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Original article

# Pilot assessment of locally acknowledged morphotypes of *Irvingia gabonensis* (Aubry-Lecomte) Baill. in southwestern Benin (West Africa)

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## Summary

*Introduction* – **This study was set up to assess the local perception on morphological differentiation within sweet African bush mango tree (*Irvingia gabonensis*) in southwestern Benin.** *Materials and methods* – **Locally acknowledged morphotypes (LAM) and local differentiation criteria were determined, using group discussions with 60 farmers. A total of 120 trees distributed between the fixed LAM were randomly sampled with farmers' aid. The trees were morphologically characterized based on their leaves (length and width), fruit (length, diameter and mass), seeds (length, diameter and mass), kernels (mass) and fruit flesh (mass and depth). The owners of the 120 trees were questioned for their LAM preference, number of owned LAM trees, propagation methods, and taboos. Data were analyzed through a multivariate analysis of variance (MANOVA).** *Results and discussion* – **Three LAM were differentiated: (1) a pasty morphotype named '*woto*', (2) an aqueous morphotype named '*shito*', and (3) an intermediate morphotype. The MANOVA revealed that contrary to farmers' perceptions, the accurate prediction of LAM on the field was hard ($P > 0.05$). However, canonical discriminant analysis indicated an overall significant morphological difference between the three LAM ($P < 0.001$). Although farmers preferred pasty and intermediate LAM, the aqueous LAM was most abundantly found on farms. Twelve taboos and their potential negative impacts were unanimously recognized in the context of *I. gabonensis* management. Most farmers admitted to have already broken these taboos, particularly the taboo prohibiting plantation of the species.** *Conclusion* – **This study highlights an ongoing but stagnating local domestication process for this species. A progressive breaking of non-profitable taboos appears to be a gate for a guided selection process.**

**Keywords**
Benin, African bush mango tree, *Irvingia gabonensis*, agroforestry system, plant domestication, local perception

## Significance of this study

*What is already known on this subject?*

- Several scholars investigated the traditional knowledge, distribution range and ecological adaptation of *Irvingia gabonensis*.

*What are the new findings?*

- The study highlights an ongoing local domestication process of *I. gabonensis* in southwestern Benin. The fruit characteristics clearly distinguish three locally acknowledged morphotypes of the species. Farmers break the non-profitable taboos for effective domestication of the species.

*What is the expected impact on horticulture?*

- Our findings contribute to understand the domestication process of indigenous fruit species.

## Résumé

### Evaluation pilote des morphotypes localement reconnus de *Irvingia gabonensis* (Aubry-Lecomte) Baill. dans le Sud-Ouest du Bénin (Afrique de l'Ouest).

*Introduction* – **Cette étude a permis d'évaluer la perception locale de la différenciation morphologique du pommier sauvage (*Irvingia gabonensis*) dans le sud-ouest du Bénin.** *Matériel et méthodes* – **Les morphotypes localement reconnus (MLR) et les critères locaux de différenciation ont été déterminés à partir de discussions de groupe avec 60 agriculteurs. Au total, 120 arbres répartis entre MLR ont été échantillonnés au hasard avec l'appui des agriculteurs. Les arbres ont été caractérisés morphologiquement en fonction de leurs feuille (longueur et largeur), fruit (longueur, diamètre et masse), graine (longueur, diamètre et masse), du noyau (masse) et de la chair du fruit (masse et profondeur). Les propriétaires de 120 arbres ont été interrogés sur leur préférence en MLR, le nombre d'arbres à MLR leur appartenant, leurs méthodes de propagation et les tabous. Les données**

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**ont été analysées par analyse de variance multivariée (MANOVA).** *Résultats et discussion* **– Trois MLR ont été différenciés: (1) un morphotype pâteux appelé '*woto*', (2) un morphotype aqueux appelé '*shito*', et (3) un morphotype intermédiaire. Contrairement aux perceptions des agriculteurs, l'identification précise des MLR sur le terrain s'est révélée difficile ($P > 0{,}05$). Cependant, l'analyse canonique discriminatoire a fait apparaître une différence morphologique globalement significative entre les trois MLR ($P < 0{,}001$). Bien que les agriculteurs préfèrent le MLR pâteux et intermédiaire, le MLR aqueux est le plus abondant. Douze tabous et leurs impacts négatifs potentiels ont été unanimement reconnus dans le contexte de la gestion de *I. gabonensis*. La plupart des agriculteurs ont admis avoir déjà brisé ces tabous, en particulier le tabou interdisant la plantation de l'espèce.** *Conclusion* **– Cette étude fait ressortir le processus de domestication en cours mais stagnant du pommier sauvage. Une rupture progressive des tabous non rentables semble être une porte ouverte sur un processus de sélection assisté.**

**Mots-clés**
Bénin, manguier ou pommier sauvage, *Irvingia gabonensis*, système agroforestier, domestication des plantes, perception locale

## Introduction

On-farm conservation and management of wild edible tree species has been the focus of many recent studies worldwide (Leakey and Page, 2006; Leakey *et al.*, 2003; Page, 2003; Pauku *et al.*, 2010) because it offers numerous opportunities in regard of human livelihood enhancement, ecosystem restoration and biodiversity conservation (Pauku *et al.*, 2010; Atangana *et al.*, 2002; Oyediran *et al.*, 2007; Leakey, 2001, 2010; Vihotogbé *et al.*, 2007, 2013, 2014). The African bush mango tree (ABMT), *Irvingia gabonensis* (Aubry-Lecomte) Baill., has been identified as the top provider of non-timber forest products (NTFP), with a high potential to alleviate poverty through direct income and agrosystem resilience enhancement in West and Central Africa (Vihotogbé *et al.*, 2012; Leakey and Tchoundjeu, 2001). This species is important because of its high food, economic and medicinal values (Franzel *et al.*, 1996). *Irvingia gabonensis* appears in the humid lowland forest areas in Sub-Saharan African countries (Vihotogbé *et al.*, 2013), from southern Senegal to Angola and South Soudan (Ainge and Brown, 2004; Harris *et al.*, 2005; Kengni *et al.*, 2011). Little information is available on the intraspecific variation in morphological, physiological and genetic traits, ecological requirements and adaptation of this tree (Atangana *et al.*, 2002; Leakey *et al.*, 2000, 2004). To improve and speed up the ongoing endogenous domestication process, there is a need to reveal intra-specific patterns which could lead to a selection of an 'ideotype', adequately responding to the socioeconomic optimization of marketable products such as fresh fruit and kernels with high oil and polysaccharide content (Atangana *et al.*, 2002; Leakey and Tchoundjeu, 2001; Leakey *et al.*, 2000, 2004).

Several studies have investigated the traditional knowledge of *I. gabonensis* over its entire distribution range (Ainge and Brown, 2004; Ayuk *et al.*, 1999) but with little regard to how local people perceive and manage its intraspecific variation. However, local perception on the value of different morphotypes of a tree might influence traditional domestication systems, since this perception strongly hinges on fruit traits (shape, size and taste), which determine choices in consumption, plantation and commercialization (Leakey *et al.*, 2003; Luckwill, 1959; Leakey, 2012; Rashidi and Seyfi, 2007). Likewise, local taboos or social representations also affect – at least at farm level – ABMT utilization and management, shaping its spatial arrangement, population size, and above all, its conservation (Vihotogbé *et al.*, 2013, 2014).

So far, the scientific as well as technical support for domestication of non-timber forest trees (Simons and Leakey, 2004) are not fully integrated in the traditional domestication processes of ABMTs in West and Central Africa. As a result, it is difficult for local farmers to secure the best ideotypes from continuous interbreeding with undesired morphotypes, which also need to be preserved in the sense of genetic resource conservation (Vihotogbé *et al.*, 2013). In the republic of Benin, located in the Dahomey gap, only the sweet ABMT has been reported (Vihotogbé *et al.*, 2013, 2014). Recently, small scale farmers of the Couffo Region (Southwestern Benin, Plateau phytogeographical district) were reported to have reached an advanced domestication stage of sweet ABMT, while in Central Africa the exploitation still relies mostly on wild populations (Vihotogbé *et al.*, 2013; Lowe *et al.*, 2000). Indeed, morphological characterization revealed a clear differentiation of populations in the Couffo region from other populations, suggesting a history of selection actions targeted towards big fruit size with heavy seeds in this region (Vihotogbé *et al.*, 2013). In Couffo, people currently distinguish two groups in sweet ABMT, based on fruit characteristics: pasty fruits and aqueous fruits (Vihotogbé *et al.*, 2007), both with very sweet and deep fruit flesh (mesocarp). On-farm, adequate differentiation of morphotypes, preferentially identifiable at the non-fruiting vegetative phase, is crucial for a targeted and fast selection process. Here, we investigated whether the morphotypes identified by the farmers in the Couffo region can be confirmed by quantitative morphological descriptors. Also, assuming that farmers of the Couffo region are able to control preferred morphotypes on their farms, we expected to find more trees of the preferred morphotype than of the non-preferred morphotype on these farms.

Our aim was to assess how farmers of the Couffo region differentiate and manage morphotypes in ABMT and how this knowledge can be integrated in a formal framework, to enhance farmers' livelihood and enhance biodiversity conservation. Specifically, we asked the following research questions: (1) What are the locally acknowledged morphotypes-LAM of ABMT fruit and which criteria do farmers use to distinguish them at the vegetative phase? (2) Can quantitative descriptors of leaves (length and width), fruits (length, diameter and mass), seeds (length, diameter and mass), kernels (mass) and fruit flesh (mass and depth) distinguish LAM identified in the Couffo region? (3) Does the local classification match with the morphological classification? (4) Does the ongoing selection process have an impact on the fruit and leaf morphological characteristics? (5) What is the preferred LAM and is this preference reflected in the number of sweet ABMT owned by farmers of the Couffo region? (6) How do farmers of the Couffo region propagate sweet ABMT? (7) What are the taboos on sweet ABMT in the Couffo region?

## Materials and methods

### Study area

The study was conducted in the western part of the phytogeographical district of Plateau (Adomou *et al*., 2006), belonging to the Guinea-Congolian phytogeographical zone in Benin (Figure 1). The climate is tropical humid and the rainfall is bimodal with a mean annual rainfall of 900–1,100 mm, a mean temperature of 25–29 °C and a high air relative humidity, reaching 85% in August (Adomou *et al*., 2006). Since this area is located in southern Benin, it entirely belongs to the Dahomey gap, a distinct eco-region reaching from Accra (Ghana) to Badagry (Nigeria) (Maley, 1996; Sowunmi, 2004). The establishment of this vast savannah within the West African/Guinea forest belt has been postulated either as a consequence of the last global climate change (Maley, 1996) or as that of human activities regarding intensive woody materials exploitation (Akoegninou, 1984; Fairhead and Leach, 1998; Jenik, 1994). Ferralitic soil with concretions is the major soil type (Adomou *et al*., 2006). Agriculture is the main activity, occupying 90% of the active population. Soil fertility is poor because of over-exploitation and high demographic pressure, which suppress fallows (Afrique Conseil, 2006a, 2006b, 2006c, 2006d). Agroforestry is an increasing practice and sweet ABMT plays a crucial role to value the soil and conserve its fertility, especially because ABMT suits the ecological conditions of the region. Sweet ABMT is a relatively widely cultivated tree in the region and its maintenance and protection in local farming systems denotes its sociocultural importance (Vodouhê, 2003). The Couffo region is dominated by *Adja* people, a socio-cultural group that has a great knowledge on sweet ABMT and highly values its products (Vihotogbé *et al*., 2014).

### Sampling and data collection

Eleven localities across four districts (Aplahoué, Klouékanmey, Lalo and Toviklin) were randomly selected within the study region (Figure 1). First, in each locality a group discussion was performed, where 15 farmers owning ABMT per district were asked to describe the locally acknowledged morphotypes (LAM) of sweet ABMT, based on fruits, and to explain the criteria used to discriminate these morphotypes. Based on this, 40 trees per LAM (120 trees in total) were randomly sampled with the help of the farmers. Following Cornelissen *et al*. (2003), ten mature leaves were randomly harvested from the sunward side down the branches of each tree, in order to assess morphological variation. To avoid any deformation during transportation and conservation, leaves were set in wet paper in a gelignite bag which has been disposed in an icebox.

Leaves were measured for their length (i) and width (ii). Methods developed by Leakey *et al.* (2000) and successfully applied in ICRAF tree-to-tree evaluation for ABMT were used to assess morphological variation in fruits, fruit flesh (mesocarp), seeds and kernels. A total of 15 to 30 ripped fruits were collected per tree in 2013 during June and July, the peak fruiting periods of sweet ABTM (Vihotogbé *et al*., 2012). Following Vihotogbé *et al*. (2012), trees were visited early in the morning to collect mature fruits that had freely fallen down during the night. Fresh fruit mass (iii) (measured on the day of collection), seed mass (iv) (measured two days after depulping and suitable drainage) and fresh kernel mass (v) (measured after careful extraction of the nut) were measured using an electronic balance of 0.0001 g sensitivity. Fresh fruit length (vi) and diameter (vii), fruit flesh (mesocarp) depth (viii), seed length (ix), maximum seed diameter (x) and minimum seed diameter (xi) were measured using

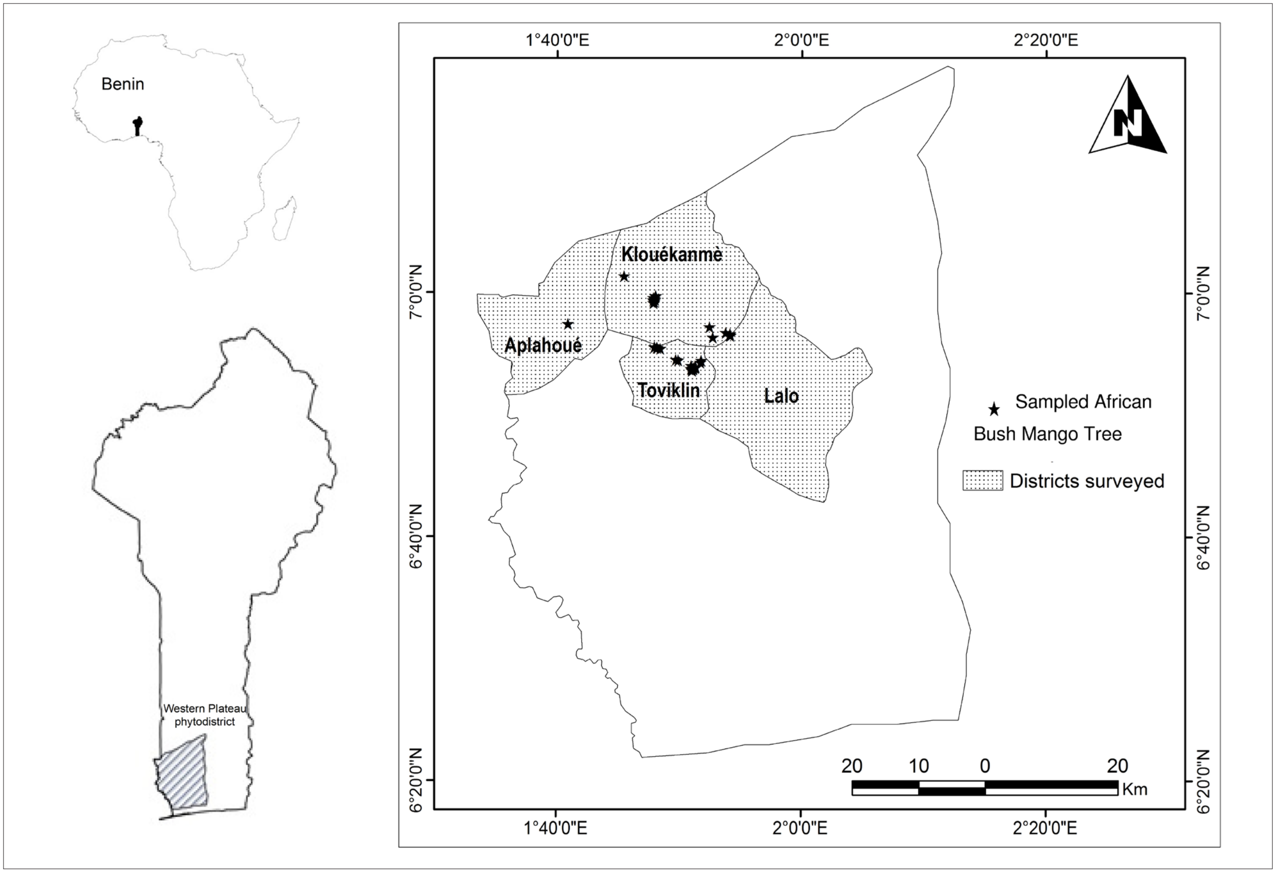

**Figure 1.** Map of the study area showing the surveyed districts and location of sampled African bush mango trees (ABMT).

an electronic caliper accurate to 0.1 mm. Fruit flesh mass (xii) was derived from fruit and kernel mass.

Owners of 120 selected LAM were identified and involved in an individual semi-structured interview. Interviews focused on preferred LAM, number of trees owned of each LAM, and the propagation methods used. The type of usage (food, cultural, medicine, fuel, pasture and services), plant parts used (leaves, fruit, kernel, seed, bark, *etc.*), and taboos on sweet ABMT were also recorded. Farmers were also asked if they inherited their trees.

### Data analysis

Locally acknowledged morphotypes (LAM) and local field differentiation traits were first analyzed using percentages. Morphological characteristics were then arranged according to LAM. Multivariate analysis of variance (MANOVA) was performed on the factor LAM (considered as fixed) to check whether the measured quantitative descriptors of sweet ABMT leaf, fruit, fruit flesh, seed and kernel allow distinguishing the LAM. The set of sampled localities was used as a random factor in the ANOVA and the percentage of the variability linked to localities was computed for each quantitative descriptor to reveal the importance of between localities variability. No data transformation was applied to the morphological characteristics variables because normality and homoscedasticity were checked without transformation using the Ryan-Joiner test of normality and the Levene test for homogeneity of variances. A Canonical Discriminant Analysis (CDA) was then performed on the three LAM in order to describe each LAM and highlight differences in their morphological characteristics.

To check whether the LAM match a morphological classification, a hierarchical clustering was performed using the 12 measured morphological descriptors. Mixed ANOVA were performed on the ABMT morphological classes obtained from the clustering procedure to check for significant difference in each morphological trait. The ABMT morphological classes were then described using a Principal Component Analysis (PCA) and a Fisher exact was then performed to test for independence between LAM and morphological classes of ABMT.

To test if the ongoing selection process (represented by farmers that actively have sown ABMT) has a significant impact on the fruit and leaf morphological characteristics, farmers were gathered into two groups (protection of spontaneous seedling versus actively sowing). A Fisher exact test was then performed to test for independence between morphological classes of ABMT and the farmer groups. All the statistical analyses were performed with the software R (R Development Core Team, 2012), using the *nlme* package for mixed modeling, the *Candisc* package for CDA analysis, and the *FactoMineR* package for PCA. The critical *P-value* was set to $\alpha = 0.05$.

The percentage of farmers preferring a specific LAM was computed and the Fisher exact test was applied to test whether preference (Yes versus No) was independent from LAM. The average number of sweet ABMT trees owned per farmer was calculated and downscaled per LAM to reveal which one dominated in the study area. A generalized linear model using Poisson error distribution was used to compare the number of individual trees owned per farmer against the number of owned LAM. The percentage of farmers who mentioned a type of use and use of a plant part were also computed. Data on propagation methods, taboos and inheritance status of sweet ABMT trees were analyzed using the percentage of each response.

## Results

### Locally acknowledged morphotypes of sweet ABMT

Three locally acknowledged morphotypes (LAM) of the sweet Africa bush mango tree (ABMT) were reported by all respondents. Local names were unanimously '*Woto*' for the pasty fruits and '*Shito*' for the aqueous fruits with the highest fibrosity and water content. The third type has no clear local name, but was described as a morphotype with mixed characteristics between '*Woto*' and '*Shito*'. According to the farmers, these three LAMs are produced by different trees, *i.e.*, an individual tree can only produce one type of fruit. In the field, farmers used leaf characteristics to distinguish the LAMs. Particularly, trees with aqueous bush mango were reported (by 100% of the respondents) to have the smallest leaf length and width, while the pasty bush mango trees were reported to have the longest and widest leaves. However, respondents were not able to distinguish between the pasty and mixed sweet ABMT using leaf characteristics.

### Quantitative morphological differences in LAM of sweet ABMT

The variance components from the MANOVA performed on the three LAM indicated that the between localities variability range from 17.2% to 44.3% of the total variability of the measured morphological traits of ABMT (Table 1). The environmental variability of ABMT morphological traits within the Couffo region has a low importance relative to between trees variability. The results of the mixed ANOVA indicated no significant difference between LAM on leaf shape (length and width), fruit length, seed mass, seed length, maximum seed diameter, and kernel mass ($P > 0.05$). However, fruit mass and fruit diameter, fruit flesh mass and depth, and the minimum diameter of the seed showed significant differences between the LAM ($P < 0.05$). The leaves of mixed and pasty sweet ABMT were longer (133.37 mm ± 21.86% and 130.37 mm ± 26.82%, respectively) and wider (57.09 mm ± 19.84% and 55.31 mm ± 24.75%, respectively) than those of aqueous sweet ABMT (length: 101.93 mm ± 22.77%, width: 48.07 mm ± 22.61%). The leaf characteristics actually lack statistical consistency to confirm the perception of the farmers.

The results of the CDA performed on the LAM showed that 100% of the information was represented in two canonical axes explaining respectively 73.7% and 26.3% of the total variability (Table 2). Overall, the two axes were highly significant ($P < 0.001$) in discriminating LAM. The first axis was positively correlated with the fruit diameter, fruit flesh depth, seed smallest diameter, seed mass, fruit flesh mass and fruit mass (correlation $> 0.5$), showing that these morphological characteristics are positively linked. The second axis was correlated with leaf length. Overall, the mixed LAM revealed the highest values for all considered morphological characteristics (Figure 2). The aqueous LAM trees had the lowest values; and the pasty LAM the medium values (Figure 2).

The hierarchical clustering procedure resulted in three morphological classes of ABMT gathering 46 ABMT-Class 1, 42 ABMT-Class 2, and 32 ABMT-Class 3 (Figure 3). The results of the mixed ANOVA showed that all the 12 morphological descriptors measured on leaves, fruit, mesocarp, seeds and kernels varied significantly between the ABMT morphological classes ($P \leq 0.001$) (Table 3). The between localities variability was relatively low ($< 50\%$) for all morphological descriptors (Table 3).

**Table 1.** Multivariate ANOVA (locality as random factor) performed on the previously identified LAM characteristics: variation in leaf, fruit, mesocarp seed and kernel of African bush mango trees (ABMT) and the three locally acknowledged morphotypes (LAM). Cv: coefficient of variation (in %); Min: Minimum; Max: Maximum; LOC: variability between localities (in %); DF: Degree of freedom; *P*: Probability.

| Plant parts | Characteristics | Statistical parameters | All trees | Aqueous | Pasty | Mixed | LOC (%) | Results of the ANOVA | | | Normality |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | DF | *F*-value | *P* | *P* |
| Leaf | Length (mm) | Mean (cv) | 109.12 (25.18) | 101.93 (22.77) | 130.37 (26.82) | 133.37 (21.86) | 24.91 | 2 | 1.84 | 0.164 ns | 0.880 |
| | | Min-Max | 57.73-168.00 | 57.73-147.08 | 66.47-168.00 | 99.16-168.00 | | | | | |
| | Width (mm) | Mean (cv) | 46.61 (23.76) | 48.07 (22.61) | 55.31 (24.75) | 57.09 (19.84) | 38.95 | 2 | 0.68 | 0.509 ns | 0.686 |
| | | Min-Max | 25.47-73.81 | 25.47-65.35 | 31.43-73.81 | 44.31-69.13 | | | | | |
| Fruit | Mass (g) | Mean (cv) | 172.62 (28.53) | 157.87 (31.58) | 175.74 (26.38) | 216.39 (14.20) | 42.55 | 2 | 4.01 | 0.021 * | 0.551 |
| | | Min-Max | 93.37-298.90 | 93.37-229.27 | 115.76-280.48 | 168.80-298.90 | | | | | |
| | Length (mm) | Mean (cv) | 66.29 (10.95) | 64.35 (11.55) | 67.22 (10.86) | 70.47 (6.93) | 36.32 | 2 | 1.32 | 0.272 ns | 0.3536 |
| | | Min-Max | 52.30-83.83 | 52.30-78.25 | 59.39-83.83 | 63.63-76.35 | | | | | |
| | Diameter (mm) | Mean (cv) | 65.29 (9.65) | 62.86 (10.24) | 65.98 (7.70) | 72.00 (5.58) | 44.30 | 2 | 5.42 | 0.006 ** | 0.190 |
| | | Min-Max | 54.95-79.75 | 54.95-79.75 | 56.13-76.24 | 67.27-77.14 | | | | | |
| Mesocarp | Depth (mm) | Mean (cv) | 20.97 (11.99) | 20.19 (12.27) | 21.02 (10.38) | 23.62 (8.74) | 34.34 | 2 | 3.34 | 0.039 * | 0.536 |
| | | Min-Max | 16.75-26.56 | 16.75-25.65 | 16.91-26.14 | 20.95-26.56 | | | | | |
| | Mass (g) | Mean (cv) | 159.90 (29.11) | 145.82 (32.36) | 163.05 (26.70) | 201.14 (14.77) | 42.30 | 2 | 3.91 | 0.023 * | 0.342 |
| | | Min-Max | 87.55-280.06 | 87.55-280.06 | 107.21-258.98 | 156.70-230.07 | | | | | |
| Seed | Mass (g) | Mean (cv) | 12.72 (27.89) | 12.05 (27.50) | 12.69 (30.40) | 15.25 (18.18) | 35.02 | 2 | 1.55 | 0.218 ns | 0.789 |
| | | Min-Max | 5.82-23.43 | 5.82-18.84 | 8.55-23.42 | 12.11-18.32 | | | | | |
| | Length (mm) | Mean (cv) | 44.41 (12.56) | 43.66 (13.77) | 44.77 (12.04) | 46.05 (11.09) | 17.19 | 2 | 0.44 | 0.646 ns | 0.300 |
| | | Min-Max | 33.49-56.01 | 33.49-53.42 | 38.33-56.01 | 40.14-51.97 | | | | | |
| | Greatest diameter (mm) | Mean (cv) | 32.83 (9.51) | 32.19 (9.45) | 32.61 (9.59) | 35.76 (5.54) | 22.23 | 2 | 2.48 | 0.088 ns | 0.087 |
| | | Min-Max | 26.20-41.68 | 26.20-38.25 | 27.30-41.68 | 33.82-37.97 | | | | | |
| | Smallest diameter (mm) | Mean (cv) | 22.09 (10.44) | 21.28 (10.68) | 22.43 (7.76) | 24.03 (12.19) | 18.47 | 2 | 3.29 | 0.041 * | 0.134 |
| | | Min-Max | 17.85-27.67 | 17.85-26.56 | 20.88-27.67 | 20.30-27.23 | | | | | |
| Kernel | Mass (g) | Mean (cv) | 3.49 (30.68) | 3.49 (28.10) | 3.47 (33.22) | 3.53 (38.51) | 39.76 | 2 | 0.15 | 0.862 ns | 0.678 |
| | | Min-Max | 1.71-5.94 | 1.71-5.18 | 1.83-5.94 | 1.83-4.93 | | | | | |

ns: not significant; *: significant at 5%.

The results of the PCA showed that 100% of the information was represented in two principal components. The first principal component explained 90.44% of the overall variability and was positively correlated with all morphological descriptors (correlation > 0.95) except seed mass (Table 4). Seed mass was positively correlated with the second principal component (correlation = 0.972) which explained 9.56% of the overall variability. Traits related to leaves (length and width), fruit (diameter, length and mass), mesocarp (depth and mass) and seeds (mass, length, largest diameter and smallest diameter) represented by the first component sorted the three morphological classes so that for these traits, class 1 < class 2 < class 3 (Figure 4). Additional to this distinction, the second component showed that Class 2 (mean kernel mass = 3.88 g; Table 4) represented ABMT which produced heavy kernel relative to Class 1 (mean = 3.23 g; Table 3) and Class 3 (mean = 3.40 g; Table 4).

The result from the Fisher exact test showed that the distribution of ABMT in the morphological classes defined using a hierarchical clustering depended significantly on the LAM (*P* < 0.001). The morphological Class 1 was of aqueous (65.22%) and pasty (34.78%) ABMT; Class 2 was mainly of pasty (47.62%) and mixed (38.10%) ABMT; and Class 3 was mainly of mixed ABMT (75.00%). The result from Fisher exact test showed that the distribution of ABMT in the morphological classes defined using a hierarchical clustering did not depend significantly on the LAM (*P* = 0.380).

### LAM preferences, number of owned LAM per farmer, propagation methods and uses of sweet ABMT

Preferences varied significantly between LAM (*P* < 0.001), depending on the fruit flesh. Indeed, more than three quarters of the farmers (77%) gave preference to pasty fruit, 15% and 9% of them gave preference respectively to mixed and aqueous fruits of sweet ABMT (Figure 5a). The total number of LAM trees owned per farmer also varied significantly (GLM, Residual deviance = 628.57 , DF = 2, *P* < 0.0001), averaging 8 ± 2 trees for the aqueous LAM, 5 ± 1 trees for the pasty one and 1 ± 1 trees for the mixed one. Overall, 58% sweet ABMTs owned by farmers produced aqueous fruits, 34% produced pasty fruits and 8% produced mixed fruits (Figure 5b). The two most important type of uses were food and medicinal uses (Figure 5c), practiced by all the surveyed farmers. The used plant parts were mostly fruit flesh and kernels for food and leaves for medicine (Figure 5d). Wood (fuel) and bark (medicine) were the least used plant parts. Propagation of the plant by seeds was reported by all farmers. A total of 56% farmers actively sow, while 35% farmers reported protection of spontaneous seedlings on farms or in home gardens. A total of 44% farmers inherited at least one of the sweet ABMT they owned.

**TABLE 2.** Canonical discriminant analysis (CDA) on ABMT morphological traits against LAM (Aqueous, Pasty and Mixed): Correlations between canonical axes (Can1 and Can2) and ABMT morphological characters; *P* = probability.

| Morphological characteristics | Can1 | Can2 |
|---|---|---|
| Fruit diameter | 0.649 | -0.112 |
| Mesocarp deep | 0.581 | -0.222 |
| Seed smallest diameter | 0.552 | -0.012 |
| Mesocarp mass | 0.524 | -0.123 |
| Fruit mass | 0.522 | -0.129 |
| Seed largest diameter | 0.458 | -0.312 |
| Fruit length | 0.400 | 0.029 |
| Leaf width | 0.378 | -0.353 |
| Seed mass | 0.577 | -0.181 |
| Leaf length | 0.294 | -0.544 |
| Seed length | 0.202 | 0.013 |
| Kernel mass | 0.012 | -0.028 |
| *P* | < 0.001 | < 0.001 |

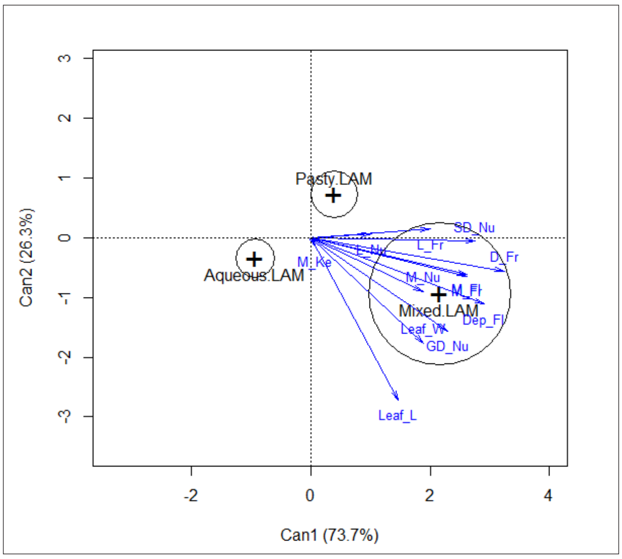

**FIGURE 2.** Results of the Canonical Discriminant Analysis on the 120 selected LAM: representation of locally acknowledged morphotypes (LAM) of African bush mango trees (ABMT) in the two-dimensional canonical plan. *Quantitative descriptors*: M_Fr fruit mass, L_Fr fruit length, D_Fr fruit diameter, Dep_Fl fruit flesh depth, M_Fl fruit flesh mass, M_Nu seed mass, L_Nu seed length, GD_Nu seed greatest diameter, SD_Nu seed smallest diameter, M_Ke Kernel mass, L_Leaf leaf length, W_Leaf Leaf width.

**FIGURE 3.** Results of hierarchical clustering based on morphological descriptors of leaves (length and width), fruits (length, diameter and mass), mesocarp (depth and mass), seed (mass, length, largest and smallest diameters) and kernel (mass) of the 120 ABMT collected from the Couffo region (Republic of Benin).

**Table 3.** Multivariate ANOVA (locality as random factor) performed on the previously identified LAM characteristics: variation in leaf, fruit, mesocarp seed and kernel of African bush mango trees (ABMT) and three morphological ABMT classes defined using hierarchical clustering. Cv: coefficient of variation (in %); Min: Minimum; Max = Maximum; LOC: variability between localities (in %); DF: Degree of freedom; *P*: Probability.

| Plant parts | Characteristics | Statistical parameters | Class 1 | Class 2 | Class 3 | LOC (%) | Results of the ANOVA | | | Normality |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | DF | *F*-value | *P* | *P* |
| Leaf | Length (mm) | Mean (cv) | 98.05 (23.95) | 121.38 (17.61) | 129.35 (22.32) | 38.20 | 2 | 13.72 | < 0.001 * | 0.571 |
| | | Min-Max | 57.73-145.93 | 101.93-168.00 | 91.60-168.00 | | | | | |
| | Width (mm) | Mean (cv) | 41.83 (20.83) | 50.78 (15.99) | 56.30 (19.83) | 39.60 | 2 | 19.23 | < 0.001 * | 0.357 |
| | | Min-Max | 25.47-58.20 | 41.35-73.81 | 38.89-69.13 | | | | | |
| Fruit | Mass (g) | Mean (cv) | 142.18 (16.71) | 181.92 (8.35) | 244.35 (8.97) | 44.98 | 2 | 223.48 | < 0.001 * | 0.312 |
| | | Min-Max | 93.37-199.74 | 166.08-206.23 | 221.63-298.90 | | | | | |
| | Length (mm) | Mean (cv) | 62.68 (7.17) | 67.33 (6.47) | 74.07 (6.62) | 43.30 | 2 | 69.58 | < 0.001 * | 0.083 |
| | | Min-Max | 52.30-71.73 | 55.80-72.97 | 67.78-83.83 | | | | | |
| | Diameter (mm) | Mean (cv) | 61.33 (5.99) | 67.02 (2.57) | 74.91 (3.13) | 48.09 | 2 | 217.83 | < 0.001 * | 0.328 |
| | | Min-Max | 54.95-67.99 | 63.06-70.15 | 70.71-79.75 | | | | | |
| Mesocarp | Depth (mm) | Mean (cv) | 19.39 (7.76) | 21.02 (4.75) | 24.65 (5.91) | 0.00 | 2 | 288.16 | < 0.001 * | 0.272 |
| | | Min-Max | 16.75-21.97 | 20.24-23.58 | 22.87-26.56 | | | | | |
| | Mass (g) | Mean (cv) | 130.98 (16.78) | 168.31 (7.96) | 228.32 (8.99) | 45.14 | 2 | 237.72 | < 0.001 * | 0.105 |
| | | Min-Max | 87.55-178.12 | 153.35-192.73 | 207.44-280.06 | | | | | |
| Seed | Mass (g) | Mean (cv) | 11.20 (21.26) | 13.61 (20.77) | 16.03 (17.28) | 38.30 | 2 | 35.45 | < 0.001 * | 0.255 |
| | | Min-Max | 5.82-14.87 | 9.31-18.32 | 13.11-23.42 | | | | | |
| | Length (mm) | Mean (cv) | 42.89 (9.77) | 44.53 (11.41) | 47.99 (9.52) | 34.25 | 2 | 16.90 | < 0.001 * | 0.054 |
| | | Min-Max | 34.00-50.85 | 33.49-51.59 | 41.66-56.01 | | | | | |
| | Greatest diameter (mm) | Mean (cv) | 31.49 (7.09) | 33.95 (7.41) | 35.89 (6.29) | 15.43 | 2 | 53.45 | < 0.001 * | 0.336 |
| | | Min-Max | 26.20-34.60 | 29.99-38.25 | 33.05-41.68 | | | | | |
| | Smallest diameter (mm) | Mean (cv) | 21.20 (8.34) | 22.52 (8.74) | 24.63 (9.39) | 0.00 | 2 | 54.93 | < 0.001 * | 0.192 |
| | | Min-Max | 17.85-26.22 | 20.30-27.14 | 21.74-27.67 | | | | | |
| Kernel | Mass (g) | Mean (cv) | 3.23 (29.98) | 3.88 (18.02) | 3.40 (40.10) | 47.94 | 2 | 11.76 | 0.001 * | 0.599 |
| | | Min-Max | 1.71-5.52 | 2.53-4.94 | 1.83-5.94 | | | | | |

ns: not significant; *: significant at 5%.

### Taboos and cultural practices on sweet ABMT

Overall, 12 ABMT-related taboos were reported (Table 5). All respondents indicated that non-respect of the taboos induces consequences including reduced fruit production, baby abortion, living in trouble, or death of a responsible person or his/her children (Table 5). To stimulate fruit production, farmers (56%) offer boiled maize (*Zea mays* L.) mixed with sugar and a white stuff to grid them to sweet ABMT trees. Three of the 60 surveyed farmers reported sacrifices of sheep or chicken to sweet ABMT trees as gratitude to their fruit production.

**TABLE 4.** Principal components analysis (PCA) on African bush mango tree (ABMT) morphological classes obtained from a hierarchical clustering: Correlations between principal components (Dim1 and Dim2) and ABMT morphological characters. In parenthesis are the contribution of each axis to the analysis.

| Morphological ABMT characters | Dim1 (90.44%) | Dim2 (9.56%) |
|---|---|---|
| Seed mass | 1.000 | 0.013 |
| Mesocarp depth | 0.999 | -0.046 |
| Fruit diameter | 0.997 | -0.079 |
| Seed largest diameter | 0.997 | 0.081 |
| Fruit length | 0.996 | -0.091 |
| Fruit mass | 0.994 | -0.113 |
| Seed smallest diameter | 0.993 | -0.117 |
| Mesocarp mass | 0.993 | -0.119 |
| Leaf width | 0.989 | 0.150 |
| Seed length | 0.982 | -0.188 |
| Leaf length | 0.958 | 0.286 |
| Kernel mass | 0.237 | 0.972 |

## Discussion

### Locally acknowledged morphotypes (LAM) of sweet African bush mango trees (ABMT)

Three LAM of sweet ABMT fruit were unanimously recognized by farmers in the study area, which are locally distinguished based on the water content and fibrosity of the fruits. A high agreement for the morphotype names proves the importance of the species and a consensus on the three LAMs. Leaf shape was the trait used by the local farmers to distinguish LAMs in the field. The observed variation in leaf shape

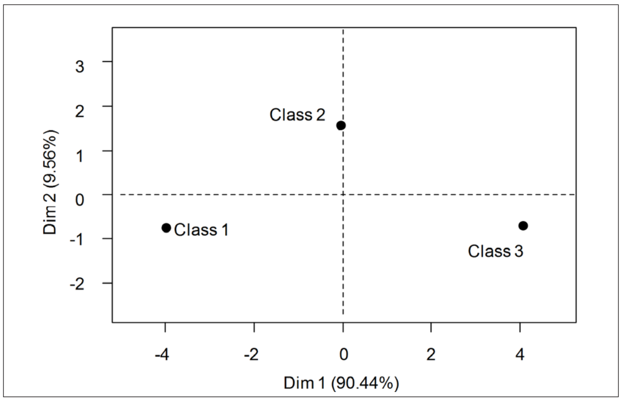

**FIGURE 4.** Results of principal components analysis (PCA) on ABMT morphological classes obtained from a hierarchical clustering (*n* = 120): Class map. The first component is positively correlated with leaf characteristics (length and width), fruit characteristics (length, diameter and mass), mesocarp characteristics (depth and mass) and seed characteristics (mass, length, largest diameter and smallest diameter). The second component is positively correlated with the kernel mass.

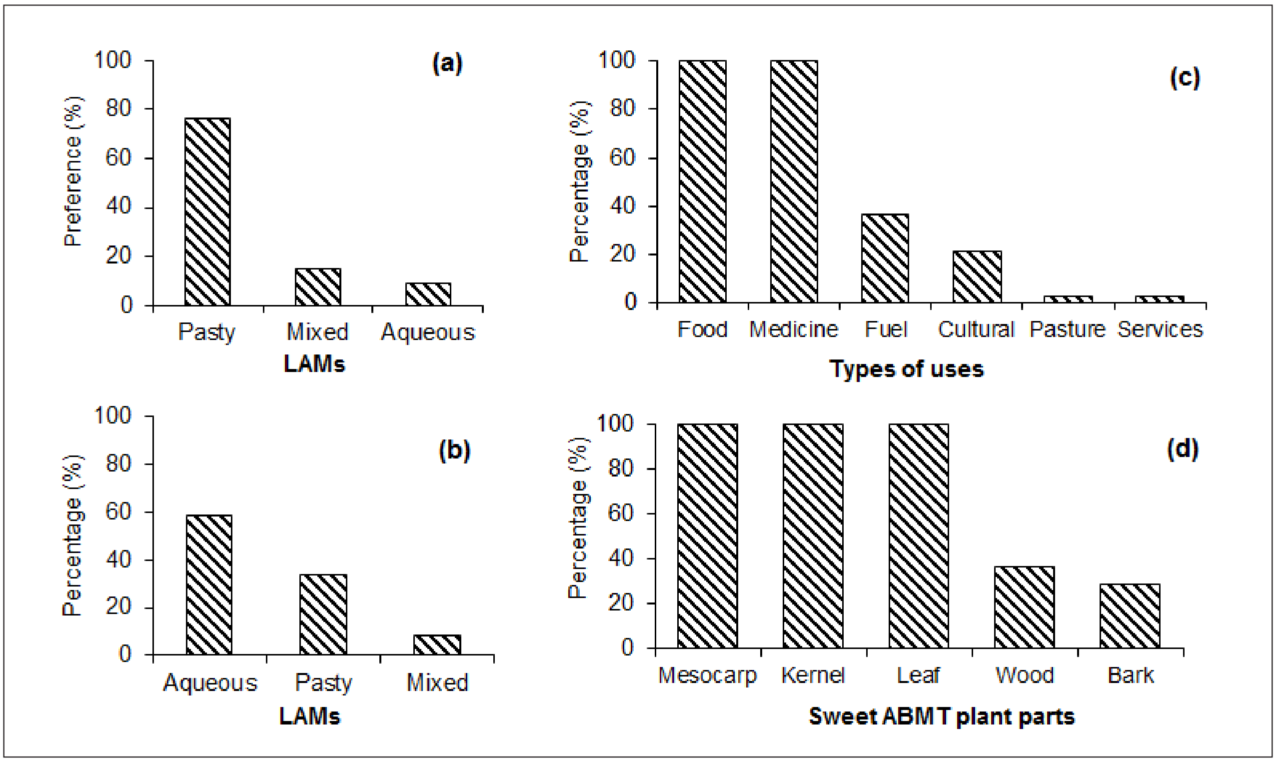

**FIGURE 5.** Preferred locally acknowledged morphotypes (LAM) of: (a) Preference of ABMT types by the respondents; (b) Percentage of LAM owned by the respondents; (c) Percentage of types of use; and (d) Percentage of plant parts used.

**Table 5.** Taboos or representations of African bush mango tree (ABMT) in the Couffo region (Republic of Benin) and associated risks in condition of non-respect.

| Taboos or representations | Risks or gains |
|---|---|
| Not to bargain fruit or tree price under the tree<br>Not to shake the tree's branches when harvesting fruits<br>Owner's nephew should not climb the ABMT<br>Not to talk about an ABMT's bad performances near the tree<br>Not to break a promise (offering an animal or other sacrifice)<br>Not to eat palm (*Elaeis guineensis*) oil before going under the ABMT<br>Not to depulp fruit or crush seed under the ABMT<br>Not to set fire around the ABMT<br>Not to knock a hoe against the ABMT | Weak fruit production |
| A woman should not use ABMT wood as fuel (only menopausal women could) | Miscarriage or death of children |
| Not to cut down an ABMT during fruit production | Death or life with troubles (without peace) |
| Not to plant ABMT | The planter will die before fruit production |
| To grid the ABMT with a white stuff and offer boiled maize and sugar, or an animal (sheep or goat, cock or hen) | Stimulate fruit production |

(5.80–16.80 cm for length and 2.50–7.40 cm for width) overlap those reported in previous studies (respectively 5.20–14.60 cm and 2.70–7.20 cm for length and width) with little overflowing on the maximum values (Vihotogbé *et al.*, 2013). Likewise, the observed values (mean, min–max) of fruit flesh depth (2.10, 1.70–2.60 cm, resp.), seed length (4.40, 3.40–5.60 cm, resp.) and seed width ([2.20–3.30], [1.80–2.60]–[2.80–4.20] cm, resp.) were close to those reported in the same area by Vihotogbé *et al.* (2013) on a population $n = 24$: mean fruit flesh depth ([2.20–2.40], [0.50–1.60]–[3.80–3.80] cm, resp.), seed length (4.30, 3.00–5.70 cm, resp.) and seed width (3.30, 2.20–5.30 cm, resp.). However, there were some noticeable differences with regard to fruit mass ([172.60, 93.37–298.90 g] *vs.* [213.70, 78.00–426.00 g], resp., in the previous study), and seed mass ([12.70, 5.82–23.43 g] *vs.* [18.10 g, 6.00–30.00 g], resp.). These differences could be related to the number of kernels per seed, which we did not investigate. The lack of consistency of the leaf shape (length and width) in distinguishing LAM in the field indicates that, contrary to farmers' perceptions, it is not possible to accurately distinguish LAM at the vegetative phase. This difficulty has been related to the large morphological variation of the sweet ABMT trees in the Dahomey gap, and to the limited number of visible distinctive phenotypic characteristics within and between populations (Vihotogbé *et al.*, 2013).

In recent years, domestication processes have been made participative, by involving farmers as well as researchers (Leakey *et al.*, 2003). Therefore, studies should now take into account local perceptions about phenotypic variations in order to capture the potential for improvement, through identification of elite cultivars (Leakey *et al.*, 2000). In the case of the Dahomey gap, where a large morphological variation of sweet ABMT is recognized (Vihotogbé *et al.*, 2013), broadening the study area and taking more ecological regions as well as more detailed characteristics into account might be a good way to accurately identify interesting local morphological patterns related to commercially important traits.

### A stagnating domestication process

The domestication process of wild tree species has been hypothetically split up in five stages identifiable through the examination of the frequency distribution of each desired trait (Leakey *et al.*, 2003). In the process, as the progeny is improved for the selected trait, a noticeable separation of the overall individuals in two or more groups in regard to the trait of interest reveals a mixture of individuals with different mean values, that is, the distinction of sub-populations within a population. The possibility to distinguish in a same population differentiated LAMs with higher, middle and lower characteristics denotes the effects of an oriented effort to design one or more groups of trees producing some given type of fruit. This suggests a second/third domestication stage where *Adja* farmers had distinctly identified profitable traits (fruit size, water content, fibrosity) and are running a selection by recognizing possible links between characteristics.

There is in fact an unavoidable association among plant quantitative morphological characteristics (Leakey *et al.*, 2004; Brown *et al.*, 2010), which farmers are aware of. For instance, aqueous fruit trees are considered to have leaves with smaller size, and are avoided by most of farmers who prefer pasty LAM; big fruits are selected by farmers willing to have trees producing big seeds (Vihotogbé *et al.*, 2013). As perceptions on these associations do not always fit the reality, and as farmers have no control on the determination of the genetic make-up of selected seeds for reproduction or survival, there is a truncated process whereby only the best individuals in the population are crossed (Futuyma, 1983). It is then a difficulty to fix desired characters and pass over second and third stages and get to the fourth stage where a selected variety is obtained (Leakey *et al.*, 2003). This emphasizes that the selection effort of farmers is being weakened by the occurrence of some undesirable morphotypes (Vihotogbé *et al.*, 2013), highlighting the need to support local domestication by oriented research and development of vegetative propagation techniques. This engaged but stagnant domestication process could explain not only the difficulty to separate the LAM by leaf as claimed by farmers, but also the very surprising fact that most of trees owned by farmers are of the aqueous LAM although most farmers rather prefer pasty sweet ABMT. This clearly shows that farmers are not controlling the ongoing selection process: genotypes involved in the process are interacting so that a vegetative propagation is necessary to fix desirable traits.

Such stagnating domestication process may have also been favored by the lack of suitable policies and incentives from the government. Indeed, very important agroforestry species are no longer been supported actively by the state government production strategy.

Still, it seems already interesting that the mixed LAM represents most of the preferred individuals of the 'mass selection' process indexed. In the Dahomey gap where ABMT is suffering from a lack of wise and efficient usage and conservation strategies (Vihotogbé *et al*., 2013), this can be a starting point in the development of a vegetative selection process of fruit morphotypes: farmers can identify by themselves 'plus trees' based on local perception and apply suitable vegetative propagation techniques to be popularized as support to the local domestication process.

### Uses and management of sweet ABMT: Non-profitable taboos breaking as a gate for a guided and effective domestication

Food and medicinal uses are the well-known uses of the ABMT, fruit flesh and kernel being the organs targeted as food (Tchoundjeu *et al*., 2002; Leakey *et al*., 2005). The leaves are generally used for medicinal application, while fuel utilization of the wood is less generalized. This might be due to one taboo, which forbids fuel utilization of sweet ABMT wood and branches by women. This taboo may have allowed the relative abundance of the aqueous LAM in the study area, since trees were not cut down even if the produced fruits were not appreciated by the owners. Though this taboo seems to have partially protected sweet ABMT against pruning, it could have also favored the aqueous LAM abundance in the region, weakening the selection towards pasty LAM, as only non-vegetative propagation methods were used.

Another taboo, the prohibition of plantation, is likewise not profitable for the species conservation and management. Although all respondents acknowledged this taboo, more and more people also reported to break it (56% of the farmers). Sweet ABMT seeds are intentionally let in fields and seedlings are selected and protected against clearing and fire. People are trying to circumvent taboos because the species is getting more and more economic value and is now targeted as an important income source, although implementation of a strategic plan of valorization is still expected. Numerous farmers who have inherited sweet ABMT (40%) have also grown it directly by seed. This shows that they are aware of the economic importance of the species and that the more trees they have, the more income it could generate. However, the traditional selection, lead by commercial opportunities, is not sufficient to boost the domestication process. It is important that institutions heading plant genetic resources conservation and management lead a guided selection process (truncated selection and vegetative propagation) while the non-profitable taboos are being broken.

## Conclusion

The study highlights an ongoing but stagnating local domestication process of ABMT within the Couffo region of Benin. While fruit characteristics can clearly distinguish the three LAMs of ABMT, the leaf characteristics usually used by farmers of the Couffo region at non-fruiting stage fail to do that, impeding consistent differentiation of the LAMs on-farm at the vegetative stage. Also, the propagation methods used, namely seeding associated with the taboo prohibiting plantation of ABMT, appear as constraints to its effective domestication in the Couffo region. Research institutions, extension services and national policies makers thus have a critical role to play in effective domestication of ABMT. While research institutions should focus on participative development of vegetative propagation methods to fix desired morphotypes, extension services should encourage farmers in planting and sensitize them on the possibility of vegetative propagation. Implementation of a national strategy for the valorization of NTFP from ABMT, especially by bringing together all stakeholders into a formal framework, would also incite farmers to plant and thereby enhance their livelihoods, contributing to poverty alleviation.

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