spontaneum* and *S. sinense*, and to these he added a fourth, *S. barberi*, which included the cultivated Indian canes of that time. In 1928 a new form growing in the wild was discovered and was described as a new species, *S. robustum*, by Grassl (1946). Described by Hasskarl in 1842 (Whalen 1991), *S. edule* was included neither by Linnaeus (who was probably aware of Rhumphius' description of 1747) nor by Jeswiet (1927). When *S. edule* is included, it raises the number of *Saccharum* species to six, two of them wild species (*S. spontaneum* and *S. robustum*) and the remaining four cultivated (*S. barberi*, *S. edule*, *S. officinarum* and *S. sinense*). In a recent taxonomic evaluation of *Saccharum*, Whalen

(1991) recognized, as have others, the possibility that *S. edule* is a form of *S. robustum* and, if this were to become accepted, by the rules of priority both forms would be included under the older name, *S. edule*. Whalen also reduced, as had Brandes (Artschwager and Brandes 1958), the status of *S. barberi* to that of a horticultural variant of *S. sinense*.

Doubt has been expressed (Grassl 1946; Artschwager and Brandes 1958; Reveal et al 1989; Whalen 1991) as to the source of material for Linnaeus' description of *S. officinarum*. Grassl (1946) stated that no type specimens exist of *S. officinarum* and cited Munro Williams as reporting in 1862 that no sugarcane specimens were found in Linnaeus' herbaria. A more recent study (Reveal et al. 1989) reported that the specimen sheet in the Linnaean Herbarium labeled by Linnaeus as *Saccharum officinarum* is *Miscanthus floridulus*, a mysterious error. A second sheet in the collection contains an anomalous leaf together with a dried culm that is sugarcane but without the necessary flower for complete identification. A third sheet in the Linnaean herbarium in Stockholm is not annotated by Linnaeus and is of unknown provenance. The authors did not find specimens in the other Linnaean herbaria in Helsinki, Moscow, Uppsala or in the Bergius foundation of Stockholm. Lacking a type specimen, the authors considered other collections and publications in which Linnaeus may have established synonymy; they noted that Linnaeus had found the illustration of sugarcane in Sloane's volume (Sloane 1707) to be excellent, and they recognized the synonymy with the illustrated sugarcane (lectotype) and maintained the traditional name and authority (Reveal et al. 1989).

Probably, neither Sloane in 1696 nor Linnaeus in 1753 would have seen the 'noble' or garden canes from the South Seas. According to historical records, the first of the noble canes left Tahiti with Bougainville in 1768, eventually arriving in the Caribbean in 1789 (Deerr 1921, 1949; Machado et al. 1987). Noble canes are those clones currently identified as *S. officinarum* and are characterized as having broad leaves, thick stems, high sugar and low fiber content, and originating in the Indonesian archipelago. The possibility was raised (Whalen 1991) that Linnaeus knew of the existence of sugarcane from the East Indies, having reported sugarcane in the Clifford herbarium in 1738. A recent search (Reveal et al. 1989) found no relevant specimens there. The probability is small that East Indian sugarcane served as the source for Linnaeus' description of *S. officinarum*. However, Hasskarl (cited in Whalen 1991) referred to a publication from 1747 by Rhumphius which includes a specimen that later would be classified as a plate of *S. edule* which is endemic to the East Indies.

The cane which both Linnaeus and Sloane saw was probably that which had been grown in southern Europe since 755 AD (Deerr 1949) and which Columbus introduced to the Caribbean on his second voyage in 1493. This was the cane which, after the introduction of the nobles, came to be called Creole, Criolla, or Crioula in French, Spanish and Portuguese, respectively. Deerr (1949) and Earle (1928) support the view that Creole originated in India and migrated westward to Persia, Arabia, Egypt and the western Mediterranean. Separate introductions to the New World were made by the Spaniards from the Canary Islands to the Caribbean and by the Portuguese from Madeira to Brazil (Machado et al. 1987). While historians suggest that Creole was the first variety in the Western Hemisphere, multiple introductions and Deerr's observation that there were three color variants in Morocco before Columbus' first voyage provide a small doubt that early cane culture in the West was based on a single variety.

Earle (1928) states that, in the Americas, Creole was quickly replaced in cultivation by the noble Otaheite, when it was brought to Jamaica from Tahiti by Bligh in 1791. Earle described Creole, presumably based on garden canes in Puerto Rico, a century after its abandonment by commercial growers. Artschwager and Brandes (1958), in their comprehensive description of 334 noble clones, did not include a detailed description of Creole, saying "The clone gradually disappeared from extensive cultivation between 100 and 150 years ago" (Artschwager and Brandes 1958). (Not all of Artschwager's descriptions were published, and some were edited by I.E. Stokes and deposited in the National Agriculture Library, Beltsville, MD, USA.) The authors cite the drawings and description of Fleischmann (1848) presenting Creole as – "a short, relatively thick-stemmed, greenish-yellow cane with erect leaves." The authors authenticated their own collections of Creole from Spain and the Dominican Republic by means of Fleischmann's drawings; however, these accessions were destroyed because of mosaic infection (specimens of Creole are not listed for the ISSCT collections in Miami, Florida, USA, nor in Cannanore, India). Artschwager's and Brandes' (1958) description of Creole was probably based more on these importations than on Fleischmann's description (Fleischmann 1848, from Brandes' library). Artschwager and Brandes (1958) further describe Creole as an – "odd sterile hybrid type with $2n = 81$ chromosomes." There is no reference to the source of this observation, and circumstantial evidence (the probable lack of the clone in the Florida collection) suggests that it is not an original observation. Brandes recognized the possibility that Linnaeus used Creole as the type specimen for *S. officinarum*, but does not call Creole a noble cane, mentioning instead confusion regarding its identity and synonymy (Artschwager and Brandes 1958).

Bremer (1929, 1932) is the probable source of Brandes' chromosome number for Creole. Bremer (1961) cites Deerr saying that Creole, Puri and Yellow Egyptian are synonymous and that the Yellow Egyptian in the Javan collection had $2n = 81$ chromosomes and the mitotic figures had a fragment of nuclear membrane which Bremer found typical of Indian canes. Bremer's claim that the Yellow Egyptian in the Javan collection was the same as Creole cannot be substantiated since the ISSCT world collection in Miami lacks Creole and Yellow Egyptian but has Creoula and Puri. The Puri at Miami is clearly an *S. barberi* clone and Creoula there matches neither Artschwager's description nor the Creoula in the Copersucar (Brazil) collection. The accession in the Copersucar collection listed as Creoula (equals Crioula, Earle 1928) is still grown as a garden cane in Bahia. Creoula had been cultivated as late as 1926 (584 ha) in the state of São Paulo (Machado et al. 1987). The morphology matches that described by Artschwager (Artschwager and Brandes 1958) for Creoula and is similar to the description of Earle (1928) and Fleischmann (1848) for Creole, and very much resembles Plate 1 in Deerr's "Cane Sugar", 1921 edition (Deerr 1921). The specimen used for the plate was obtained from Dr. F. S. Earle in Puerto Rico in 1920.

Brandes (Artschwager and Brandes 1958), Bremer (1929, 1932), Deerr (1921, 1949) and Earle (1928) imply a closer relationship of Creole with the Indian canes than with the noble canes from Southeast Asia. Brandes hypothesized that the noble canes could have been carried by humans in the last 10 millennia from New Guinea to India, where it could have hybridized with *S. spontaneum* to produce the *S. barberi* – *S. sinense* group. Whalen (1991) discards this hypothesis for the evolution (selection) of the cultivated Indian and Chinese forms from *S. spontaneum*, but the presence of noble varieties in the gardens of southeast Asia at least up to the 24th parallel supports Brandes' theory.

Characterization of *Saccharum* species

Species are defined differently in different sources. General dictionaries define a species as a number of animals or plants with a high degree of similarity; the members of which interbreed among themselves and show persistent difference from members of other species. A genetic definition would have a species be a reproductively isolated breeding population while a taxonomic definition of a species would be a phenotypically distinctive group of co-existing individuals (King and Stansfield 1985).

The species of *Saccharum* accepted by sugarcane technologists are interfertile, producing vigorous hybrids which are the mainstay of the modern cane sugar industry. *S. officinarum* was first crossed with *S. spontaneum* over a century ago and the progeny led to varieties with new levels of vigor and disease resistance. Virtually all modern cultivars are interspecific hybrids which have these species as parents. *S. barberi*, *S. robustum* and *S. sinense* are listed as ancestors in some cultivars, but *S. edule* is not.

Characteristics used to separate species of *Saccharum* include floral parts, sugar content, chromosome numbers and hair groups. The floral characteristics used include the presence or absence of long hairs on the main axes, spikelets with both lemmas present or absent, sequence of flowering in the floret pairs, lodicules ciliate or not and glumes 2- or 4-ribbed (Jeswiet 1927; Earle 1928; Artschwager and Brandes 1958; Kandasami et al. 1983; Whalen 1991). Jeswiet's key (1927) to the species of *Saccharum* uses floral characteristics to separate *S. officinarum* from the other species. The primary character is that of the paired florets, the sessile floret opens before the pedicellated one. Brandes' (Artschwager and Brandes 1958) amendment to Jeswiet's key uses these same characteristics as an umbrella for three species, separating *S. robustum* from the others by its being wild and having a high fiber and a low sugar content. Recent keys (Whalen 1991) use the prior opening of the sessile floret as characteristic of *S. officinarum* and *S. robustum*, and prior opening of the pedicellate floret as characteristic of *S. spontaneum* and *S. sinense*, with the caveat that in all four the florets may open simultaneously. Scientists at Coimbatore found that the prior opening of the sessile floret is maternally inherited in crosses with *S. officinarum* × *S. spontaneum*, and removed four questionable accessions in the world collection from *S. officinarum* by crossing them with *S. spontaneum* and noting prior opening of pedicellate florets in the progeny (Kandasami et al. 1983).

While taxonomists emphasize floral characteristics under the Linnaean system, their use in distinguishing the six species of *Saccharum* is sometimes questionable. There are forms of *S. barberi*, *S. officinarum* and *S. sinense* that do not flower and, by definition, none of the forms of *S. edule* reach anthesis. These non-flowering forms have been assigned to species by vegetative characteristics. The flowering sequence of florets is sometimes unreliable since simultaneous flowering sometimes occurs in all *Saccharum* species. Intergrades in the hairiness of floral axes are common and this character may be useful only when the extremes are expressed.

The use of sugar content as a species characteristic is of no value due to the wide variation in all species and the strong genotype and environmental interaction. A widely used estimate of sugar content, Brix, measures soluble solids including sugars, other organic compounds and salts. In the wild species, *S. spontaneum* and *S. robustum*, Brix measurements as low as 3.0 and 0.8 respectively have been observed (Kandasami et al 1983 b; Ramana Rao et al. 1985, and unpublished data). Brix values as low as these have not been reported in the other *Saccharum* species or their interspecific hybrid cultivars. However, clones of both *S. spontaneum* and *S. robustum* have also been described with surprisingly high Brix values. Figure 1 shows the range of Brix values reported (Kandasami et al. 1983 b;

Ramana Rao et al. 1985; Sreenivasan and Nair 1991; GRIN and unpublished data) for five species of *Saccharum*; the overlapping values between the two wild species and the cultivated ones are striking. I could find no data for Brix in *S. edule*, but published data for sucrose in five clones (Ramana Rao et al. 1985) suggests that Brix values would fall at the low end of the range for *S. robustum*. The most significant conclusion drawn from Fig. 1 is that a broad overlap exists in the ranges of Brix for the five groups, suggesting that sugar content is not a reliable characteristic for separating species of *Saccharum*. Brix values in *S. officinarum* overlap all other groups in Fig. 1, and over one third of its range overlaps that of *S. spontaneum*, a species commonly regarded as lacking sugar.

The Brix values for the smaller populations of *S. barberi* and *S. sinense* extend below the range of *S. officinarum* but are otherwise similar. Roach and Daniels (1987), reviewing the origin of sugarcane, noted that the proposals to designate *S. barberi* and *S. sinense* as horticultural groups had not been accepted. Jeswiet (1927) found no consistent floral characters that separated these species but, in order to separate them, he used highly variable vegetative characters (height, leaf width, internode shape and stalk color). Naidu and Sreenivasan (1987) lament the pending extinction of these forms, saying that they now exist only in collections. As will be discussed later, these two forms, like modern varieties, are hybrids of *S. officinarum* and *S. spontaneum.*

Arguing from the position that *S. officinarum* and *S. robustum* represent distinct populations, this overlap in sugar content demands explanation. One possibility is that the clones of *S. robustum* in the upper Brix range and clones of *S. officinarum* in the lower range are either misidentified or are natural hybrids between the two species. A second explanation is that the two groups, which occupied a restricted geographic area, represent a segregating natural population with clones of *S. officinarum* having been selected, propagated and protected by natives. This is compatible with *S. robustum* as the ancestral form of *S. officinarum* (Artschwager and Brandes 1958), the latter arising through a genetic change which caused photosynthate destined for growth and fiber to be stored as sugar. If the changes occurred more than once they could explain populations variable in both Brix, fiber, and morphological characteristics.

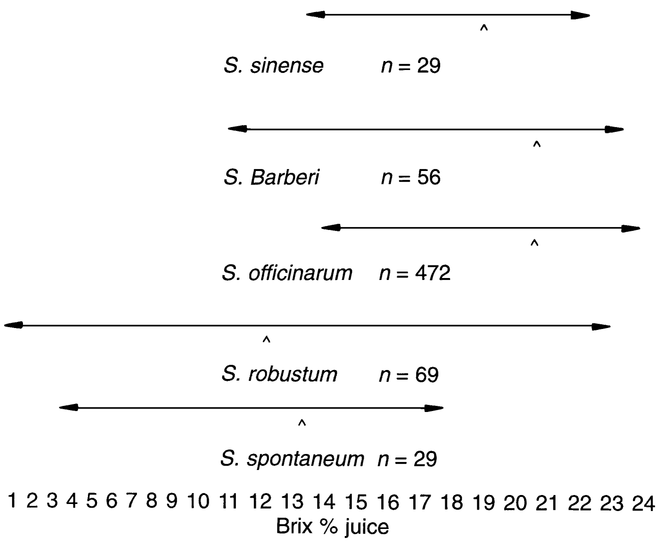

Fig. 1 Range and maximum frequency ( ) of Brix values in five species of *Saccharum*: n = number of accessions measured (data from 23, 28, 34, GRIN and unpublished data)

Data from ten sources on chromosome numbers among *Saccharum* species are compared in Table 1, with the species designations used by sugarcane technologists. A glance at the table reveals the great diversity in chromosome numbers in *Saccharum*, with a range of $2n = 36$ to 170. The greatest ranges are found in the two wild species, *S. spontaneum* ($2n = 36$–128) and *S. robustum* ($2n = 60$–170). Among the cultivated forms, chromosome numbers of *S. officinarum* ($2n = 70$–140) range the widest, but 92% of its chromosome counts are $2n = 80$, suggesting that the New Guinea/Irian Jaya aborigines, in selecting high sugar and low fiber canes for their gardens, also inadvertently selected for clones with $2n = 80$ chromosome numbers. So striking is the high percentage of $2n = 80$ in *S. officinarum* that some technologists believe that the number is characteristic of the species and that clones with other numbers are hybrids with other taxa. To exclude noble clones with chromosome numbers other than 80 would require that chromosome number be the primary taxonomic criterion for this species. (Clones of *S. officinarum* that did not fit its botanical description as reported by Kandasami et al. 1983 a are not included in Table 1.)

In addition to *S. officinarum*'s high frequency of $2n = 80$ counts, this count also occurs in *S. spontaneum*, *S. robustum* and *S. edule*, suggesting an evolutionary link. This would support the basic number of either $x = 8$ or $x = 10$ for *Saccharum* as proposed by Whalen (1991), but there is no obvious series involving multiples of ten in any of the species. However, there is a series involving multiples of eight in *S. spontaneum.* With no diploid, triploid or tetraploid counts reported there is, in Table 1, a series including $2n = 40$, 48, 56, 64, 72, 80, 88, 96, 112, 120 and 128 which accounts for 77% of the data reported for this species in Table 1 and suggests a polyploid series with a basic number of $x = 8$. Da Silva et al. (1993), identified eight homologous groups in a study of progeny derived from a cross of *S. spontaneum* ($2n = 64$) with a haploid of itself. Their RFLP data produced 44 linkage groups and 29 of these (DaSilva et al. 1993) were placed on eight putative homologous chromosomes. They also showed that *S. spontaneum* is an autopolyploid. Whalen (1991) recognized the possibility of a series with a basic number of

Table 1 Distribution of 2n chromosome numbers in *Saccharum*[a]

2n	*S. spontaneum*	*S. robustum*	*S. edule*	*S. officinarum*	*S. barberi*	*S. sinense*
36	1					
40	3					
48	6					
50	2					
51	1					
52	2					
54	29					
56	10					
58	2					
60	36		21		1	
60–64			1		1	
62	1					
63	2					
64	172					
66–70		1				
68–70		1				
70		1	15	1		
70–72	7	1				
70–76			1			
72	6					
73		1				
74			1			
74–76				1		
78	1					
78–80				2		
79–80				3		
80	86	34	6	459		
80–81				1		
80–82			1	1		
81	1			1		
82				1	9	
82–83					2	
82–84				1		
83					3	
83–85		1				
84		1	1			
84–86		1				
84–88			1			
85				1		
86–92		2				
88	1	2				
90	1	2	1	1		
90–94			1			
90–100		1				
91					1	
91–92					2	
92		2		1	2	
92–94				1		
95		1				
96	10					
97–98		1				
97–117				1		
98		1		1		
98–100		1		1		
99–102				1		
100		7		1		
101		1				
103–110		1				
104				1		1
105	1					
105–107	1					
106–108				1		
107					1	
107–114				1		
108					1	
108–110		1				

Table 1 Continued

2n	*S. spontaneum*	*S. robustum*	*S. edule*	*S. officinarum*	*S. barberi*	*S. sinense*
109						1
110		2				4
110–112				1		
111					1	1
112	9			4		
112–116						1
113	1					2
114				2		1
114–116						1
114–128						1
115						1
115–116				1		
116				4	1	6
116–118		1				2
116–119						1
116–122			1			
117						8
117–118						1
118–120						1
118–124						1
119					1	
120	3			1		
120–122						1
121					1	
122–128						1
124					2	1
124–128	1					
126	1					
128	1					
140		1			1	
156–157		1				
162		1				
163–164		1				
164–165		1				
170		1				
Total	398	96	31	497	27	37

[a] Data from Artschwager (1948), Bremer (1929), Grassl (1946), Jeswiet (1927), Kandasami et al. (1983 b), Ramana Rao et al. (1985), Roach (1972), Sreenivasan and Nair (1991), Sreenivasan and Sreenivasan (1994) and unpublished data from the records of the Hawaiian Sugar Planters Association furnished by P.H. Moore

n = 8, but found it rare (among Andropogoneae) and favored $x = 10$ for *Saccharum.*

Assuming *S. spontaneum* to be the ancestral form, one might expect the most common chromosome number in the series to be significant in the evolution of the genus. However, while 43% of the counts for *S. spontaneum* listed in Table 1 are of 2n = 64 chromosomes, there are none reported as 2n = 64 from the other five species. The second most frequent count in *S. spontaneum* is 2n = 80 with 22% of the total, and this count is found in 15% of *S. robustum*, 19% of *S. edule* and 92% of *S. officinarum*, suggesting an evolutionary progression. The place of the *S. sinense–S. barberi* group is equivocal since there are no 2n = 80 counts reported for these forms, and within themselves the *S. barberi* clones have lower numbers than most of the *S. sinense* clones with 78% of the *S. barberi* below 2n = 110 and 95% of the *S. sinense* higher. The wide variation in chromosome numbers in the wild species of *Saccharum* and somewhat less variation in the cultivated species suggests that the cultivated groups were subject to selection pressures that damped the variability in numbers. Bremer (1929, 1932), who wrote in the early days of sugarcane cytology, focused on the frequency of 2n = 80 clones in *S. officinarum* and concluded that all members of the species had that number of chromosomes. However, he had far fewer *S. officinarum* clones to study than did later cytologists. His rigid classification was perhaps based on his notion that only germ cells with n = 40 were viable (Bremer 1932). Probably because he categorized *S. robustum* as having 80 chromosomes, he felt comfortable in saying – "there is no compelling reason for not regarding it (*S. robustum*) as a sub-species of *S. officinarum*" (Bremer 1961). His argument seems a case of special pleading considering the variations noted in Table 1. If chromosome number were used for species identification, the wild *Saccharum* canes would be sorted into continuous arrays of new species, and the *S. sinense–S. barberi* group would be badly splintered. It seems illogical to apply a standard to one species and not to the others in the genus.

The epidermal hair groups studied by Jeswiet (1927) and Artschwager (1948) have been used to identify clones and to separate species in taxonomic keys (Jeswiet 1927; Artschwager 1948; Whalen 1991). Hair group 67, which occurs on the leaf blade, is characteristic of *S. edule* and *S. robustum* (Artschwager 1948). However, not all clones of these species have hair group 67, and it has also appeared in interspecific hybrid cultivars in Brazil. Crosses with these made at Copersucar's Camamu station in Bahia showed a 1:1 F_1 segregation, reinforcing the simple inheritance suggested by Artschwager (1948). However, morphological characters of the vegetative plants are affected by environment and age of plant, and would be weak characteristics for species identity (Gallacher 1997).

Resolving the dilemma

Viewing the uncertainties described above and the use of highly variable characters to describe species, we must ask how interbreeding groups of *Saccharum* should be classified. Brandes (Artschwager and Brandes 1958) suggests that *S. edule*, *S. officinarum* and *S. robustum* are closely related, with *S. robustum* the progenitor of the other two. The question is whether these three forms merit species rank on the basis of physiological characteristics.

Technologists at the Sugarcane Breeding Institute, Coimbatore, India, say that forms classified as *S. edule* at Cannanore sometimes flower when moved from Cannanore to Coimbatore, and some forms may produce an inflorescence when treated with gibberellic acid. This would change species status by manipulating the physiological response. It is odd to give species rank to a group that cannot produce sexual progeny and participate in a gene pool, and we should consider *S. edule* an aberration rather than a species. *S. officinarum* can be separated from *S. edule* by having a normal flower, low fiber and high sucrose. *S. edule* is described as having an aborted inflorescence, more or less pubescent leaf blades (hair group 67) and low sucrose (Artschwager 1948). Roach and Daniels (1987) suggest that *S. edule* is a complex group with 60, 70 or 80 chromosomes and some aneuploidy, with possible parental forms being *S. robustum*, *S. officinarum* and *Miscanthus* sp. The hair group is described by Artschwager (1948) as a trait encountered in *S. robustum* and is probably of simple inheritance. The trait is found in other unrelated taxa. Several authors (Artschwager 1948; Artschwager and Brandes 1958; Whalen 1991) have suggested that *S. edule* is derived from *S. robustum* and Brandes notes that the latter produces rhizomes in its natural riverbank habitat.

Sucrose and fiber contents have been used to separate *S. robustum* and *S. officinarum*. Brandes (Artschwager and Brandes 1958) suggests that only the intergrades will present difficulties in separating *S. robustum* from *S. officinarum* and he presumably wrote about the putative hybrids between these two species that were collected during the 1928 expedition (Artschwager and Brandes 1958). The data presented in Fig. 1 show that there is a wide range of sugar (Brix) content in both species, with considerable overlap. Characteristics that can be modified by cultural practices or physiological manipulation produce a broad range of phenotypic expression, and sucrose concentration is governed by multiple genes strongly affected by environmental interaction. These characters should not be used to support species status for the four species that only exist in cultivation. Lumping these four into one species would make sense, and Brandes (Artschwager and Brandes 1958) stated that "A more factual systematic treatment would be to exclude from the genus as species all but *S. spontaneum* and *S. robustum* (both wild ancestral forms) and recognize the others as horticultural classes."

Of the six species of *Saccharum*, *S. edule* cannot meet the requirement that individuals of the species breed among themselves. *Saccharum sinense* and *S. barberi*, both horticultural forms with a common origin in India (Earle 1928; Deerr 1949), differ enough to be distinct (Glaszmann et al. 1990) but not enough to be classified as separate species (Whalen 1991). *S. officinarum* and *S. robustum* are closely related in morphology, cytology and physiology, differing primarily in fiber and sugar content. With the exception of *S. edule*, these species will cross among themselves and with *S. spontaneum*, forming a large interfertile group that has been exploited by breeders for over 100 years. These interrelationships suggest that the six species should be lumped into one, with each group given sub-specific rank or less. This would conform to the broad biological definition of a species, that is, a population whose members interbreed and show persistent differences from others.

Rather than lumping the six into one species, there may be merit in recognizing two species, both described by Linnaeus and suggested by Brandes (Artschwager and Brandes 1958). The first of these is the putative ancestral form, *S. spontaneum* L., which has a very wide natural range and is morphologically distinct from other *Saccharum* forms. Cytoplasmic DNA sequences in *S. spontaneum* differ from the other forms; chloroplasts (Sobral et al. 1994), mitochondria (D'Hont et al. 1993), and ribosomal DNA (Glaszmann et al. 1990) from *S. spontaneum* differ in base-pair sequences from those of *S. officinarum*, *S. robustum* and *S. sinense–S. barberi*, and these four are indistinguishable from each other.

Cluster and principal component analyses of restriction fragment length polymorphisms of nuclear DNA indicate wide genetic differences between *S. spontaneum* and the other groups (Burnquist 1991; Moore and Irvine 1991). Burnquist's dendrogram shows the genetic distances among 125 clones representing *Erianthus* sp., five of the six species of *Saccharum* and a range of interspecific hybrids from ten breeding programs in seven countries. The dendrogram lends itself to be broken into four distinct groups. The first group is composed entirely of five *Erianthus* clones, and this group is well distanced from all others. The second group is composed solely of 12 clones of *S. spontaneum* representing 86% of *S. spontaneum* clones in the total sample. The third group is a mixture having two clones of *S. spontaneum*, two of hybrids between *S. barberi* × *S. spontaneum*, two of *S. barberi*, four of *S. sinense* and one of *S. officinarum*. The fourth and largest group has 86 clones of which 19 are *S. officinarum* (96%) and 67 interspecific hybrids (100%), all having *S. officinarum* as an ancestral female parent. The dendrogram clearly separated groups based on genetic distance, with *Erianthus* and *S. spontaneum* the more distant and *S. officinarum* and its hybrids more close. These data and the fact that all taxa used are interfertile show that they share a common gene pool.

The basic number of chromosomes for *S. spontaneum* has been established as $x = 8$ (Da Silva et al. 1993), while a case can be made for $x = 10$ (Al-Janabi et al. 1994) as the basic number for *S. officinarum*. An anther-derived *S. spontaneum* clone ($2n = 32$) was found to have four satellite chromosomes and four nearly identical chromosomes suggesting a tetraploid with a basic number of $x = 8$ (P. Moore, personal communication). *S. spontaneum* has chromosomes which usually fail to pair with those of *S. officinarum* in interspecific hybridization (Bremer 1929, 1932, 1961) and the $2n + n$ pairing behavior of the chromosomes which results does not occur when *S. officinarum* is crossed with the other *Saccharum* species (Bremer 1961) or with commercial hybrids (Burner and Legendre 1993). The gametes are usually an unreduced female and a reduced male gamete. Pairing in crosses of *S. officinarum* × *S. spontaneum* is autosyndetic and usually as bivalents, and intergeneric crosses in the Saccharinae, with or without *Saccharum*, produce gametes that are $n = n$, $2n + n$ and $2n = 2n$ (Gill and Grassl 1986).

Working with an interspecific commercial hybrid, R570, D'Hont et al (1996) showed that 10% of the chromosomes from the two species pair, and a few have segments of chromosomes of both parents as shown by fluorescent in-situ hybridization analyses (FISH). Recent work (D'Hont, personal communication), using FISH analyses and the probes for identifying the chromosomes of *S. officinarum* and *S. spontaneum*, showed that *S. sinense* has chromosomes from both species. The ancient and modern sugarcane varieties used in sugar production may be hybrids of the same ancestors, as was suggested by Brandes (Artschwager and Brandes 1958). Cases of preferential pairing were also noted (D'Hont et al. 1996) in the *S. spontaneum* chromosomes in R570 but were mentioned as absent in *S. spontaneum* by others (DaSilva et al. 1993; Moore 1996; R. Ming, personal communication) but present in *S. officinarum* and *S. robustum* (Al-Janabi et al. 1994; R. Ming, personal communication). In *S. officinarum* ($2n = 80$), multicolor in-situ hybridization with ribosomal gene probes gave eight simultaneous hybridization sites, indicating a basic number of $x = 10$ (P. Moore, personal communication).

Phenotypic, cytological, and molecular marker analyses suggest that the autopolyploid, *S. spontaneum*, differs from the other *Saccharum* species and hybrids sufficiently to retain species rank. Further advances in molecular genetics may reveal that the other wild species, *S. robustum*, together with the land races *S. officinarum*, *S. edule*, *S. barberi* and *S. sinense*, belong together in one species to which nomenclatural priority may assign the name *Saccharum officinarum*.

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