# Ethnobotanic and genetic diversity of sugarcane in French Polynesia

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**Ethnobotany Research and Applications 29:8 (2024)** - http://dx.doi.org/10.32859/era.29.8.1-15
Manuscript received: 12/01/2024 - Revised manuscript received: 02/05/2024 - Published: 03/05/2024

## Research

## Abstract

*Background*: In French Polynesia, traditional tō *(Saccharum officinarum*) have been re-exploited in the recent years to produce organic certified rum. Former botanists have described the sugarcane which were spread by Polynesians during their migrations of the Eastern Pacific. One of them, referred by botanists as Otahiti was the main cultivar grown for sugar production until the 1880s.

*Methods*: Between 2013 and 2017, we collected 15 sugarcane accessions in the Society Islands and examined their taxonomic status to establish the correspondence with those described by former botanists. Nine morphological traits were repeatedly measured including stalk colour, tillering, stalk height, stalk diameter, and internode lengths. We also analyzed them using flow cytometry, PCR markers and in one case molecular cytogenetics.

*Results*: The results showed 4 modern hybrids cultivars, 9 traditional S. *officinarum* and one intergeneric hybrid between S. *officinarum* and the wild genus *Miscanthus floridulus*, Tō 'ā'eho. Among the traditional S. *officinarum* sugarcane cultivars, we suggested that Polynesian sugarcane called Tō 'irimotu and Tō re'are'a could correspond to Otahiti.

*Conclusions*: The studies of processing characteristics also revealed the high Brix of the Tō 'ā'eho and its potential for producing rum. These types of hybrids support the hypothesis of Pacific being a satellite center of sugarcane diversity.

Key words: *Saccharum officinarum*, noble sugarcane, *Saccharum maximum*, French Polynesia, Otahiti

## Background

In the past ten years, interest in sugarcane production has risen in French Polynesia. Owners and producers are organizing themselves under quality standards such as certified organic agriculture and a recognized geographic origin. The high price of sugarcane production locally doesn't allow for economically viable raw sugar production and the only interest is for high-value rum production (Vitrac et al. 2022). One of the main specificities is the use of local noble *Saccharum officinarum* cultivars which are required for the rum to be certified as a "rum of French Polynesia".

French Polynesia was populated between year1000-1300 before Christ by Polynesians coming from the Western Pacific (Wilmshurst et al. 2010). In their canoe expeditions from island to island, Polynesians brought with them several plants such as coconuts, bananas, yams, taro, breadfruits and sugarcane. Sugarcane are generally called tō (Henry 1928; Whistler 2009) and were used in medicine, ceremonies (Ellis 1831; von den Steinen 1898), as a carbohydrate resource (Lincoln 2020) and to sweeten food (Vitrac et al. 2018a). It was a plant of major importance for Polynesians, and they had probably selected and disseminated several cultivars for specific purposes prior, during and after their migrations from island to island over the years.
When the first European navigators arrived in the French Polynesian islands, starting in the late eighteenth century following native Polynesian's knowledge, botanists gave some descriptions of the S. *officinarum* cultivars and closely related wild species (S. maximum and *Miscanthus floridulus*) they discovered (Wray 1853).

In Tahiti, between 8 to 10 cultivars (Table 1) were described by former botanists such as Cuzent (1860), Nadeaud (1873) and Henry (1928) and 14 in the Marquesas (Brown 1931) with no correspondence in the Polynesian names due to the different languages used between archipelagos. One of the S. *officinarum* cultivars was called "Otahiti" (Bougainville 1771) without any reference to its Tahitian name and the European explorers spread it all around the world, where it became the main crop of S. *officinarum* for sugar production until the years 1880s (Stevenson 1965) because of its high sugar production rate, robust growth, and excellent ratooning.

At the beginning of the twentieth century, noble S. *officinarum* cultivars used for industrial purposes were replaced worldwide initially by intraspecific hybrids and later by interspecific hybrid between S. *officinarum* and S. *spontaneum* (herein "modern cultivars") developed by breeders, which were more resistant to disease and with a better yield for sugar production (Stevenson 1965).

As sugarcane was reproduced using setts (stalk cuttings) and without any rules regarding world plant exchanges, many S. *officinarum* from different regions and modern cultivars were spread, particularly in all the Pacific islands, following the navigator's travels. In French Polynesia, the Otahiti cane was used for sugar production until the end of the nineteenth century (Ellis 1831; Nollinberger 1857; Cuzent 1860) and the decline of Atimaono plantation in Tahiti (Vitrac et al. 2015). The Otahiti cultivar, and indeed all noble S. *officinarum* cultivars, were no more used for sugar or rum production (Fahrasmane & Ganou-Parfait 1997), after this period.

Rum producers today hope that growing traditional Polynesian S. *officinarum* cultivars, including cultivar Otahiti, can enhance the marketability and branding of local products. However, in such a context, it is difficult to be sure which of the cultivar used today can be regarded as Otahiti sugarcane.

The objectives of this study were to i) collect, record and characterized the diversity of *Saccharum* and its close relatives currently present in French Polynesia, with a special focus on S. *officinarum;* ii) to try and make correspondence between the accessions we collected and those described by former botanists. To this end, we used morphological descriptions, process indicators and molecular tools.

Table 1. Taxonomy and descriptions of the sugarcane cultivars and associated wild species in Tahiti Island by former botanists

| | Cuzent (1857, 1860) | | Henry (1928) | |
|---|---|---|---|---|
| **Scientific name** | **Tahitian name** | **main characteristics** | **Tahitian name** | **main characteristics** |
| *Saccharum officinarum* | Tō ‘irimotu | green color, brittle skin, urticating hairs | Tō ‘irimotu | purple with brittle skin |
| *Saccharum officinarum* | Tō rurutu<br>Tō rutu | slightly purple and purple leaves | Tō tea<br>Tō rutu | light greenish-yellow |
| *Saccharum officinarum* | Tō pi’avare / pi’avere | slightly red, small internodes, small diameter | Tō pi’avare / pi’avere | grape colored, white bloom |
| *Saccharum officinarum* | Tō ‘ōura / ‘o ‘ura | purplish with yellow bands, large diameter | Tō ‘ōura / ‘o ‘ura | striped green, white, and purple |
| *Saccharum officinarum* | Tō ‘ute | violet skin and medulla, big stem, lots of juice, imported from Batavia by Bougainville | Tō 'ute | dark red |
| *Saccharum officinarum* | Tō Vaihī<br>Tō Vaihī-‘uo’uo<br>Tō ‘uo’uo | white, lots of sugar, imported from the Sandwich Islands | Tō ha’avai | no description |
| *Saccharum officinarum* | Tō ‘avae | yellowish, green stripes | | |
| *Saccharum officinarum* | | | Tō 'ofe | great light greenish-drab, resembling a bamboo |
| *Saccharum officinarum* | | | Tō rā'au | light maroon color, very hard |
| *Saccharum officinarum* | | | Tō ’ō’opu | very dark purple |
| *Saccharum maximum* | Tō ‘ā’eho | green (white), slender stem, mountain cane, | Tō ‘ā’eho | light green, wild, resembling a reed |
| *Saccharum maximum* | Tō patu | violet (red), slender stem, mountain cane, | | |
| *Miscanthus floridulus* | 'ā'eho | reed | | |

## Materials and Methods

**Material**

Between 2013 and 2017, we prospected the islands of Tahiti, Moorea, Raiatea and Taha’a in the Society archipelago, to collect all sugarcane and wild species from *Saccharum* or close genera we could find.

We collected 15 accessions which are described in Vitrac et al. (2018b, 2019a, 2019b) and were tentatively classified as eight noble cultivars (*S. officinarum*), four modern cultivars (*Saccharum* spp.) and two wild accessions (*S. maximum* and *Miscanthus floridulus*) (Table2). In addition, two noble canes, ‘Batavia’ and ‘Black Cheribon’, and one modern cultivar B69566 were imported from the Visacanne® quarantine (CIRAD, Montpellier), and leaves, from the ‘Lahaina’ noble *S. officinarum* from the HARC collection (Hawaiian Agricultural Research Centre). DNA from the modern cultivar R570 was used in Montpellier for the genetic analysis. The canes were cultivated at farm scale under the same cropping standards described in Vitrac et al., (2019a) at two separate locations (respectively “collection plot” and “plantation plot” described in Vitrac et al., (2023)).

**DNA fingerprinting and PCR diagnostic markers**

DNA extractions were done at the laboratory of the “Epic Vanille” in Raiatea Island and at CIRAD according to the protocol of Hoisington (1992). DNA fingerprinting with microsatellites was performed at the AGAP institute Genotyping Platform GPTR of CIRAD (Montpellier, France) as described by Kagy et al. (2016). Six microsatellites markers were used: CV29, CV37 and CV38 (from Macheroni et al. 2007) and 3 developed by CIRAD (mSScir_14, mSScir_19, mSScir_164). After amplification with a set of M13 tailed fluorescent labelled primers, fragment sizes were estimated using internal size standard on a DNA

analyser (ABI 3500xL, Applied Biosystems), and allele scorings were analyzed using Genemapper v4.1 software (Applied Biosystems).

A *Miscanthus* PCR diagnostic marker was developed from a *Miscanthus* inter Alu type transposable element sequence (Alix et al. 1999). Two primers (5'-GTGACTCCTGCTGTGACTCC-3' and 5'-GAACATGATCGGAGGCCCTC-3') were designed in the *Miscanthus* sequence MsCIR2 (EMBL Y17576, Alix et al. 1999). These primers used on *Miscanthus floridulus* or *Miscanthus sinense* DNA produced of band of around 300 bp and no amplification was observed with *Saccharum* DNA. The amplification reaction was performed in a final volume of 25µl, containing 25ng of sugarcane DNA, 0.2mM dNTP mix, 2mM MgCl2, 80mM Tris-HCl buffer, each primer at 0.1µM and 0.06U of Taq polymerase (FIREPol®). The PCR was carried out with the following program: 94°C for 4 min; 35 cycles of 94°C for 30 s, 60°C for 45s, 72°C for 1min; a final cycle of 72°C for 10min. PCR products were separated on 1% agarose gel and visualised after staining with ethidium bromide.

*Morphological analysis*

Table 2: Sugarcane and wild accessions collected in French Polynesia or imported, and methods used to characterize them.

| | Year | Names | ref. | Process | Morphology | PCR markers | Flow cytometry | Origin |
|---|---|---|---|---|---|---|---|---|
| | | *Saccharum officinarum* | | | | | | |
| collected | 2013 | Verte à Bandes Pourpres | VBP | x | x | x | x | 17°32'01.1"S 149°25'52.1"W |
| | 2013 | Rouge à Bandes Vertes | RBV | x | x | x | x | 17°45'2.80"S 149°21'11.9"W |
| | 2013 | VErte | VE | x | x | x | x | 17°30'47.4"S 149°30'3.18"W |
| | 2013 | Trois(3) Couleurs | 3C | x | x | x | x | 17°40'34.4"S 149°18'28.3"W |
| | 2013 | Jaune à Rayure Pourpre | JRP | x | x | x | x | 17°45'37.0"S 149°22'02.7"W |
| | 2013 | POurpre | PO | x | x | x | x | 17°30'53,9"S 149°28'10.3"W |
| | 2014 | Jaune à Taches Rouges | JTR | x | - | x | - | 17°36'59.3"S 149°18'8.04"W |
| | 2014 | ROuge | RO | x | - | x | x | 17°43'44.0"S 149°18'51.1"W |
| | 2017 | Rapa JFB | | - | - | x | - | Rapa island |
| imported | 2017 | BATtavia | BAT | x | - | x | x | CIRAD Visacane |
| | 2017 | Black Cheribon | BC | - | - | x | x | CIRAD Visacane |
| | 2017 | Lahaina | | - | - | x | - | HARC Hawaii |
| | | *Saccharum* spp. | | | | | | |
| collected | 2013 | Rouge Reflets Verts | RRV | x | x | x | x | 16°44'09.5"S 151°26'19.9"W |
| | 2013 | Jaune Roseau | JR | x | x | x | x | 17°45'56.0"S 149°28'00.3"W |
| | 2014 | Blanche | Bla | *x* | - | x | x | 17°45'56.0"S 149°28'00.3"W |
| | 2014 | HAWaii | HAW | - | - | x | - | 17°44'60.0"S 149°21'41.0"W |
| imported | 2016 | B69566 | Ble | x | x | x | x | CIRAD Visacane |
| | 2018 | R570 | R570 | - | - | x | - | CIRAD AGAP |
| | | *Saccharum maximum* | | | | | | |
| collected | 2016 | Tō 'ā'eho | | x | - | x | x | 17°49'12.3"S 149°08'06.3"W |
| | | *Miscanthus floridulus* | | | | | | |
| | 2016 | ‘ā 'eho | | x | - | x | x | 17°37'56.4"S 149°36'48.0"W |

x: done ; -: not done

To compare our plant material to the descriptions made by the former botanists for all the sugarcane observed, we used the UPOV (2005) sugarcane varietal repository (using Artschwager & Brandes (1958) standards). These sheets are not presented in this study, being too large (54 traits), but it was the first step of identification and comparison to descriptions given by former botanists. The main traits described were: stalk color, stalk diameter, stalk height, tillering (number of stalks per plant), ratoon ability, internodes length, leaf color, leaf bunch appearance and flowering occurrence. We also compare our observations to the recent descriptions made by Lincoln (2020) who described all the Hawaiian sugarcane.

For nine varieties as described in Table 2 ("morphology" column), ten stalks of each variety and each plot were sampled from the plantation plots in August 2015 (first plantation, 12 months) and August 2016 (first ratoon, 24 months). The stalk height, the stalk diameter and the internode length as well as the tillering were measured.

Data was analyzed using the statistical software XLSTAT 19.4.45191. A population probability law (normal distribution) and descriptive statistical parameters such as means and standard deviations were processed. Mean comparison tests of Mann Whitney (samples<30) were used to compare stalk height, tillering, stalk diameter, and internode length. A factorial analysis was also done.

**Flow cytometry**

Leaves were sampled from both collection and plantation plots and sent fresh to AGAP laboratory to be analyzed by flow cytometry method accorded to Ochatt (2011) to determine their nuclear DNA content and evaluate chromosome numbers. Leaves from accessions of *Miscanthus sinense* were used as standard.

**Genomic In Situ Hybridization (GISH)**

Genomic hybridization was performed according to D'Hont et al. (1996) on chromosomes of the wild *Saccharum maximum* accession Tō 'ā'eho using as probes 200ng of *Miscanthus sinense* NG7722 genomic DNA (labeled with Biotin and detected with avidin-Texas Red) and 200ng of S. *officinarum* BN3066 genomic DNA (labeled with digoxigenin and detected with anti-digoxygenin-FITC). The chromosomes were counterstained with 4'-6 diamidino-2-phenylindole (DAPI; Vectashield Mounting Media with DAPI), and fluorescent images were then captured separately using a cooled high-resolution CCD camera (ORCA Hamamatsu) attached to a Leica DMRXA2 fluorescent microscope.

**Process indicators**

Three stalks for each cultivar (Table 2) of the collection plots were milled (laboratory stainless steel miller) to determine the juice yield (weight of juice / weight of milled cane), the fibre content (weight of fibre residue after milling / weight of cane before milling) and the Brix degree (soluble dry extract, with the ATAGO® "pocket" digital refractometer) according to traditional milling methods (Rein 2017).

## Results and discussions

**DNA fingerprinting**

DNA fingerprinting of the 15 collected accessions was performed using 6 *Saccharum* microsatellites markers to determine if some of the collected accessions could be identical or correspond to somaclonal variants (Figure 1).

For all accessions except the *Miscanthus* accession, an amplification was obtained. The absence of amplification for the *Miscanthus* accession was expected since these markers are specific to the *Saccharum* genus. Very similar fingerprints were obtained for 'Verte bandes pourpres (VBP)', 'Verte (VE)' and 'Jaune à taches rouges (JTR)'. However, 'Verte bandes pourpres' is striped green and purple, while the two others are solid colored. This difference may thus be due to somaclonal variation. 'Rapa JFB' and 'Trois couleurs (3C)' had also very similar fingerprints as well as 'Jaune roseau (JR)' and 'Hawaii (HAW)'. 'Rapa JFB', 'Jaune à taches rouges' and 'Hawaii' were not included in further analysis.

**Morphological and phenological comparison of cultivars**

Eight of the collected accessions and one imported modern cultivar were cultivated at farm scale under the same cropping standards, firstly to compare them to the descriptions made by the former botanists and secondly to characterize them using standard/classical descriptors. After two years of cultivation for most of the cultivars in two separate sites, we encountered some difficulties establishing a "standard" morphologic identification. Environmental factors such as sunlight exposure, rainfall, and soil fertility have been reported to influence morphological characteristics (Lincoln 2020). Also, the maturation stage and age of the plant have a large influence. However, some characteristics are both distinctive and relatively consistent,

and it is the combination of all which finally allows us to identify a cultivar with accuracy. This is similar to the approach by Lincoln et al. (2022), in which 95 morphological traits were recorded but they found that the best separation of cultivar classifications occurred when using only 19 parameters. Producing the variety sheets (following Artschwager & Brandes 1958 In: UPOV 2005), we observed some discriminant characteristics as it is resumed in Table 4: stalk color, leaf bunch size and color, stalk diameter, tillering, internode length, flowering, special characteristics, and potential ratoon. We paid particular attention for morphological characteristics linked to agronomy.

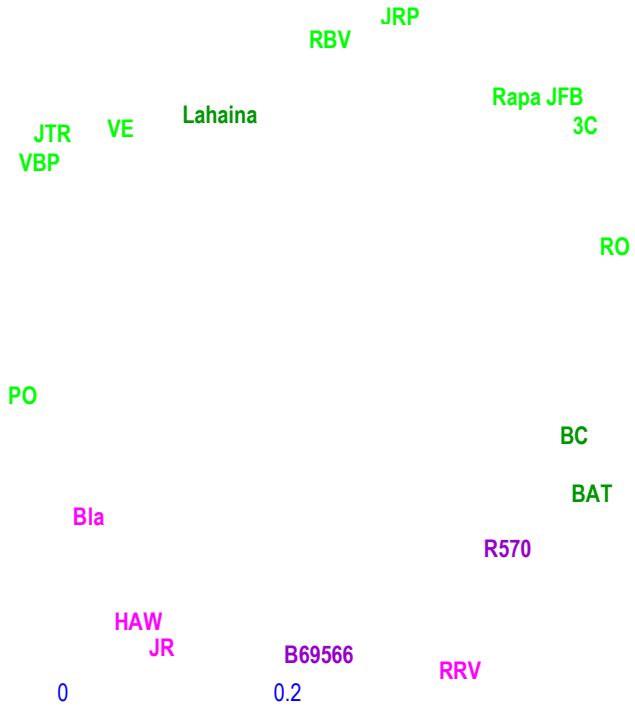


Figure 1. DNA fingerprinting of the 15 collected accessions (performed using 6 *Saccharum* microsatellites markers). *Saccharum officinarum* (green color, collected and dark dark green color, imported) and *Saccharum* spp. (pink color, collected and purple color, imported).

We were surprised that most of former botanists did not mention flowering of sugarcane. Moreover Lincoln (2020) mentioned that he could not consistently observe the canes throughout the year so could not be confident in his observations of flowering. In our case, we observed that flowering did not occur every year for most of the cultivars. This criterion helped us to distinguish two morphologically very similar varieties: Tō ‘irimotu (VE, Table 4) which flowers every year whereas ‘Jaune à rayures pourpres’ (JRP) a cane we propose to call Tō re’are’a (which means Yellow in Polynesian language) has never flowered since 2014. We did not find mention of this particular cane by Polynesians nor former botanists, which is very easy to confuse with Tō ‘irimotu because of their similar nodes zone and stalk colour. We found that flowering and a few additional agronomic characteristics (tillering, size of internode length and ratoon ability) allowed us to make the distinction.

Table 3 sums up the measurements done in 2015 and 2016 regarding agronomic characteristics for the sugarcane in the plantation plots. A factorial analysis based on these morphological characteristics is shown in Figure 2. The first axis of the factorial analysis (explaining 49.31% of variation) separated two groups. Group 1 was composed by ‘Rouge à Bandes Vertes’ (RBV), JRP, VBP, VE, 3C and ‘Pourpre’ (PO), which we previously classified based on morphological characteristics as S. *officinarum* and Group 2 was composed by ‘Rouge à Reflets Verts’ (RRV) and JR, which we previously classified as modern cultivars, and B69566 (a modern cultivar imported from CIRAD visacane). On the second axis (explaining 27.99% of the variation), JRP (Tō re’are’a) and RBV (Tō ‘ute, Table 4) cultivars are separated from the other noble sugarcane. According to our literature interpretations, Tō ‘ute variety (which corresponds to ‘Cavengerie’, (Lincoln 2020)) is probably not from an ancient Polynesian introduction and there is still doubt regarding Tō re’are’a (JRP).

In accordance with literature regarding the morphological differences between noble sugarcane and modern cultivars, Group 1 has poor tillering (2.80 to 8.83 stems par plant), large stalk diameter (2.73 to 3.61cm), small internodes (5.10 to 7.82cm) and small stalk height (1.02 to 1.58m except JRP 1.89m) and is significantly different (p=0.05) from the Group 2: rich tillering (5.37 to 15.00), medium stalk diameter (2.61 to 2.99cm), medium internodes (8.56 to 12.37cm ) and big stalk height (1.82 to 1.98). Only the noble sugarcane JRP height is similar to Group 2 heights. Vitrac et al. (2019b) showed that main components of Polynesian *Saccharum officinarum* yield are height and tillering. Tō re'are'a (JRP) cultivar seems to be different from all others from the Group 1 regarding height. It can be an ancient Polynesian introduced variety or introduced from elsewhere from an unknown area. Without significant differences, Table 3 shows that sugarcane of Group 2 globally increased all their characteristics from first plantation (2015) to first ratoon (2016) while sugarcane from Group 1 showed the opposite. For our S. *officinarum* cultivars, the best agronomic results were obtained in first plantation which is confirmed by Vitrac et al. (2019b).

Table 3. Results of measured morphologic characteristics for the different studied cultivars.

| **Cultivars** | **Stalk height (m)** | | **Tillering** | | **Stalk diameter (cm)** | | **Internodes length (cm)** | |
|---|---|---|---|---|---|---|---|---|
| Group 1 | 2015 | 2016 | 2015 | 2016 | 2015 | 2016 | 2015 | 2016 |
| RBV | 1.58 ns | 1.49 ns | 5.27 a | 6.80 ac | 3.44 c | 3.42 ns | 7.10 a | 6.75 a |
| JRP | 1.88 b | 1.89 c | 3.03 ns | 2.80 ns | 3.58 c | 3.61 ns | 5.89 ab | 7.82 ns |
| VBP* | - | 1.20 a | - | 8.83 d | - | 2.97 c | - | 6.19 ac |
| VE | 1.36 a | 1.21 a | 5.10 a | 5.00 a | 2.73 a | 2.75 a | 6.46 a | 6.44 a |
| 3C | 1.34 a | 1.02 ab | 6.73 a | 5.03 a | 2.83 ab | 2.79 ab | 5.73 b | 5.14 b |
| PO | 1.13 ns | 1.04 b | 4.07 ns | 4.93 a | 3.53 c | 3.22 ns | 5.10 b | 5.64 bc |
| Group 2 | | | | | | | | |
| RRV | 1.94 b | 1.90 c | 7.07 a | 15.00 b | 2.95 d | 2.99 c | 8.56 ns | 8.97 d |
| JR | 1.88 b | 1.98 c | 5.37 a | 7.37 cd | 2.93 bd | 2.61 b | 12.37 ns | 9.06 d |
| B69566** | - | 1.82 c | - | 13.33 b | - | 2.76 ab | - | 10.53 ns |
| Std. | 0.19 < σ 2015 < 0.34 | | 1.69 < σ 2015 < 4.42 | | 0.23 < σ 2015 < 0.39 | | 1.05 < σ 2015 < 2.52 | |
| deviation | 0.17 < σ 2016 < 0.35 | | 1.47 < σ 2016 < 5.02 | | 0.22 < σ 2016 < 0.79 | | 0.62 < σ 2016 < 1.87 | |

*a, b, c, d, ns: Mann Whitney (p< 0.05) results ; * : not cultivated in 2015 ; ** : introduced in 2016*

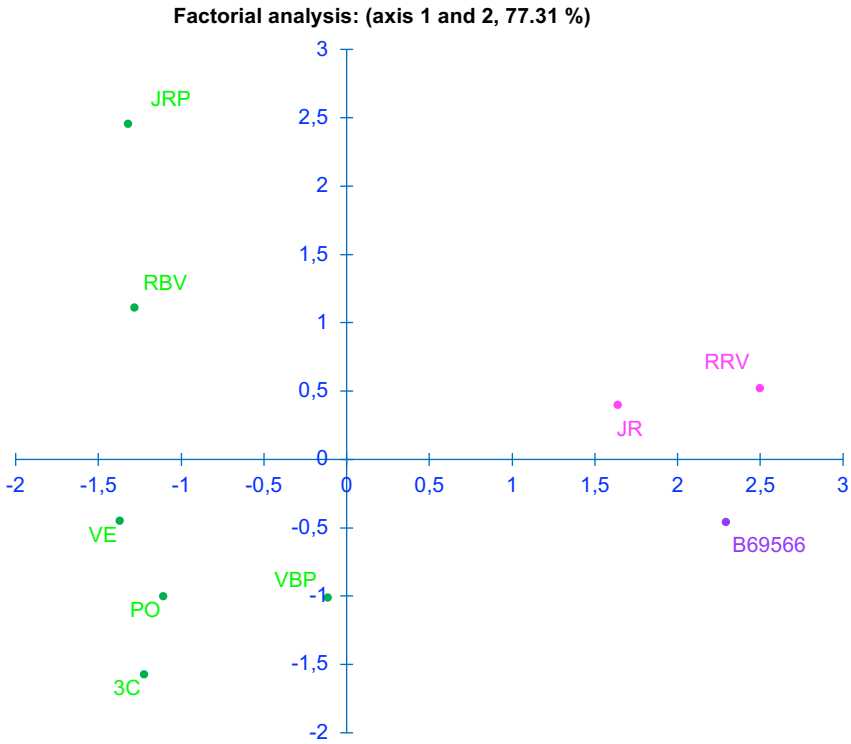


Figure 2. Factorial analysis following morphological characteristics of the varieties cultivated in the plantation plot. *Saccharum officinarum* (green color) and *Saccharum* spp. (pink color, collected and purple color, imported).

**Chromosome number estimation through flow cytometry measurement**

To further confirme our classification of the collected accessions in S. *officinarum* versus modern hybrid cultivars, we analyzed them with flow cytometry. Flow cytometry allows to determine nuclear DNA content which can be related to chromosomes numbers. S. *officinarum* typically has 80 chromosomes with some small variation and a nuclear DNA content of around 7.6 picograms while modern cultivars have around 110-120 chromosomes with a nuclear DNA content of around 10 picograms (D'Hont and Glaszmann 2001). The results presented in Figure 3 and Table 4 showed that the 7 collected accessions that we suspected based on morphological characteristic to belong to S. *officinarum*, as well as the two standard we used for S. *officinarum* ('Batavia (BAT)' and 'Black Cheribon (BC)'), all have nuclear DNA content typical of S. *officinarum*. The three collected accessions that we suspected based on morphological characteristic to be modern cultivars, as well as the two standards we used for modern cultivars (R570 and 'Bleue (Ble) B69566'), all have nuclear DNA content typical of modern cultivars.

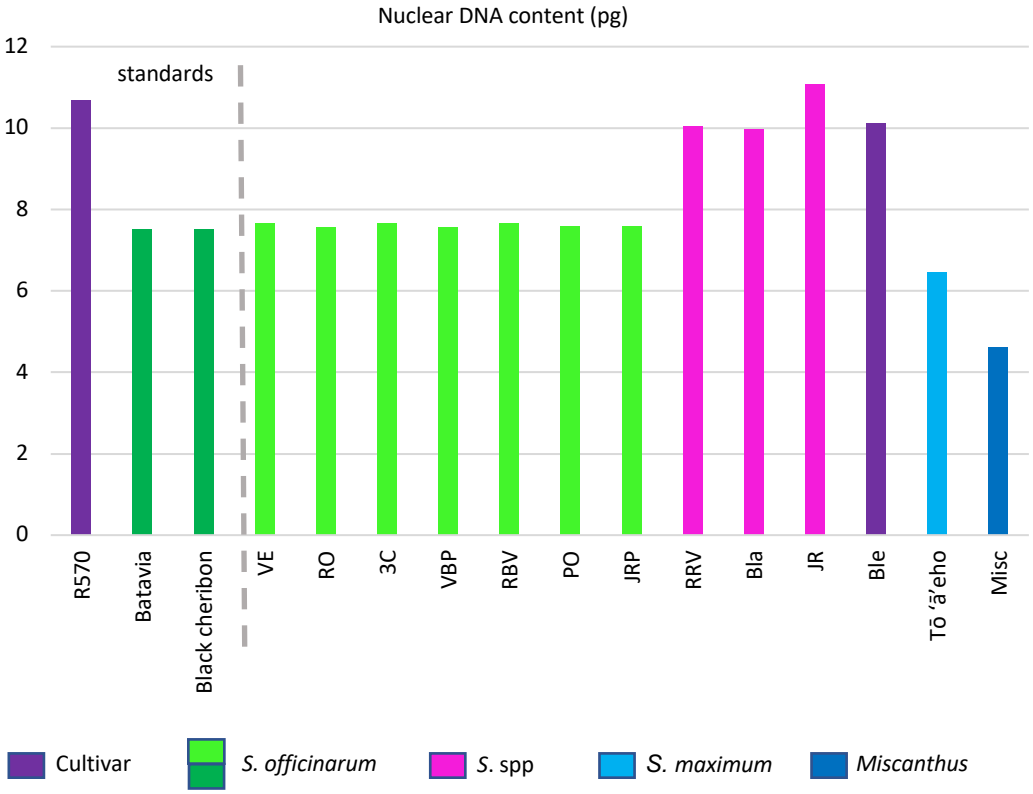


Figure 3 Flow cytometry results of S*. officinarum* versus modern hybrid cultivars and wild species.

**Characterization of the *Saccharum maximum* accession**

Former botanists have noted the presence of atypical sugarcane in mountains that they related to *Saccharum spontaneum* (Cuzent 1860; Guillemin 1837). The origin of these types of accession have long been debated, having been related to S. *spontaneum*, *Erianthus* or *Miscanthus*, and they were attributed different taxonomic names, the most commonly used currently being *Saccharum maximum* (Price and Daniels 1968; Grassl 1946). We found one such accession, call Tō 'ā'eho in Polynesian language. In Polynesian language, 'ā'eho is the name for *Miscanthus floridulus* and tō the name for S*. officinarum*. Tō 'ā'eho thus signifies a possible hybrid between 'ā'eho and Tō. This together with absence of S. *spontaneum* in Society Islands suggested that Tō 'ā'eho could be an intergeneric hybrid between S. *officinarum* and *Miscanthus floridulus*.

To further verify this hypothesis, we used microsatellite markers specific to the *Saccharum* genus and a PCR markers specific to *Miscanthus* genus. Both types of markers produced an amplification strongly suggesting that this accession is a hybrid between the two genera.

We also performed a hybridization on the chromosomes of Tō 'ā'eho with one probe consisting of total DNA of S. *officinarum* (detected in green) and one probe of total DNA of *Miscanthus floridulus* (detected in red). The results presented figure 4 clearly show that Tō 'ā'eho is an intergeneric hybrid with around 40 chromosomes inherited from S. *officinarum* and 19

inherited from *Miscanthus*. Price & Daniels (1968) analyzed an accession, Raiatea 1, collected in Raiatea Island in 1935 and based on the observation 2n = 60 chromosomes, they suggested that it could derived from hybridization between *Saccharum* and *Miscanthus.* These results also confirmed, Grassl (1946) hypothesis of the involvement of *Miscanthus* in *Saccharum maximum*.

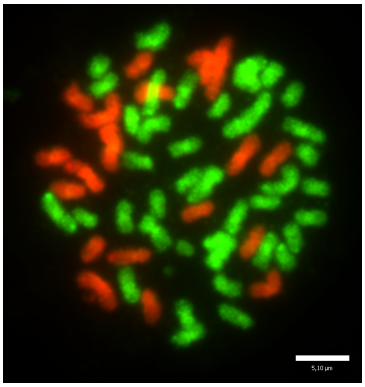

Figure 4. Chromosome preparation of Tō ‘ā’eho accession after in situ hybridization with *Miscanthus floridulus* total DNA (detected in red) and S. *officinarum* total DNA (detected in green).

**Processing characteristics of the studied accessions**

Figure 5 resumes the measurements done (2015 and 2016 as a mean) regarding processing characteristics about cultivated cultivars in the collection plot.

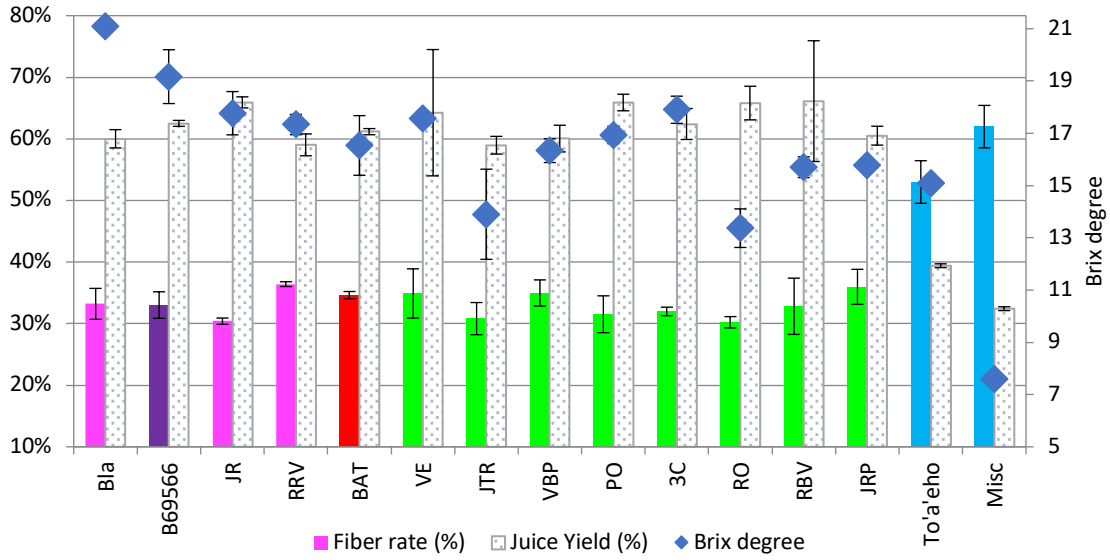


Figure 5. Processing characteristics (Brix degree, fiber rate and juice yield) of the studied accessions. Purple: introduced modern hybrid cultivars; pink: collected modern hybrid cultivars; red: Noble *Saccharum officinarum* introduced from visacane®; Green: collected noble Polynesian *Saccharum officinarum*; Blue: wild accessions

The fibre content was almost the same for both S. *officinarum* and modern hybrid cultivars with around 30-35% (Figure 5). For *Saccharum maximum* Tō ‘ā’eho, this rate is about 50% and for *Miscanthus floridulus* 60%. Also, the juice rate is about 60-65% regarding both S. *officinarum* and modern hybrid cultivars even for the introduced cultivars (B69566 and Batavia). So, these process indicators are not relevant here to distinguish S. *officinarum* from modern hybrid cultivars with laboratory material we used. Vitrac et al. (2019b) found the opposite with more effective juice extraction for noble S. *officinarum* sugarcane. They also found no difference regarding Brix degree, which is richer in modern hybrid cultivars in our study, although classically Brix is higher in modern cultivars. These discrepancies may be coming from the milling equipment and refractometer we used and thus not relevant here for taxonomic distinction between S. *officinarum* and modern hybrid cultivars.

However, the wild species *Saccharum maximum* (Tō ‘ā’eho) and *Miscanthus floridulus* displayed large differences: Tō ‘ā’eho has 40% juice extraction yield which is 20% less than sugarcane and a valuable Brix degree of about 15, comparable to most sugarcane cultivars. Tō ‘ā’eho can thus be regarded as an interesting variety for rum production because of its high sugar content.

Table 4: Identification and characterization of the sugarcane and wild species of the study.

| Species | origin | Polynesian name | ref. | common name | stalk color | leaf bunch | leaves | diameter | tillering | internodes | flowering | specials | ratoon | nuclear DNA content (pg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *S. officinarum* | F.P.* | Tō ‘irimotu | VE | verte | green | falling back | large, green | large | 3 to 10 | small | every time | brittle skin | 1 to 3 | 7.66 |
| *S. officinarum* | F.P. | Tō rutu | RO | rouge | red | falling back | large, purple | large | 3 to 6 | small | every time | - | 0 | 7.56 |
| *S. officinarum* | F.P. | Tō pi’avare | 3C | trois couleurs | red, brown and yellow | falling back | large, green | small | 3 to 10 | small | sometime | - | 1 to 3 | 7.66 |
| *S. officinarum* | F.P. | Tō ‘ōura | VBP | verte à bandes pourpres | green with abundant large purple stripe | falling back | large, green | large | 3 to 10 | small | no | - | 1 to 3 | 7.56 |
| *S. officinarum* | F.P. | Tō ‘ute | RBV | rouge à bandes vertes, Cavengerie | red with large low abundant large purple stripe | falling back | large, green | large | 3 to 10 | large | rare | - | 1 to 5 | 7.65 |
| *S. officinarum* | F.P. | Tō ’ō’opu | PO | pourpre, Badila | very dark purple | falling back | large, green | large | 3 to 10 | very small | sometime | - | 1 to 3 | 7.58 |
| *S. officinarum* | F.P. | Tō re’are’a** | JRP | jaune à rayure pourpre | yellow with abundant very thin purple stripe | falling back | large, green | large | 3 to 6 | small | no | - | 1 to 5 | 7.59 |
| *S. officinarum* | CIRAD | - | BAT | Batavia | yellow with abundant large purple stripe | falling back | large, green | large | 3 to 10 | small | no | - | 1 to 3 | 7.52 |
| *S. officinarum* | CIRAD | - | BC | Black Cheribon | purple | falling back | large, green | large | 3 to 10 | small | no | - | 1 to 5 | 7.51 |
| *S. maximum* | F.P. | Tō ‘ā’eho | Tō ‘ā’eho | - | green, brown and red | erected | thin, green | very small | 10 to 30 | large | every time | pubescent | > 5 | 6.46 |
| *M. floridulus* | F.P. | ‘ā’eho | ‘ā’eho | - | green | - | thin, green | very small | 10 to 30 | large | every time | - | - | 4.62 |
| *Saccharum spp.* | unknown | - | RRV | Rougereflets verts | red as purple | falling back | large, green | large | 7 to 20 | large | no | green stripe (rare) | > 5 | 10.05 |
| *Saccharum spp.* | CIRAD | - | Bla | blanche | white | erected | thin, green | small | 7 to 20 | large | everytime | cerusia | > 5 | 9.96 |
| *Saccharum spp.* | Unknown | - | JR | jaune roseau | yellow | erected | thin, green | small | 7 to 20 | large | no | cerusia | > 5 | 11.07 |
| *Saccharum spp.* | CIRAD | - | Ble | B69566 | blue | falling back | thin, green | small | 7 to 20 | large | no | cerusia | > 5 | - |
| *Saccharum spp.* | CIRAD | *** | R570 | - | - | - | - | - | - | - | - | - | - | 10.69 |

* : French Polynesia ; ** : no descriptions in literature ; ***: not cultivated, from literature

## Discussion

In this study we characterized the *Saccharum* diversity we could collect in part of the Society Islands (Vitrac et al. 2019b), tried to make correspondence between theses accessions and the one described by former botanists, and tried to distinguish traditional S. *officinarum* Polynesian cultivars from more recently introduced S. *officinarum* and modern hybrid cultivars.

Sugarcane has been propagated vegetatively through cutting by farmers since their arrival on these Polynesian islands some 1000 years ago. Over this period, mutations occurred through somaclonal variations which when favorable or attractive (bright color for example) could have been selected by farmers. In addition, although S. *officinaru*m is generally not very fertile, it can sometimes flower when environmental conditions are favourable and result in some progenies from which farmers could also select attractive clones. The occasional generation of somaclonal variants, the frequent exchange of material between islands often associated with a change of Polynesian names and the frequent mix-up of materials make correspondence between accessions over time or regions quite difficult. It is Even more difficultto differentiate accessions introduced originally by the first Polynesian from more recently introduced ones. Lincoln et al. (2022) have reported on these difficulties while analyzing the sugarcane diversity in Hawaii and highlight the need to combine several lines of evidence including, morphological characteristic, genetics characteristics as well as ethnological and historical research.

We collected 7 *Saccharum officinarum*, 1 *Saccharum maximum*, 3 modern hybrid cultivars *Saccharum* spp. and 1 *Miscanthus floridulus* (Table 4). These numbers are very close to what former botanists described (Cuzent 1860; Nadeaud 1873; Pancher 1855; and Henry1928). Among the 7 S. *officinarum*, a few had identical fingerprints, some of them representing somaclonal variants with clear distinct morphological characteristics.

Regarding the modern cultivar *Saccharum* spp. group which were introduced in French Polynesia before 2013, we have few information about them, and it was impossible to know their true origin. The 'Blanche' (Bla) variety came from CIRAD and was introduced in the 1970s. At the same period, the JR variety was introduced maybe from Australia or from Hawaii as well (personal information from a sugarcane producer). We don't have any information about the RRV.

Some S. *officinarum* described in old literature (Table 1) as Tō 'avae, Tō rā'au, Tō vaihī, Tō ha'avai, Tō 'ofe were not found, observed or identified during our study and fieldwork. They may have disappeared because not cultivated anymore or difficult to link to the ones we collected because of traits variation due to environment or maturation stage when observed. We can also note some contradictions and oddities between sources: for example, according to Cuzent (1860), Tō rutu ('Rouge' (RO)) has red stalk contrary to Henry (1928) observation as green. Also, for Henry (1928) Tō 'irimotu (VE) is purple contrary to Cuzent (1860) observation as green. But maybe they were talking of the same variety for which color may depend on conditions. For example, the one we called Tō re'are'a (JRP) can be green or yellow and sometimes with abundant thin purple stripes.

Lincoln (2020) mentioned around 50 traditional Hawaiian *Saccharum officinarum*, 12 introduced S. *officinarum* and 7 recognized modern cultivars. This result was supported by Schenk et al. (2002) genetic diversity study who found 41 old/ traditional S. *officinarum* with several of them being clustered together in genetic analyzing suggesting that they differed by somaclonal variations. Moreover, Wilfong in 1883 found 50 varieties of ancient Hawaiian introduction. It is surprising to see that former botanists mentioned no more than 8 to 14 S. *officinarum* varieties in French Polynesian islands as opposed to around 50 in Hawaii. We would have expected the opposite since Polynesians first arrived in Marquesas and Society islands and then went to Hawaii. The diversity of native varieties in Hawaii that arose most probably through somaclonal variation is likely driven by the importance of sugarcane in the pre-European context in Hawaii, as well as the ecological diversity that varieties would have needed to be selected for. In addition, we can suppose that many more introductions of noble varieties from other pacific islands or countries occurred in the 18th century in Hawaii, before the creation of the breeding stations. It is to be noted that *Saccharum maximum* was not found in Hawaii (Wagner et al. 1999) and is known in Marquesas, Society, Austral and Cook archipelagos.

Although, we can find some contradictions in historical records, they can help distinguish accessions introduced originally by the first Polynesian from more recently introduced ones.

The sugarcane multiplication is vegetative so, following Polynesian migrations from Tahiti and Marquesas Islands to Hawaii, we would expect to find there most of Marquesan and Tahitian varieties in Hawaii. It seems to be the case based on morphological characteristics for Tō 'ute ('ie'ie, 'Cavengerie' or RBV), Tō 'ō'opu ('Badila' or PO) according to Lincoln (2020) but not regarding other noble varieties. However, we can note some similitudes between Tō rutu (RO) and 'Honua'ula' which

is the only Hawaiian sugarcane that has purple leaves too. Tō ‘ōura (VBP), green with big purple stripes, is similar to ‘Not Laukona’ and ‘Hawaiian *officinarum’*, and of uncertain origin and evocated by Wray (1853) as an introduced sugarcane in Tahiti by Bougainville from Batavia (current Jakarta) in 1769, the molecular fingerprint showing the opposite (VBP very close to VE).

Regarding Tō ‘ute (RBV) and Tō ’ō’opu (PO). These canes are described by Lincoln (2020) as introduced Hawaiian S. *officinarum.* Tō ‘ute is called Kō ‘ie’ie or Cavengerie (Kō is Tō in Hawaiian language) and was introduced in Hawaii from New Caledonia while it was introduced in Tahiti from Batavia Island (Cuzent 1860). However, we can note some contradictions as Lincoln (2020) describe ’ie’ie with a small diameter and poor ratooning which is contrary to Tō ‘ute from Tahiti.
Tō ’ō’opu (PO), imported in the 1920s in Hawaii, is called Badila and is one of the important S*. officinarum* used in breeding programs to produce *Saccharum* spp. modern cultivars, like Black Cheribon and ‘Lahaina’ (Heinz 1987).

Lahaina is an another introduced variety in Hawaii, which is recognized as Otahiti cane and coming from Marquesas Islands in 1853 (Wilfong 1883). It is surprising to see that Brown (1931) doesn’t mention any Otahiti cane in the Marquesas islands. He actually mentions 14 sugarcane in the Marquesas with no name correspondence with names collected in the Society islands.

For Nadeaud (1873), Tō ‘uo’uo, vaihī and rurutu (rutu, RO) are imported and for Cuzent (1860) only Tō ‘ute (RBV) was imported following Wray (1853). In a letter from Pancher (former botanist of Tahiti and New Caledonia) to his colleague Decaisne at the beginning of 1855 (unpublished data), some more important indications can help us regarding identification of noble Polynesian canes: the importation from Sandwich Islands (current Hawaii Islands) of avahi variety is mentioned and seems to be accurate. Pancher indicates that this variety avahi (different spelling of vaihī or ha’avai) is named ’uo’uo by the young Tahitians and we then conclude that Tō ha’avai (Henry 1928), vaihī, ‘uo’uo (Cuzent 1860) and avahi are the same variety which doesn’t exist anymore nowadays. He also mentions that Tō pi’avare (3C) and Tō ‘irimotu (VE) are among the oldest Polynesian introduced varieties. Tō pi’avare (3C) which is recognized as a medicinal cane (Vitrac et al. 2018a) is often confounded with other sugarcane. For example, in a recipe for traditional medicine, Hooper (1995) mention Tō patu from Raiatea (described as a wild species in Tahiti by Cuzent, 1860 and Nadeaud, 1873) as Tō pi’avare from Tahiti, vernacular names being different in a single archipelago. It is also maybe called Tō rā’au by Henry (1929) because of its medicinal use (the word rā’au in Polynesian language meaning a medicine), the description corresponding to the observations we made but Tō rā’au being actually Tō pi’avare (3C). Lincoln (2020) documents how in Hawaii, names for certain cane varieties were tied to their usage, and it is possible that certain names were applied to multiple different cane varieties when they were used in a particular way.

Cuzent (1860) says that Otahiti sugarcane cultivated in the Caribbean French territories has a green or a yellow stripe, which is only the case regarding Tō ‘irimotu (VE) and Tō re’are’a (JRP). Cuzent (1860) and Henry (1928) also mention that cultivated fields presented flowers from May to July without any other distinctions. We then can suppose that the main cultivated sugarcane were the Otahiti ones, with green or yellow stripe, which is only the case for Tō ‘irimotu (VE) and Tō re’are’a (JRP) and as only Tō ‘irimotu (VE) is flowering every year (and Tō re’are’a (JRP) not), we can suppose that Otahiti could be Tō ‘irimotu (VE).

Tō re’are’a (JRP) is one of the most productive noble sugarcane cultivated in Tahiti (Vitrac et al. 2019b) and looks very similar to Yellow Caledonia described by Lincoln (2020) which is an introduced famous productive cane from New Caledonia. However, Lincoln (personal discussions) says that Yellow Caledonia cultivar is definitely different from Tō re’are’a (JRP).
We finally can ask the question of Otahiti cultivar as a single variety or group of varieties? Wilfong (1883) and Lincoln (2020) say that Lahaina is the Otahiti sugarcane introduced in Hawaii in 1853 from the Marqueseas. Tō ’irimotu (VE) seems to be this Otahiti sugarcane, but we also can note that Tō re’are’a (JRP) is morphologically very similar to Tō ’irimotu (VE), the difference being the flowering. We then can suppose that Tō re’are’a (JRP), if from ancient Polynesian introduction, is also a probable Otahiti sugarcane, especially because of its higher agronomic and sugar productivity than other Polynesian S. *officinarum* cultivars.

In consideration of all these points, the Polynesians sugarcane regarded as having been introduced by ancient Polynesians are: Tō ’irimotu (VE), Tō pi’avare (3C), Tō rutu (RO) and Tō ‘ōura (VBP). Tō re’are’a (JRP) is not described in old literature or has been confounded with another cultivar. The 19th century introduced sugarcane are: Tō ‘ute (RBV) and Tō ’ō’opu (PO). All the modern *Saccharum* spp. cultivars are recently introduced (>1900, date of the very first hybridization stations): (i) with unknown origin: rouge reflets verts (RRV), jaune roseau (JR), and (ii) with known origin: Blanche (Bla).

## Conclusion

Tahitian sugarcane cultivars were not kept in a collection and have not been in cultivation for long, this lead to difficulties in recording of their names and origins i.e. introduction or not.

In this study, we were able, using agro-morphological traits and molecular tools, to distinguish, among the 15 collected accessions, we recently collected, the ones corresponding to S. *officinarum*, modern hybrid cultivars and *Saccharum maximum*. We could characterize 7 distinct S. *officinarum* accessions/cultivars.

We were also able to tentatively make correspondence between the collected S*. officinarum* and the one reported in ancient literature. The morphological approach suggested that original Otahiti could be Tō 'irimotu (VE) or Tō re'are'a (JRP). Some distinctive points such as flowering (no flowering for Tō re'are'a) indicate that Tō 'irimotu could be the probable Otahiti described and exported around the world by Bougainville. On the other hand, Tō re'are'a could also be the probable Otahiti because of its high agronomic potential that must have attracted former farmers.

We also confirmed that the wild species *Saccharum maximum* is a hybrid between S. *officinarum* and *Miscanthus floridulus* and revealed that it has good Brix degree and juice production to produce rum.

In French Polynesia, the characterization of the current cultivars will help significantly the sugarcane and rum producers to be sure of what they are growing and to keep safe their recognized geographic origin label that imply the use of the traditional Polynesian S*. officinarum* cultivars.

## Declarations

**List of abbreviations:** AGAP: Amélioration génétique et adaptation des plantes méditerranéennes et tropicales; BAT: Batavia; BC: Black Cheribon; Bla: Blanche ; Ble: Bleue; CCD: Cooled high-resolution Camera; CIRAD: Centre International pour la Recherche Agronomique et le Développement; DAPI: Vectashield Mounting Media; DNA: Desoxyribo Nucleic Acid; GISH: Genomic In Situ Hibridization; HARC: Hawaiian Agricultural Research Center; JFB: Jean François Butaud; JR: Jaune Roseau; JRP: Jaune à Rayure Pourpre; JTR: Jaune à Taches Rouges; PO: Pourpre; PCR: Polymerase chain reaction; RBV: Rouge à Bandes Vertes; RO: Rouge; RRV: Rouge Reflets Verts; *S.: Saccharum;* Spp.: species; Std.: Standard; UPOV: Union internationale pour la protection des obtentions végétales; VBP : Verte à Bandes Pourpres; VE: Verte HAW: Hawaii; 3C: Trois Couleurs ;

**Ethics Approval:** To respect the ISE Code of Ethics Guidelines, before any field sampling, we first got the authorization of local authorities ("Direction de l'Agriculture" of French Polynesia) and secondly ask the agreement of every people where we found the sugarcanes before collect.

We everytime to everybody explained our objectives as first renew knowledge about ancient sugarcanes used by local people and secondly help to develop organic rum production by a recognized geographic origin procedure.

We kept cuttings of all varieties and create some collections in the local administrations ("Direction de l'Agriculture") and museums ("Musée de Tahiti" and "Fare Natura"). We also expect to export them in a quarantine center to protect them (CIRAD visacane®).

We also will produce a poster showing the list of cultivars found with their Polynesian names, exposed in these special places. We finally will publish the list and the characteristics of the cultivars in the local scientist journal which name is "bulletin de la société des océanistes".

**Consent for publication:** All authors consent for publication

**Availability of data and material:** All data and material can be produced in transparency.

**Competing interests:** The Authors declare no competing interests.

**Funding:** The research was supported by both CIRAD and University of French Polynesia.

**Author's contributions:** Mr Vitrac Marotea realized the experimentations, he drove the study and wrote the paper; Mr TeaiTaivini contributed to the aim of the study and the global design; Mrs Shili-Touzi Ines contributed to the writing of the paper and corrections as well**;** Mrs Hervouet Catherine done the genetic analysis and contribute to the writing of the paper**;** Mr Butaud Jean-François contribute to the morphologic observations and interpretations. He also corrected the paper**;** Mr Goebel Francçois-Régis drove the paper and contribute to original design with statistics**;** Mrs D'Hont Angélique drove the paper as well and contribute to the global design. She drove the genetic items and contribute to write the paper.

## Acknowledgments

We thank Susan Schenk, former researcher at the HARC who send us the leaves of Lahaina in 2016 and Noa Kekeuewa Lincoln (Botanist researcher, UH Manoa, Hawaii) for his help identifying the varieties common between Hawaii and Tahiti.

We also thank Sandra Lepers Andrzejewski (genetic researcher) for the DNA extractions done at the Epic Vanille de Tahiti of Raiatea laboratory.

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