



# A Review of Recent Molecular Genetics Evidence for Sugarcane Evolution and Domestication

Laurent Grivet, C. Daniels, J.C. Glaszmann, and A. D'Hont

## Abstract

In 1987, J. Daniels and B. T. Roach published an exhaustive multidisciplinary review of evidence permitting the domestication and the early evolution of sugarcane to be traced. We try here to synthesize the new data that have been produced since, and their contribution to the understanding of the global picture. It is now highly probable that sugarcane evolved from a specific lineage restricted to current genus *Saccharum* and independent from lineages that conducted to genera *Miscanthus* and *Erianthus*. The scenario established by E. W. Brandes in 1958 is very likely the right one: Noble cultivars (ie. *Saccharum officinarum*) arose from *S. robustum* in New Guinea. Humans then spread these cultigens over large distances. In mainland Asia, natural hybridization with *S. spontaneum* occurred, and gave rise to the North Indian (*S. barberi*) and Chinese (*S. sinense*) cultivars. Relationships between *S. spontaneum* and *S. robustum* in situations of sympatry are still not well understood.

## Introduction

Sugarcane is an important crop plant cultivated throughout the world for its sugar-rich stalks. The Western world first learnt of the existence of this plant during Alexander the Great's conquests about two millennia ago. Since then historians have traced its extension towards North Africa, Europe and to the Americas through documentary evidence. What occurred before, that is, the evolutionary process that led to wild ancestors of sugarcane, and the domestication of those wild ancestors remained obscure until recently, and has been actively debated.

Like many tropical plants that are consumed for their vegetative organs, few remnants of sugarcane have been reported from archeological contexts. Moreover, distinction between wild and cultivated plant artifacts are problematic. Most information has therefore come from

living wild and cultivated sugarcane plants and from written history and linguistic evidence for relatively recent events. In 1987, J. Daniels and B. T. Roach published a comprehensive review of hypotheses and arguments regarding sugarcane evolution and domestication, based on the available botanical, genetic and historical evidence. Since then, new data, particularly in the field of molecular genetics, have made it possible to reconsider evolution and domestication of sugarcane.

## State of the Art

### Relevant germplasm

From a practical point of view, sugarcane genetic resources can be divided into three groups: (1) traditional cultivars, (2) wild relatives, and (3) modern cultivars.

Traditional cultivars have almost disappeared from cultivation but remain important as progenitors of modern cultivars and as potential sources of traits for future breeding. Historically, they descend in straight line from

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primary domesticates. They are clones propagated by stem cuttings. They can be divided into two groups:

- The Noble cultivars. These generally have a chromosome number of  $2n=80$  and brightly colored thick stalks, rich in sugar. They are still used in traditional agriculture, especially in Melanesia. The highest diversity is undeniably in the island of New Guinea. The term 'Noble' was given by the first Dutch breeders in Java. Those clones are formally designated by the species binomial *S. officinarum* L.
- The North Indian and Chinese cultivars. These generally have thinner stalks and leaves, flatter colors and lower sugar content than Nobles, a chromosome number  $> 80$  and a better adaptation to sub-tropical environments. They were formerly cultivated in mainland Asia, especially North India and South China, which are probably also where sugar-making industries were born. Nowadays, they are confined to germplasm collections. Five morpho-cytological groups have been described, Mungo, Sarethia, Nargori, Sunnabile and Pansahi (Barber, 1922). The binomial *S. barberi* Jesw. usually refers to the first four groups, endemic to India. The fifth group is either included in *S. barberi* or referred to as *S. sinense* Roxb. It was common in China, and was introduced to India at the close of the 18th century.

A vegetable currently eaten in Melanesia is morphologically similar to sugarcane. It is cultivated for its edible aborted inflorescence and has no sugar content. Vernacular designations vary from island to island: It is for example 'naviso' in Vanuatu and 'pitpit' in New Guinea. We will use the name 'naviso' since 'pitpit' is also used to designate others plants, which may be confusing. The botanical designation of this cultigen is *S. edule* Hassk.

Wild plants related to traditional sugarcane cultivars and potentially included among their progenitors have been assembled into an informal taxonomical group, the 'Saccharum complex', first defined by Mukerjee (1957) and further extended by Daniels et al. (1975b). This includes:

- *S. spontaneum* L., a species presenting diverse morphologies and ecological adaptations. Stalks are usually thin and their sugar content is very low. *S. spontaneum* has a wide distribution range covering some Pacific islands, Melanesia, Tropical Asia, the Middle East and part of Africa (Panje and Babu, 1960). Chromosome complements vary between  $2n=40$  and  $2n=128$ , the multiple of eight being more frequent.
- *S. robustum* Brandes and Jeswiet ex Grassl, a species presenting usually long, thick stalks with little or no sugar. Its distribution extends from Kalimantan (where it is rare), to Sulawesi, New Guinea and associated Melanesian islands. Chromosome number vary, but two cytotypes predominate ( $2n=60$  and  $2n=80$ ).

- Species from the genera *Erianthus*, *Miscanthus*, *Sclerostachya* and *Narenga*. These genera have wide distribution ranges, from Himalaya to Melanesia, and for some, as far as the Pacific islands or Siberia. They generally have no sugar content and stalk morphology is variable depending on species. A particularly high concentration of species from these genera is encountered in the Northeast of the Indian sub-continent (Panje, 1953).

Modern cultivars have progressively replaced traditional cultivars during the 20th century. Most of the former were produced by artificial crosses between traditional cultivars and *S. spontaneum* clones, followed by several generations of clonal selection. The production of sugar has increased so much thanks to plant breeding, that traditional cultivars are now most often considered as relics and their use has become very limited as planting material and as progenitors in current selection programs. As modern cultivars have well-known and very recent origins, they are not useful for investigating the origins and domestication of sugarcane and are not considered further here.

#### Scenarios for domestication

Daniels and Roach (1987) reviewed hypotheses proposed in the last century concerning geography and process of sugarcane domestication. The most popular scenario has been the one developed by E. W. Brandes: Noble cultivars were domesticated from *S. robustum* in New Guinea and were then dispersed in the Pacific and mainland Asia during human migrations. In mainland Asia they hybridized with local *S. spontaneum* giving rise to North Indian and Chinese cultivars (Brandes, 1958).

The direct emergence of Noble cultivars from *S. robustum* is now generally accepted and it has been hypothesized that *S. robustum* was the result of complex introgressions between *S. spontaneum* and other genera, particularly *Erianthus* and *Miscanthus* (Daniels et al., 1978; Daniels and Roach, 1987). The emergence of Noble cultivars from a wild species other than *S. robustum* was considered a minor hypothesis. In this scenario, *S. robustum* populations may be secondary hybrids formed by crosses between Noble clones and wild related genera (Daniels and Roach, 1987).

Alternative scenarios for the emergence of the North Indian cultivars have been proposed. The first one is a direct selection from *S. spontaneum*, for at least some of the forms, particularly the Sarethia group. The second one is hybridization between *S. officinarum* and a species of the genus *Erianthus*, most probably *E. elephantinus*, which is confined to the foothills of Assam and Nepal (Daniels and Roach, 1987). Parallel scenarios have been proposed for the emergence of Chinese cultivars, with either a de novo selection from unknown local wild species (Daniels and

Daniels, 1993) or an alternative hybrid origin involving *S. officinarum* and *Miscanthus sacchariflorus* as wild progenitor, instead of *S. spontaneum* (Grassl, 1964).

**Naviso** is suspected to have emerged as a mutant within *S. robustum* or through interspecific hybridization between *S. robustum* and another species (Daniels and Roach, 1987).

## The Evolutionary Path Leading to Sugarcane

Molecular data that clarify relationships between cultivated sugarcane and wild related species have been accumulating in the last ten years or so. The data generally do not support an evolutionary path through distant crosses involving representatives of several genera. Current living species of the genera *Saccharum*, *Erianthus* and *Miscanthus* are clearly distinct in analyses of molecular variation in different sequence type and genome compartments. The nuclear genome has provided the greatest diversity of sequence types for analysis: low copy number sequences (Glaszmann et al., 1989; Lu et al., 1994), ribosomal RNA genes (Glaszmann et al., 1990) and repeated non-coding DNA (D'Hont et al., 1995). Mitochondrial and chloroplast genomes have also been analyzed (D'Hont et al., 1993). Most of those studies were conducted with few representatives of genera other than *Saccharum*. However, the Southern hybridization of repeated Alu-like and Satellite elements specific from the nuclear genome of *Erianthus* and *Miscanthus* did not show any trace of those genomes in any representative of *Saccharum* (Alix et al., 1998; Alix et al., 1999). Finally, an extensive survey of diversity in *Erianthus* was carried out with nuclear low copy-number DNA. This showed that *Erianthus* is probably monophyletic and highly divergent from genus *Saccharum* (Besse et al., 1997).

Recent genetic data support the existing view of genus *Saccharum* as a well-defined lineage that include cultivated sugarcane plus two wild species, *S. spontaneum* and *S. robustum*. This lineage diverged from other lineages, such as those leading to the genera *Erianthus* and *Miscanthus*, over a long course of evolution. The implication of this is that cultivated sugarcane very likely emerged from wild *Saccharum* species, and secondary introgressions with other genera are not likely pathways.

This, however, does not mean that inter-generic hybridizations are impossible in the wild and may not account for some local peculiarities. Giant fencing clones of *S. robustum* from New Guinea highlands with high chromosome numbers, and clones of **naviso** (*S. edule*) are candidates for derivation from inter-generic hybridization. This suggestion can be easily checked with molecular markers.

Restriction fragment analysis of the chloroplast genome (Sobral et al., 1994) as well as sequencing data for nuclear satellite DNA (Alix et al., 1998) and hybridization intensity signal with genus-specific Alu-like elements (Alix et al., 1999) indicate that *Saccharum* is likely more closely related to *Miscanthus* than to *Erianthus*.

The concept of a '*Saccharum* complex' may have contributed to an overestimation of the contribution of other genera to the emergence of cultivated sugarcane. This concept was first developed based on geo-botanical considerations (Mukherjee, 1957; Daniels et al., 1975b) and later received the apparent support from analysis of leaf flavonoids (pigments). However morphological traits and flavonoids can be misleading when they are used as single diagnostic markers, especially in polyploid species. They provide few independent tests of genetic variation and their genetic determinants are unknown, although possibly polygenic and complexly regulated. For example, the flavone C-glycoside compound F13, which is assumed to be diagnostic for *Erianthus*, occasionally appeared in the progenies of crosses *S. officinarum* x *S. spontaneum*, although it was not transmitted by the parents (Williams et al., 1974). Such a marker should be used cautiously because introgression may not always be distinguishable from homoplasmy or artifacts. Similar caution should be taken with morphological characters when they are used as diagnostic markers. In the past, morphology has often been misleading in the interpretation of the results of artificial inter-generic crosses, especially those involving *Saccharum* and *Erianthus* (D'Hont et al 1995; Piperidis et al., 2000).

## Origin of Noble Cultivars

### The genus *Saccharum* is bipolar

Two wild species are included in the genus *Saccharum*: *S. spontaneum* and *S. robustum*. Morphologically, *S. robustum* is distinguished from *S. spontaneum* by the "lack of rhizomes, larger inflorescence, smaller spikelet structures, greater thickness of stalk, and greater height" (Daniels and Roach, 1987). These differences are essentially quantitative. However, when allopatric samples are considered, *S. spontaneum* and *S. robustum* have been clearly differentiated in all molecular tests used so far. There is thus some genetic support for the taxonomic bipartition. Indeed, *S. spontaneum* collections from India and Southeast Asia (regions where *S. robustum* is absent), are strongly differentiated from *S. robustum* with nuclear low copy DNA revealed by RFLP (Lu et al, 1994) and mitochondrial DNA (D'Hont et al., 1993), and to a lesser extent, with the differential hybridization intensity of a repeated and dispersed nuclear element, SoCIR1 (Alix et al., 1998) and ribosomal RNA (Glaszmann et al, 1990). Moreover, the basic chromosome numbers are different in *S. spontaneum* ( $x=8$ ) and *S. robustum* ( $x=10$ ). This was

established by physical mapping, using fluorescent in situ hybridization (FISH) of two families of tandemly repeated ribosomal RNAs (D'Hont et al., 1998).

Data from leaf flavonoid are also interesting to consider here, even if they should be interpreted cautiously, because they have been more extensively used than any other type of genetic descriptor. We assembled scoring data that could be found in the literature for *S. spontaneum* and *S. robustum* (Daniels et al., 1975b; Daniels et al., 1978; Daniels et al., 1980; Daniels et al., 1989) and treated them together through a multi-variate analysis. By limiting the investigation to closely related material we expected to limit the effect of homoplasy. By analyzing the frequency of compounds in populations, instead of their presence vs absence in individuals, we expected to limit the effect of individual peculiarities (Figure 1). This permitted us to show that a bipolar structuring of wild *Saccharum* accessions is observed like that for other molecular descriptors. The case of population 'Kalimantan', a set of wild clones collected through the island of Kalimantan, is interesting to consider here because its classification in *S. spontaneum* or *S. robustum* has been debated (Daniels et al., 1989). It is grouped here in the *S. spontaneum* pole. This is in line with the cytoplasmic pattern for two of these clones (D'Hont et al., 1993) and this also fits with the initial description as "atypical *S. spontaneum*" by collectors in the field (Berding and Koike, 1980).

#### **Sympatric *S. spontaneum* and *S. robustum***

Genetic distinctions between the two wild *Saccharum* species (*S. spontaneum* and *S. robustum*) are less clear in regions of sympatry, that is in the islands ranging from Borneo (Kalimantan) to New Britain. However, relevant data are still sparse. In New Guinea, field observations show that extreme types are still easily distinguished, but that variation in the two species overlap and some individuals present intermediate characteristics and are difficult to classify (Henty, 1969).

Recently, D'Hont et al. (1998) showed that *S. spontaneum* clones from New Guinea, with  $2n=80$  chromosomes, have a typical basic chromosome number of  $x=8$ , like *S. spontaneum* in other areas. However, they show just the same intensity of hybridization signal as *S. robustum* clones with the *S. officinarum* satellite element SoCIR1 (Alix et al., 1998). They appear more closely related to *S. robustum* than to any *S. spontaneum* clones with nuclear low copy DNA (Besse et al., 1997), and they transmit 'n' chromosomes when crossed with Noble cultivars, although a high proportion of '2n' gametes transmission is generally observed in crosses involving Noble cultivar and *S. spontaneum* (Daniels et al., 1975a).

Above data are heterogeneous but they suggest that at least some *S. spontaneum* populations, that are sympatric

with *S. robustum*, are genetically closer to this species than allopatric populations. The simplest interpretation is that the sympatry between those two clearly differentiated species is recent and permits genetic exchanges. A more unlikely interpretation would be that the bipolar organization of wild *Saccharum* germplasm is a somewhat simplistic image due to biases in samples analyzed to date with markers and that the reality is more complex. An extensive molecular study of *Saccharum* germplasm is still needed to settle once and for all.

#### **Noble cultivars and wild *Saccharum***

Several types of DNA sequence representing different genome compartments have been used to compare Noble cultivars and wild *Saccharum* accessions. In tests with mitochondrial genes, a single haplotype was detected among Noble clones (D'Hont et al. 1993). The same haplotype was the most frequent of two detected in *S. robustum*, and was different from all six haplotypes revealed in *S. spontaneum*.

With nuclear single copy DNA, Noble cultivars appear very close to *S. robustum*. Although the samples were distinct on the multi-variate representation, the average similarity between a Noble clone and a *S. robustum* clone is about the same as the average similarity between two *S. robustum* clones (Lu et al., 1994). The Noble clones used by Lu et al. (1994) appear representative, as can be judged from the comparison with additional clones from Indonesia and New Caledonia (Jannoo et al. 1999). In contrast, the *S. robustum* sample may not be fully representative, which may explain the small difference observed between Noble clones and *S. robustum*.

The basic chromosome number in Noble clones ( $x=10$ ) is the same as in *S. robustum* and is different in *S. spontaneum*, as was shown by physical mapping (D'Hont et al., 1998).

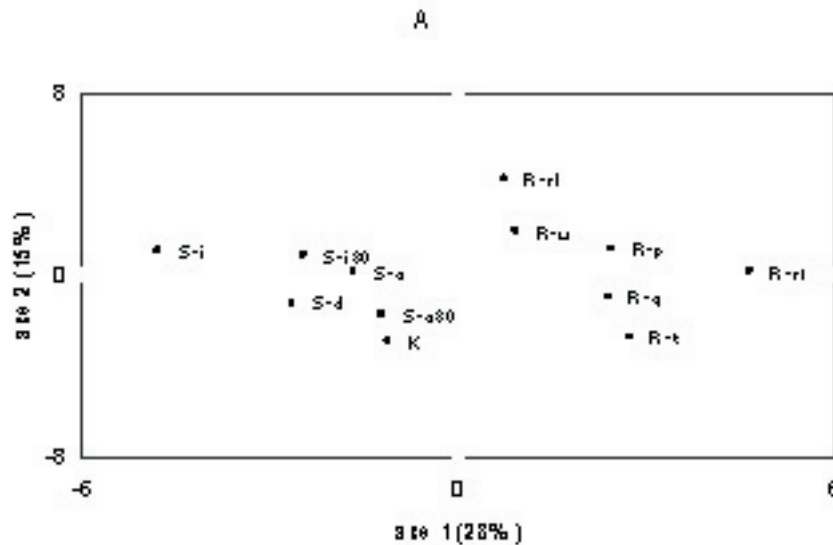
Leaf flavonoids were used to describe more clones than any other biochemical or molecular technique. With the cautious analyzes presented in Figure 1, they also show a close relationship between Noble clones and *S. robustum*. Thus multiple lines of molecular evidence support a direct descent of Noble clones from the wild species *S. robustum*. Direct selection from *S. spontaneum* in mainland Asia is excluded, as well as a descent via hybridization between *S. spontaneum* and other genera.

Some observations are not perfectly in line with the present conclusions, but are unlikely to alter them in any substantial way. A very small number of RFLP bands present in Noble clones were not detected in any tested wild *Saccharum*, and a sub-sample of these did occur in *Erianthus* or *Miscanthus* (Lu et al., 1994). This may indicate limited introgression from those genera.

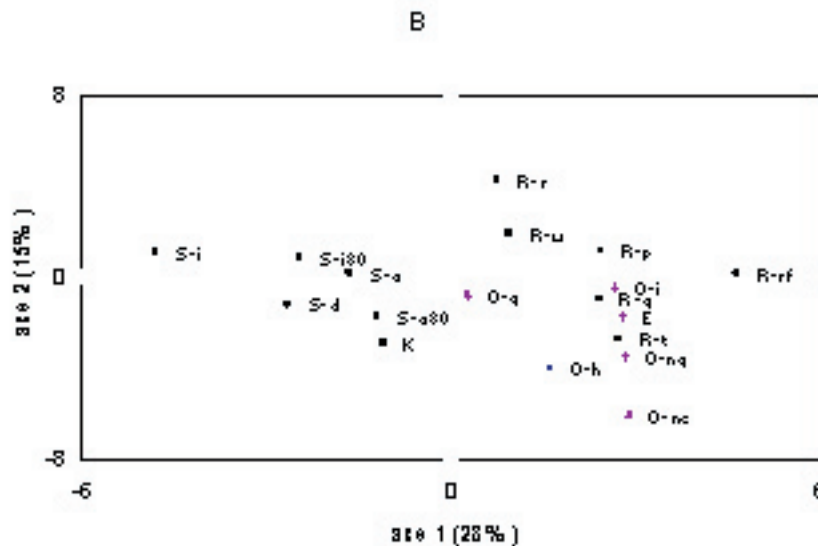


**Figure 1.** *Saccharum* germplasm analyzed with flavonoid compounds. Sources of data are given in the text.

**A.** First plane of a Factorial Analysis performed on the frequency of 25 leaf flavonoid compounds in populations of *S. spontaneum* and *S. robustum*. Codes for species and populations are as follow (sample size is given in parenthesis): R is for *S. robustum*; with populations rl, for Red-leafed (4); w, for Wau-Bulolo (6); p, for Port-Moresby (6); rf, for Red-fleshed (5); g, for Goroka (6); t, for Teboe-Salah (12). S is for *S. spontaneum*; with populations i, for India cytotype 2n=40 to 64 (24); i80, for India cytotype 2n=80 (9); a, for Southeast Asia (12); a80, for New Guinea 2n=80 (15); d, for diverse (4).



**B.** Same data with projection of Noble clones and **Naviso** (*S. edule*) populations. O is for Nobles clones with populations nc, for New Caledonia (4); ng, for New Guinea (10); h, for Hawaii (28); l, for Indonesia (12); g, for clones involved in genealogy of modern cultivars (20). K is for population Kalimantan (10). E is for **Naviso** (7).



However, the proportion of demonstrated cases is so small that other explanations must also be considered: (1) the limited sampling of wild *Saccharum* representatives might have missed some RFLP bands present in Noble cultivars, and (2) co-migration of bands that correspond to different alleles in different taxa i.e. homoplasy- is possible since these polyploid species display many RFLP bands.

### Origin of North Indian and Chinese Cultivars

Molecular data clearly show that North Indian and Chinese cultivars are the result of interspecific hybridizations between representatives of the two *Saccharum* poles, *S. spontaneum* at one end, and the complex of wild and domesticated *S. robustum* and Noble clones at the other end. This is based mostly on data from low copy nuclear DNA and genomic in situ hybridization (GISH) (Lu et al., 1994; D'Hont et al., 2002). As the region where North Indian and Chinese cultivars are encountered is outside the natural distribution range of *S. robustum*, the scenario of Brandes provides the simplest explanation of the data: Noble cultivars were transported by man to mainland Asia where they hybridized with local *S. spontaneum*. It is likely that resulting clones are first-generation hybrids because no -or very few- interspecific chromosome exchanges have been detected with GISH, in contrast with modern cultivars (D'Hont et al., 1996). Owing to mitochondrial haplotypes, it is most likely that, in all cases, Noble clones acted as females and *S. spontaneum* clones acted as males in founding crosses (D'Hont et al., 1993).

Low copy nuclear RFLP data suggest that morphocytological groups among North Indian and Chinese cultivars each represent a set of somatic mutants derived from a single founding hybrid (D'Hont et al., 2002). The Pansahi cultivar group is not particularly distinct from the other groups in test with RFLPs. The North Indian and Chinese cultivars are thus all derived from a similar process that may have occurred repeatedly in different geographical regions.

These data exclude a direct emergence of North Indian and Chinese cultivars from *S. spontaneum* alone. Moreover, genetic contributions by either *Erianthus* or *Miscanthus* are very unlikely, as demonstrated by the Southern hybridization of *Erianthus* and *Miscanthus* genus-specific satellite and Alu-like repeated elements (Alix et al., 1998; Alix et al., 1999). Altogether, the recent studies indicate that the sugar-producing ability in cultivated sugarcane has a unique origin, the Noble clone, which was further transmitted to North Indian and Chinese cultivars and to the cultivars generated by modern breeding efforts. The evidence leaves little space for a hypothetical 'second path'.

### Origin of Naviso (*S. edule*)

Few molecular data are available for tracing the origin of **Naviso**, alias *S. edule*. The mitochondria haplotype has been established for one clone and was identical to the more frequent of the two haplotypes detected in *S. robustum*. It was therefore identical to the haplotype of Noble clones (D'Hont et al., 1993). The chloroplast RFLP restriction pattern of another **Naviso** clone led to a similar conclusion (Sobral et al., 1994). Evidence for the nuclear genome is provided by flavonoids (Williams et al., 1974), which suggest that the domestication process for *Naviso* may have been like that for Noble clones (Figure 1). Clearly, this implies a direct selection from *S. robustum* alone. However, an interspecific origin, with *S. robustum* providing the female gamete, can still not be excluded at this stage.

### An Actual Scenario for Sugarcane Origin and Domestication

The genus *Saccharum* is the sole lineage from which cultivated sugarcane emerged, and is distinct from the closely related genera, *Erianthus* and *Miscanthus*. As defined here, *Saccharum* encompasses two sister wild species, *S. spontaneum* and *S. robustum*.

The current geographical range of *S. robustum* is included in that of *S. spontaneum*. The two species have different ecological adaptation within the region of sympatry: *S. robustum* is a "fresh-water swamp grass favoring moving water" and *S. spontaneum* is adapted to better-drained soils and is a key component of coastal savannas, which are probably "fire-disclimax replacing forest after repeated gardening and burning" (Paijmans, 1976).

The sympatry could result from recent events linked to human activity, for example, direct transport (wild *Saccharum* species are used by people for many purposes) or a natural expansion in habitats disturbed by human activities (*S. spontaneum* is considered as an invasive species in Asia and a growing number of other places). Indeed, *S. robustum* may only recently have extended to Kalimantan (Daniels and Roach, 1987), and *S. spontaneum* may only recently have extended to New Guinea (Berding and Koike, 1980). This would give late Pleistocene allopatric distributions for *S. spontaneum* and *S. robustum*. As the biogeography of South-East Asia and Melanesia is rich and complex with many islands and mountains, the speciation of *Saccharum* by isolation can easily be conceived. Moreover, as the Wallace line may have separated the putative ancestral distributions, so we can suggest a particular scenario for speciation. The Wallace line lies between two continental shelves, the Sunda shelf (mainland Southeast Asia, Java, Sumatra and Kalimantan) and the Sahul shelf (Australia, New Guinea and close islands). Each shelf was repeatedly unified into

a single continental mainland during cyclic lowering of sea level that accompanied ice ages of quaternary era, but no earth bridge ever connected the two shelves. Ice age cycles gave opportunities to repeatedly establish genetic exchanges between separated populations on each shelf but exchanges between populations of the two shelves remained constantly limited during the three million years of the quaternary era. As a consequence, two sister species in the *Saccharum* lineage may have had the opportunity to differentiate in isolation after dispersal of a common ancestor thus giving rise to *S. spontaneum* on the Sunda shelf and *S. robustum* on the Sahul shelf. Recently, it has been becoming more and more obvious that quaternary climatic variation played an important role in the genetic structuring of populations and species that exist today (Hewitt, 2000).

In the island of New Guinea (Sahul), domestication of the wild local plants, i.e. *S. robustum*, would have led to the Noble cultivars. New Guinea is a well-established domestication center for several other important crops (Lebot, 1999). More than just a snack, the crop may have constituted a major source of carbohydrates for pigs and humans (Daniels and Daniels, 1993). The Noble clones could then reach Sunda and the Pacific islands in association with human migration or plant exchange. *S. robustum* also crossed the Wallace line to Kalimantan as a semi-domesticated plant used for medicine or fence building. In Sunda, the introduced Noble clones could hybridize with local wild *S. spontaneum*, producing feral interspecific hybrids. Spontaneous occurrences of such natural hybrids have been reported in Java (Stevenson, 1965) and in eastern India (Mukherjee, 1957).

Contact between cultigens and the wild species was probably frequent as *S. spontaneum* is an aggressive weed in sugarcane fields (Barber, 1920). In sub-tropical climates, hybrids proved to be better adapted to local conditions than Noble clones. Unlike the stalks of Noble clones, the stalks of hybrids could reach full maturity, enabling accumulation of saccharose, a crystallizable sugar. Adoption of hybrid cultivars was thus a pre-requisite for the emergence of a sugar-making industry (Daniels, 1996). Hybridization and subsequent sugar manufacture may have occurred in one or several places in mainland Southeast Asia, probably in an area delimited by North India, Assam and North Myanmar, up to Yunnan in South China. This region encompasses all the known or suspected primary centers of sugar industry, *S. spontaneum* is present (Panje and Babu, 1960) and the latitudes are still favorable for flowering. The region was also crossed by a trade route since at least the first century A.D., if not earlier, giving many opportunities for circulation of plants and techniques.

In this scenario, *S. spontaneum* is a recent arrival in New Guinea. The plant dispersed easily in humanly disturbed habitats, which were frequent in lowlands. A single

cytotype,  $2n=80$ , has been founded in New Guinea. This is consistent with a recent founding effect. Introgression between *S. robustum* and *S. spontaneum* is likely to account for wild *Saccharum* populations reported to present intermediate characteristics.

## Conclusion

Molecular markers are very helpful for understanding the domestication of crop plants. In the case of sugarcane, they have not suggested new evolutionary schemes but have helped to choose between previous scenarios that were based on plant and historical knowledge. There is now little doubt that sugarcane emerged within a specific *Saccharum* lineage, independent from the lineages of *Erianthus* and *Miscanthus*, and that the scenario established by Brandes to account for the origin of traditional cultivars is largely correct. Although samples have sometimes been small in studies so far, it is unlikely that an enlarged study will dramatically modify the picture. Now that robust molecular techniques are well established, the limiting factor for comprehensive understanding of plant domestication is often access to relevant germplasm.

The status of *S. spontaneum* in New Guinea and the relationships between wild *S. spontaneum* and *S. robustum* in the region of sympatry are still not completely clear. The scenario favored above presumes that introgression between the two *Saccharum* wild species does occur. However, other scenarios, more complex, may also account for current data. There is no doubt that new studies targeted toward the investigation of interactions between *S. spontaneum*, *S. robustum* and Noble cultivars in New Guinea, Sulawesi and Kalimantan will help to fully understand the dynamic process of sugarcane domestication.

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