

Morphological variation of fruit in Mexican populations of *Cocos nucifera* L. (Arecaceae) under *in situ* and *ex situ* conditions

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Abstract

Morphological variation of the coconut fruit measured *in situ* has been used to estimate genetic diversity, and generate hypotheses about the evolutionary and geographical diffusion of coconut. Some authors have questioned the validity of this methodology due to the possibly high effect of the environment on the morphological characteristics of the fruit. The general aim of this study is to validate this methodology through: (1) characterizing the pattern of morphological variation of the fruit under homogeneous growing conditions *ex situ*; (2) comparing this pattern with those already reported *in situ*; (3) estimating the heritability values for the components of fruit in coconut. Results are also discussed in comparison with *ex situ* leaf variation and biochemical and molecular variation patterns previously studied. Principal components and discriminant analyses indicated that the characters that best differentiate groups are basically the same *in situ* and *ex situ*. Grouping patterns obtained with principal components and cluster analysis were similar for both growing conditions. They were also similar to the grouping pattern obtained with *ex situ* leaf characters. No significant differences were found in the variation coefficients of fruit characters between the same populations *in situ* and *ex situ*. Consistency was found between patterns of morphological variation of fruit *ex situ* and *in situ*, and those obtained using iso-enzymatic and molecular characteristics. The results are also consistent with hypotheses on the origin and diffusion of the germplasm introduced to Mexico. High values of heritability were found in nine characters. Weight and water percentage showed the highest values (0.88 and 0.883), with a strong correlation to the mass and the roundness of fruit and seed, suggesting that human selection of these characteristics led to the differentiation of domesticated populations. We conclude that morphological characterization of the coconut fruit *in situ* is useful to estimate its genetic variability because of its simplicity, speed and ease of application in the field and in remote areas.

Introduction

The coconut palm (*Cocos nucifera* L.) is widely distributed in all tropical areas of the world. A considerable amount of effort has gone into characterizing, collecting, and establishing germplasm collections from different regions of the world (Zizumbo-Villarreal and Arellano Morín 1995; Ohler 1999). The characterization of the morphological characteristics of the fruit in sites where they are grown (*in situ*) has been used to estimate the pattern

of variation and levels of genetic diversity using numerical and statistical analyses (Ashburner et al. 1997a; Zizumbo-Villarreal and Piñero 1998; Vargas and Blanco 2000). This methodology has been the basis for establishing germplasm collecting programs (Whitehead 1966, 1968; Foale 1987; Zizumbo-Villarreal et al. 1993) based on the assumptions that fruit characters have a high heritability (Whitehead 1966; Harries 1978) and that the fruit has been subject to strong pressures of selection, both natural and human (Harries 1990), and on the

ease with which the technique is applied in the field and in remote areas (Ashburner et al. 1997a).

Based on the patterns of morphological variation obtained with this methodology, hypotheses have been developed regarding the evolutionary history of the species and its geographical diffusion throughout the world (Harries 1978, 1992). However, some doubt has arisen regarding the consistency and validity of this methodology, mainly due to the possibility of a strong environmental influence on the fruit morphological characteristics, since these studies have been carried out in different time periods and under different environmental conditions of rainfall, temperature, soil, and agronomic management. Similarly, a high phenotypical plasticity has been reported in other morphological characteristics in the species (Zizumbo-Villarreal and Colunga-GarcíaMarín 2001).

Different methodologies for the estimation of genetic variation have been developed based on the analysis of DNA, in an attempt to eliminate the environmental effects (Ashburner et al. 1997b; Perera et al. 1998, 2001; Lebrun et al. 1998; Rivera et al. 2000). However, their application is limited in tropical countries and in remote areas with a low level of technology, in contrast with the methodology based on the morphological characteristics of fruit, which is simple and inexpensive. For this reason, investigating the usefulness of this methodology is of great relevance in the exploration, collection, and conservation of the coconut germplasm, as well as in evolutionary studies of the species.

High values of heritability have been reported for the weight of solid endosperm or copra (Liyanage and Sakai 1961; Meunier et al. 1984; Bourdeix 1999). It is important to determine heritability values for all the components of the fruit, since this information could provide insights regarding the evolutionary impact of human selection carried out on the different fruit components during the process of domestication, and regarding the possibility of success to be expected in the improvement programs aimed at the productive diversification of the plant.

This work focuses on comparing the value of morphological characterization *in situ* of the coconut fruit by: (1) characterizing the morphological variation of the fruit under homogeneous growing conditions *ex situ*; (2) comparing this pattern with those already reported for the morphological variation of

fruit obtained *in situ*, with those for variation of leaf characteristics *ex situ*, and with those for patterns of biochemical and molecular variation; and (3) estimating the heritability in the fruit components.

Material and methods

Collection of data

In 1989, morphological variation was studied in 41 populations of Mexican coconuts and six imported coconuts, under *in situ* conditions, distributed on both Mexican coasts (Zizumbo-Villarreal et al. 1993, 1998). 17 morphological characteristics were studied using the methodology proposed by Harries (1978), on one fruit from each of an average of 20 palm trees per population. Based on this previous study, 16 populations were selected covering the variation range of the plant in Mexico: 15 of the *Typica* variety (tall) and one of the *Nana* variety (C5) (Figure 1 and Appendix 1). Two hundred fruits per population were collected and planted in July 1989 under nursery conditions in Merida, Yucatan, Mexico. In January of 1991, the plants were transplanted to an experimental plot located at 21°21'11" North and 89°10'16" West, 100 m from the northern coastline of the Peninsula of Yucatan. The plants were established 9 m apart in contact with the water table to maintain conditions of soil water availability favorable to the plant. Agronomic management was comprised of eliminating competition by weeds twice a year. There was no fertilization. The climate at the site is dry and warm with an annual mean rainfall of 700 mm and an annual mean temperature of 23 °C, with rains in the summer and a high percentage of winter rains (García 1973). The soil is regosol sandy calcareous, with the water table 1 m deep (Duch 1991).

In the summer of 2002, when the plants were 10 years old and in full production, one fruit from each of 28 palm trees was evaluated. The data was obtained in the same way as for the *in situ* study in 1989. Only those fruits with a similar maturation stage were included, i.e., when the fruit color turned from fresh (green, yellow, or red) to dry (brown), but the fresh color remained at least on the calyx. Eleven characteristics were evaluated directly: total mass of the fruit, mass of the mesocarp, mass of the endocarp or shell, mass of the seed, mass of the water or liquid

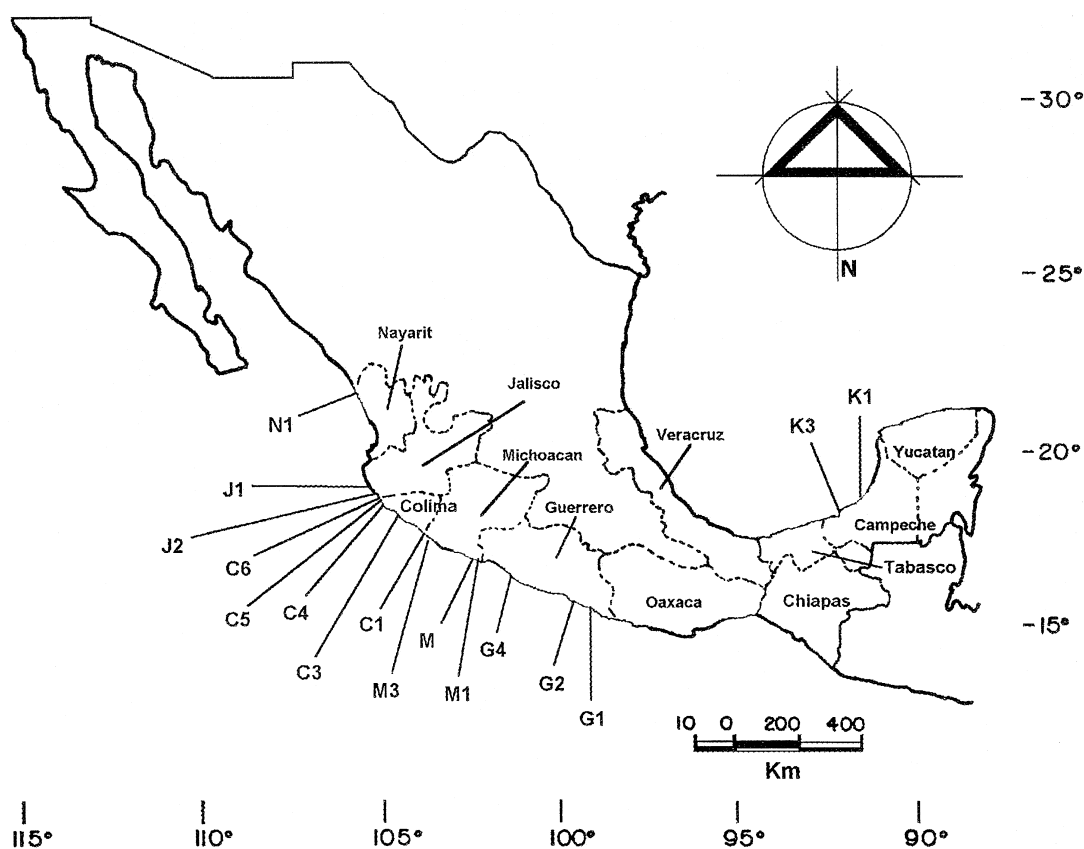


Figure 1. Areas and sites sampled for the morphological variation analysis of 16 coconut populations studied in Mexico.

endosperm, mass of the meat or solid endosperm, length and width of the fruit, length and width of the endocarp, and thickness of the mesocarp. Based on this information, six ratios were obtained: percentage of mesocarp in fruit, percentage of endocarp in fruit, percentage of water in fruit, percentage of meat in fruit, length:width ratio of fruit, and length:width ratio of endocarp.

Numerical and statistical analyses

The numerical and statistical analyses were carried out using the Statistical Analysis System Software Release 6.04 (SAS 1992) following Colunga et al. (1996). The normality of the data was tested on residuals, using the UNIVARIATE procedure, grouping together all the populations. Data for the following characteristics were distributed normally with an $\alpha \geq 0.05$: mass of seed, mass of endocarp, mass of solid endosperm, length of fruit, length and width of endocarp, thickness of mesocarp, percentage

of mesocarp, percentage of endocarp, percentage of meat and percentage of water. Data for mass of the mesocarp, mass of water, and width of fruit became normally distributed after square root transformation. The length:width ratio data of the fruit became normally distributed after logarithmic transformation. The length:width ratio data of endocarp became normally distributed after arcsine transformation, and the data for the weight of fruit was normalized by reciprocal transformation.

The analyses of the patterns of variation, their discontinuity and clustering of groups, were carried out by the following methods: (a) one-way ANOVA with general linear method was performed to test for significant differences among populations for each one of the 17 variables. Multiple comparison means was done with Tukey's studentized range method and α significance levels were adjusted to account for the simultaneous inferences made for each analysis ($\alpha = 0.05/17$; Miller Jr 1981). (b) Principal components

analysis (PCA). The two first components were obtained using the PRINCOMP procedure. (c) Cluster analysis (unweighted pair group method analysis, UPGMA). The elements of the population's matrix of means were standardized to mean 0 and standard deviation 1, and from this the matrix was obtained using as an indicator of similarity the square of the Euclidian distance. The groupings were then represented in a dendrogram. (d) Stepwise discriminant analysis was then performed with the STEPDISC procedure to establish which morphological characters contributed most to the differentiation of the groups. Variables were chosen to enter or leave the discrimination model among groups if the square partial correlation (R^2) for predicting the variable under consideration from the group classificatory variable (controlling for the effects of the variables already select for the model) was ≥ 0.15 . (e) A comparison was also made of the levels of variability among populations and characteristics (Sokal and Braumann 1980), using the coefficients of variation (CVs) of the 16 populations and 17 variables with a randomized block design and two-way ANOVA. The tests of media separation for each path were carried out using Tukey's method ($\alpha = 0.05$).

Heritability values (h^2) for each character were calculated as the slope of the simple linear regression in a comparison of the mean values of each character in the parents (*in situ*) with the mean values of the progeny (*ex situ*), taking into consideration all the populations in both growing conditions following Hedrick (2000). Finally, the correlation values between the characters with high heritability values and all the characteristics studied were calculated.

Results

Patterns of variation and clustering under ex situ conditions

Means and CVs of the 17 characters studied are presented in Appendix 2. The analysis of variance indicated the existence of significant differences among populations in all of the 17 characters studied ($P < 0.05/17$) (Table 1). The two first components of the PCA account for 87% of the variation. The first component explains 53%, and the characters that contribute most to the model (with a coefficient in

Table 1. One-way ANOVA for each character between 16 coconut populations from Mexico.

| Character | R^2 | F | P |
|-----------------------|-------|------|--------|
| Fruit mass | 0.66 | 57.5 | 0.0001 |
| Mesocarp mass | 0.51 | 30.1 | 0.0001 |
| Endocarp mass | 0.32 | 13.9 | 0.0001 |
| Seed mass | 0.46 | 24.8 | 0.0001 |
| Water mass | 0.47 | 25.8 | 0.0001 |
| Meat mass | 0.57 | 37.7 | 0.0001 |
| Fruit length | 0.25 | 10 | 0.0001 |
| Fruit width | 0.42 | 21.1 | 0.0001 |
| Endocarp length | 0.32 | 13.6 | 0.0001 |
| Endocarp width | 0.56 | 36.9 | 0.0001 |
| Mesocarp thickness | 0.14 | 5 | 0.0001 |
| % Mesocarp | 0.39 | 19.1 | 0.0001 |
| % Endocarp | 0.34 | 9.3 | 0.0001 |
| % Water | 0.35 | 29.4 | 0.0001 |
| % Meat | 0.49 | 12 | 0.0001 |
| Length:width fruit | 0.21 | 7.7 | 0.0001 |
| Length:width endocarp | 0.45 | 24.3 | 0.0001 |

Table 2. Percentage of the total variation explained by the first and second principal components, and characters that contributed most to the model (coefficient in the function greater or equal to the absolute value of 0.30).

| | <i>Ex situ</i> | <i>In situ</i> |
|-----------------------------------|----------------|----------------|
| <i>First principal component</i> | 53% | 49% |
| Width of fruit | 0.32 | ^a |
| Meat mass | 0.31 | 0.33 |
| Fruit mass | 0.31 | 0.34 |
| Seed mass | 0.30 | 0.35 |
| Endocarp mass | 0.30 | 0.32 |
| Endocarp width | 0.30 | ^a |
| Water mass | 0.30 | 0.33 |
| <i>Second principal component</i> | 34% | 31% |
| % Meat | 0.36 | 0.39 |
| Length:width of endocarp | 0.35 | 0.33 |
| Length:width of fruit | 0.35 | ^a |
| % Mesocarp | 0.32 | 0.44 |
| Mesocarp mass | 0.32 | 0.39 |

^a Coefficient in the function < 0.30 .

Data *in situ*, from (Zizumbo-Villarreal and Piñero 1998).

the function higher or equal to the absolute value of 0.30) were: width of fruit, mass of meat, total mass of the fruit, mass of the seed, mass of the endocarp, width of endocarp, and mass of the water. The second component accounted for 34% of the variation and the characteristics that contributed most to the model were: percentage of meat, length:width ratio of endocarp length:width ratio of fruit, percentage of mesocarp, and mass of the mesocarp (Table 2).

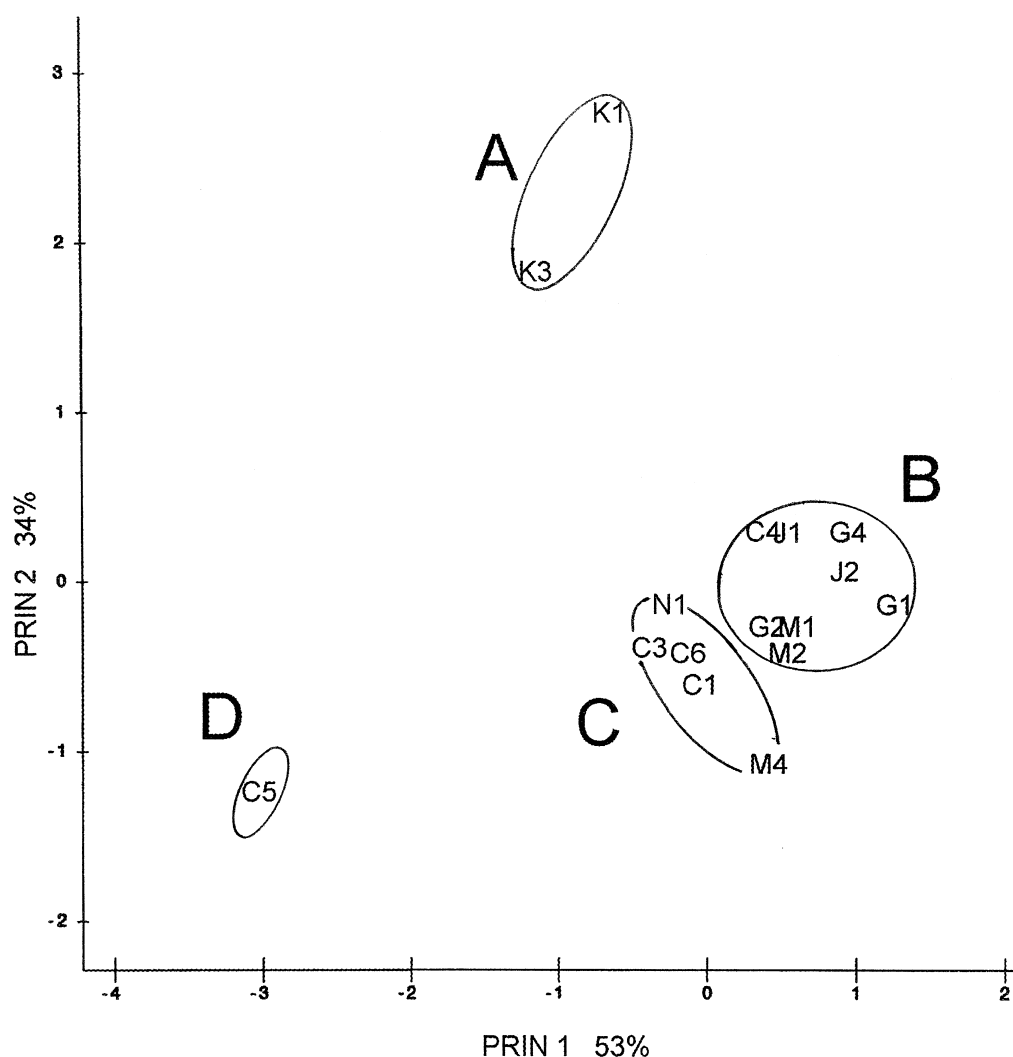


Figure 2. First and second principal components of the analysis of 16 coconut populations in Mexico. Analysis using mean values from 17 characters of fruit. The first and second principal components account for 53 and 34% of the total variation, respectively. A – Atlantic Tall; B – Pacific Tall 1; C – Pacific Tall 2 and D – Malayan Dwarf morphotype.

The graphic analysis defined four groups (Figure 2). The populations K1 and K3 of the Campeche state presented positive values in the two components, forming group 'A' or Atlantic Tall. This group is distributed on the coasts of the Gulf of Mexico, mainly in the states of Campeche and Tabasco. The populations of Guerrero, G1, G2, and G4, those of Michoacan, M1 and M2, Colima, C4 and Jalisco, J1 and J2, has positive values in the first component and positive or negative in the second component, forming group 'B' or Pacific Tall 1, while populations of Colima, C1, C3, C6, Nayarit, N1, and Michoacan M4 with

negative values in both components, except the last one, formed group 'C' or Pacific Tall 2. Finally, the population C5 or Malayan Dwarf with high negative values in both components separated from all the other groups forming group 'D'.

The results of the cluster analysis were consistent with the PCA analysis (Figure 3). In the first step the analysis separated the Malayan Dwarf population from the tall populations. The second step separated the tall populations into two groups: one group comprising the populations of the coasts of the Gulf of Mexico (Atlantic Tall or 'A'), and the other group comprising all the populations

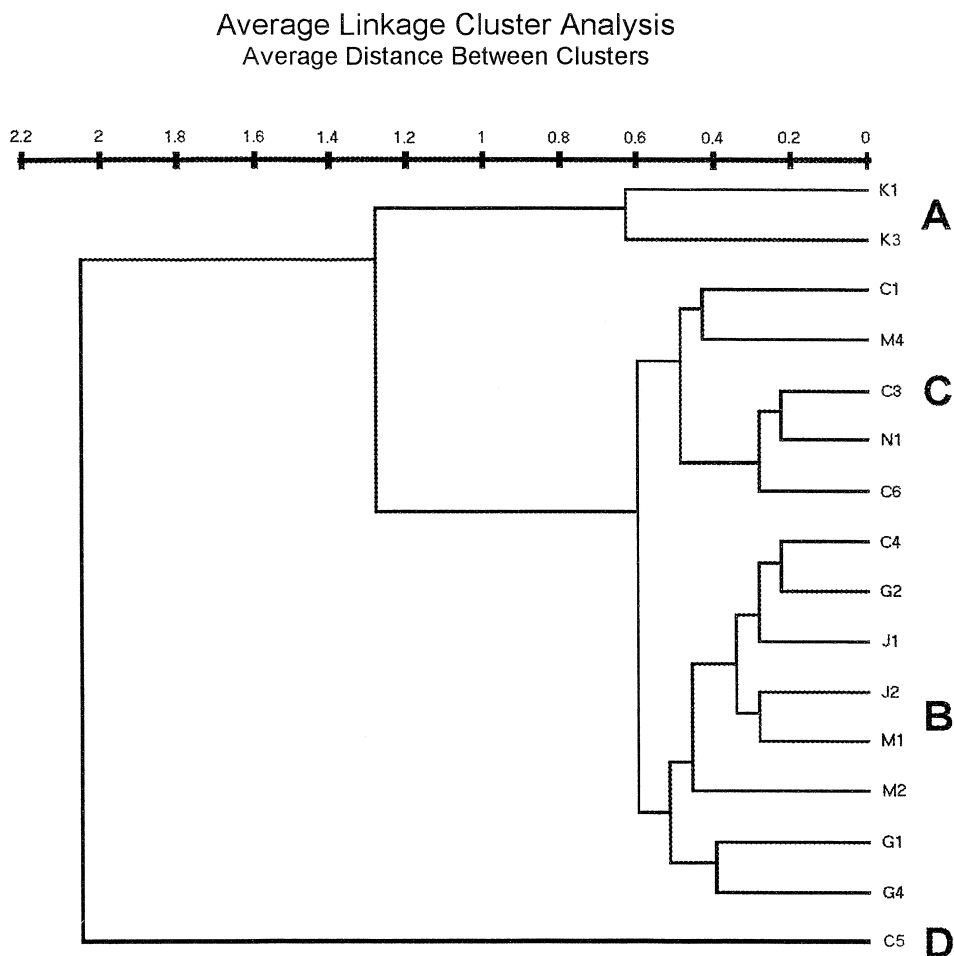


Figure 3. Dendrogram of 16 coconut populations in Mexico. Average linkage cluster analysis based on 17 characters of fruit. A – Atlantic Tall; B – Pacific Tall 1; C – Pacific Tall 2 and D – Malayan Dwarf morphotype.

distributed on the Pacific coasts. In the third step, the Pacific populations separated into two groups: the populations G1, G2, G4, M1, M2, J1, J2, and C4 (Pacific Tall 1 or 'B'), distributed in the southern portion of the Pacific coasts and the populations C1, C3, C6, M4, N1 (Pacific Tall 2 or group 'C') distributed towards the north. In the state of Colima and neighboring valleys (Cohuayana and Cihuatlán), where the geographic location divides the southern and northern portions of the Pacific coast, populations from both groups can be found (Figure 1).

Differences between dwarf and tall coconuts

The analysis of variance indicated that all the tall populations had significantly higher values of

fruit and seed characters. Only in the proportions of mesocarp, endocarp, and length:width ratio of the endocarp were there no significant differences (Table 3). The dwarf coconut had a higher percentage of solid endosperm. The stepwise discriminant analysis showed that the characters: total mass of the fruit, mass of seed, and mass of mesocarp, were the most important in the differentiation between the two groups (Table 4).

Differences between the morphotypes Atlantic Tall and Pacific Tall 1

Of the 17 characteristics evaluated, only four were not significantly different when comparing Atlantic Tall and Pacific Tall 1: length of fruit, length of

Table 3. One-way ANOVA's for all characters studied. Comparisons between Tall/Dwarf (T/D); Atlantic/Pacific (A/P); Atlantic/Pacific 1 (A/P1); Atlantic/Pacific 2 (A/P2); Pacific 1/Pacific 2 (P1/P2) coconut ecotypes from Mexico.

| Character | T/D | | | | A/P1 | | | | A/P2 | | | | P1/P2 | | | |
|-----------------------|-------|-------|-----|-------|-------|------|-----|-------|-------|------|------|-------|-------|------|------|-------|
| | R^2 | F | P | Pis | R^2 | F | P | Pis | R^2 | F | $P1$ | Pis | R^2 | F | $P1$ | Pis |
| Fruit mass | 0.6 | 704 | *** | *** | 0.15 | 49 | *** | *** | 0.02 | 4.8 | ns | *** | 0.1 | 40.4 | *** | *** |
| Mesocarp mass | 0.18 | 100 | *** | *** | 0.08 | 22.8 | *** | ns | 0.24 | 61.8 | *** | *** | 0.06 | 24.5 | *** | *** |
| Endocarp mass | 0.31 | 202 | *** | *** | 0.45 | 13.2 | *** | *** | 0.001 | 0.2 | ns | ns | 0.05 | 20.4 | *** | *** |
| Seed mass | 0.2 | 113.8 | *** | *** | 0.42 | 205 | *** | *** | 0.42 | 138 | *** | *** | 0.06 | 23.4 | *** | *** |
| Water mass | 0.21 | 121 | *** | *** | 0.51 | 292 | *** | *** | 0.46 | 167 | *** | *** | 0.08 | 34.2 | *** | *** |
| Meat mass | 0.21 | 120 | *** | *** | 0.32 | 130 | *** | *** | 0.31 | 90 | *** | *** | 0.02 | 8.4 | ** | *** |
| Fruit length | 0.16 | 82.1 | *** | *** | 0.005 | 1.5 | ns | *** | 0.07 | 15.1 | *** | *** | 0.05 | 19.2 | *** | *** |
| Fruit width | 0.27 | 166.3 | *** | *** | 0.096 | 30 | *** | *** | 0.005 | 1.5 | ns | *** | 0.12 | 49 | *** | *** |
| Endocarp length | 0.26 | 157.4 | *** | *** | 0.001 | 0 | ns | *** | 0.25 | 5.2 | ns | *** | 0.03 | 9.7 | *** | *** |
| Endocarp width | 0.2 | 111.9 | *** | *** | 0.5 | 280 | *** | *** | 0.46 | 164 | *** | *** | 0.05 | 18 | *** | *** |
| Mesocarp thickness | 0.04 | 20.8 | *** | *** | 0.008 | 2.5 | ns | ns | 0.06 | 13.1 | *** | *** | 0.04 | 14 | *** | ns |
| % Mesocarp | 0.007 | 3.2 | ns | *** | 0.43 | 206 | *** | *** | 0.48 | 181 | *** | *** | 0.002 | 0.67 | ns | ns |
| % Endocarp fruit | 0.01 | 5.1 | ns | *** | 0.03 | 8.4 | ns | ns | 0.03 | 5.8 | ns | *** | 0.004 | 1.5 | ns | *** |
| % Water in fruit | 0.07 | 31.6 | *** | ns | 0.6 | 355 | *** | *** | 0.54 | 227 | *** | *** | 0.025 | 9.5 | ** | *** |
| % Meat in fruit | 0.04 | 20.3 | *** | *** | 0.19 | 66 | *** | *** | 0.34 | 99.7 | *** | *** | 0.05 | 17.3 | *** | *** |
| Length:Width fruit | 0.06 | 28 | *** | ns | 0.04 | 10.8 | *** | *** | 0.16 | 37.5 | *** | *** | 0.06 | 23.1 | *** | ns |
| Length:Width endocarp | 0.02 | 1.6 | ns | *** | 0.53 | 308 | *** | *** | 0.52 | 218 | *** | *** | 0.004 | 1.6 | ns | ns |

*** $P > 0.003$; ns – not statistically significant.

Pis – results of the same test from data *in situ* from Zizumbo-Villarreal and Piñero (1998).

Table 4. Characters selected by the Stepwise discriminant analysis.

| Ecotype | Growing condition | | R^2 | <i>In situ</i> | | R^2 |
|-------------------------------|-----------------------|--|-------|-----------------|--|-------|
| | <i>Ex situ</i> | | | | | |
| Dwarf/Tall | Fruit mass | | 0.61 | Mesocarp mass | | 0.60 |
| | Seed mass | | 0.20 | Fruit mass | | 0.25 |
| | Mesocarp mass | | 0.20 | Endocarp length | | 0.24 |
| Atlantic Tall/Pacific Tall 1 | % Water | | 0.60 | Endocarp width | | 0.62 |
| | Length:width endocarp | | 0.20 | % Water | | 0.15 |
| Atlantic Tall/Pacific Tall 2 | % Water | | 0.50 | % Mesocarp | | 0.41 |
| | Length:width endocarp | | 0.20 | and % Water | | 0.36 |
| Pacific Tall 1/Pacific Tall 2 | % Meat | | 0.40 | Fruit mass | | 0.41 |
| | | | | Endocarp length | | 0.33 |
| | | | | Seed length | | 0.33 |

Criteria to enter the model: square partial correlation value $R^2 = 0.15$. Data *in situ* from Zizumbo-Villarreal and Piñero (1998).

endocarp, thickness of mesocarp, and percentage of endocarp (Table 3). The Pacific Tall 1 populations had greater mass of the fruit, endocarp, seed, water and solid meat, as well as greater width of fruit and higher percentages of water and meat. The Atlantic Tall populations had a greater mass and higher percentage of mesocarp. The populations of the morphotype Pacific Tall 1 had a lower width:length ratio both for the fruit and the endocarp, indicating a more spherical fruit. The stepwise discriminant analysis indicated that the percentage of water and the length:width ratio of the endocarp are the most

important characteristics for differentiating these morphotypes (Table 4).

Differences between the morphotypes Atlantic Tall and Pacific Tall 2

Of the 17 characteristics evaluated, only five were not significantly different when comparing these two groups: mass of fruit, mass of endocarp, width of fruit, length of endocarp, and percentage of endocarp (Table 1). The Atlantic Tall had significantly higher values of: mass of the mesocarp,

length of fruit, length of endocarp, percentage of mesocarp, length:width ratio of the fruit, and endocarp, as well as significantly lower values of: mass and percentage of seed, water and meat, and width of endocarp. Stepwise discriminant analysis indicated that the percentage of water and length:width ratio of the endocarp were the characteristics that best differentiate these two groups (Table 4).

Differences between the morphotypes Pacific Tall 1 and Pacific Tall 2

The analysis of variance indicated significant differences between these two groups in 13 characteristics (Table 3). Only the mass of meat, percentages of mesocarp and endocarp, and the length:width ratio of the endocarp were not statistically different. The Pacific Tall 2 had significantly lower values in all the characteristics of fruit and seed. It had a higher percentage of meat and a lower percentage of water. Stepwise discriminant analysis indicated that the percentage of meat and the width of fruit are the characters that best differentiate these morphotypes (Table 4).

Levels of variation within populations

The two-way analysis of variance using the coefficients of variation indicated significant differences among populations ($P = 0.0001$). The Tukey test media separation indicated the presence of two populational groups with a significantly different profile of variability: (1) populations with low variation in the 17 characteristics, with a range of variation from 12 to 15% (G1, C1, C3, C4, J1, M3, J2, N1, G2 and K3), and (2) one population with high variation profile (20.8%): K1. The rest of the populations, including the population of Malayan Dwarf, showed a variability range of between 16 and 19% and were not different from the first two groups.

Variation profile among characteristics

Significant differences were found between three groups of characteristics ($P = 0.0001$). The first group had high CVs of between 26.7 and 29% and included the mass of endosperm and mesocarp. The second group had medium variability, between 16 and 21%, and included the mass of seed, percentage of water, mass of endocarp, percentage of

Table 5. Heritability (h^2) values for 17 characters of coconut fruit.

| Character | h^2 |
|-----------------------|-------|
| Water mass | 0.88 |
| % Water | 0.83 |
| Seed mass | 0.82 |
| Endocarp width | 0.75 |
| Length/width endocarp | 0.74 |
| Meat mass | 0.67 |
| % Mesocarp | 0.64 |
| Fruit width | 0.57 |
| % Endocarp | 0.51 |
| % Meat | 0.51 |
| Endocarp mass | 0.50 |
| Fruit mass | 0.48 |
| Length/width fruit | 0.47 |
| Endocarp length | 0.42 |
| Mesocarp mass | 0.39 |
| Fruit length | 0.36 |
| Mesocarp thickness | 0.36 |

mesocarp, mass of the meat, mass of the fruit, and thickness of mesocarp. The third group had low variation coefficients, between 7.6 and 10.6%, and included the length:width ratio of fruit, width and length of fruit, length:width ratio of the endocarp, and width and length of endocarp. The percentage of endocarp and meat varied between 13.6 and 13.7%, respectively, and were not significantly different from the first two groups.

Heritability values of the fruit components

High values of heritability were found in nine characters ($h^2 > 0.5$). The quantity and percentage of water in the fruit showed the highest values, the mass of seed and meat, the roundness of fruit and seed and the percentage of mesocarp also presented high values (Table 5). The quantity of water presented a high positive correlation with the mass of fruit, seed and meat, and with the width of fruit and seed; but a negative correlation with the percentage of mesocarp (Table 6). The correlation values between characters with high heritability and the rest of the characteristics are presented in Table 6.

Discussion

Principal component and cluster analyses carried out initially on the parent populations under *in situ*

Table 6. Correlation values between characters with high heritability values ($h^2 = 0.60$) and the rest of characters of fruit.

| Character | Water mass | % Water | Seed mass | Endocarp width | Length/width endocarp | Meat mass | % Mesocarp |
|-----------------------|------------|---------|-----------|----------------|-----------------------|-----------|------------|
| Fruit mass | 0.84 | 0.61 | 0.87 | 0.83 | -0.29 | 0.87 | -0.36 |
| Mesocarp mass | 0.10 | -0.23 | 0.13 | 0.07 | 0.51 | 0.15 | 0.54 |
| Endocarp mass | 0.65 | 0.43 | 0.72 | 0.69 | -0.14 | 0.77 | -0.33 |
| Seed mass | 0.99 | 0.91 | 1.00 | 0.99 | -0.69 | 0.98 | -0.76 |
| Water mass | 1.00 | 0.93 | 0.99 | 0.97 | -0.72 | 0.94 | -0.75 |
| Meat mass | 0.94 | 0.84 | 0.98 | 0.97 | -0.61 | 1.00 | -0.74 |
| Fruit length | 0.38 | 0.07 | 0.45 | 0.40 | 0.24 | 0.53 | 0.09 |
| Fruit width | 0.75 | 0.51 | 0.79 | 0.77 | -0.27 | 0.81 | -0.30 |
| Endocarp length | 0.57 | 0.29 | 0.65 | 0.60 | 0.08 | 0.72 | -0.10 |
| Endocarp width | 0.97 | 0.92 | 0.99 | 1.00 | -0.74 | 0.97 | -0.80 |
| Mesocarp thickness | 0.14 | -0.14 | 0.21 | 0.17 | 0.35 | 0.29 | 0.24 |
| % Mesocarp | -0.75 | -0.90 | 0.76 | -0.79 | 0.90 | -0.70 | 1.00 |
| % Endocarp fruit | -0.08 | -0.15 | 0.02 | 0.03 | 0.23 | 0.15 | -0.04 |
| % Water in fruit | 0.93 | 1.00 | 0.91 | 0.91 | -0.89 | 0.84 | -0.90 |
| % Meat in fruit | 0.24 | 0.50 | 0.25 | 0.32 | -0.73 | 0.84 | -0.78 |
| Length:Width fruit | -0.76 | -0.78 | -0.72 | -0.77 | 0.80 | -0.65 | 0.65 |
| Length:Width endocarp | -0.73 | -0.89 | -0.69 | -0.74 | 1.00 | -0.61 | 0.90 |

conditions, indicated four populational groups of coconut in Mexico; these groups showed a strong morphological similarity with four genotypes which were introduced recently to Mexico from the same geographical areas which supposedly gave origin to the Mexican populations (Zizumbo-Villarreal and Piñero 1998). The pattern of variation revealed by PCA and cluster analysis were similar both in *ex situ* conditions and *in situ* conditions, because in both studies the populations formed four conglomerates or morphotypes: Atlantic Tall, comprising the populations K1 and K3; Pacific Tall 1 with the populations G1, M1, M2, J1, and J2; Pacific Tall 2 with the populations C1, N1, and M4; and Malayan Dwarf with the population C5. Only the populations C3 and C6 changed from the morphotype Pacific Tall 1 in *ex situ* conditions to Pacific Tall 2 under *in situ* conditions and the populations G2 and G4 changed from the Pacific Tall 2 group to the Pacific Tall 1. These inconsistencies may be due to an environmental effect, or because these populations have grown in close proximity to populations of the other morphotype and therefore could have hybridized.

In both environmental conditions a high proportion of the variability was explained by the two first principal components, and the same characters contributed most to the model: the mass of fruit, seed endocarp, meat and water (Table 2). The stepwise discriminant analyses, under both *ex situ*

and *in situ* conditions, indicated that basically the same characters differentiated the morphotypes (Table 4). The mass of mesocarp and the mass of fruit differentiated the Dwarf population from the Tall populations. The percentage of water differentiated the morphotype Atlantic Tall from the two Pacific morphotypes. Inconsistencies were found between the two conditions only in the characteristics which differentiated the morphotype Pacific Tall 1 from the Pacific Tall 2, because under *ex situ* conditions, it was the percentage of meat that differentiated these two groups best, while under *in situ* conditions, it was the total mass of fruit. We consider that this inconsistency has little relevance. Under both growing conditions, the morphotype Pacific Tall 1 had a greater quantity of water and the Pacific Tall 2 had a greater quantity of meat, identifying the first as a genotype with better qualities for the production of fruit, and the latter with better qualities for the production of copra.

On respect to the one-way ANOVA, we found that, under both growing conditions, there were significant differences among the ecotypes in the majority of the characters (Table 3). This indicates that the characters used in the study are useful for the morphological characterization and that the differentiation between ecotypes covers a large number of characters.

The comparison of average variability of the 17 characters under *in situ* and *ex situ* conditions, indicated that there were no significant differences among the populations of the ecotypes Atlantic Tall (*in situ* 18%, *ex situ* 16%); Pacific Tall 2 (*in situ* 16.8%, *ex situ* 15.8%) and Malayan Dwarf (*in situ* 15%, *ex situ* 19%). Only in the populations of the ecotype Pacific Tall 1 were there significant differences (*in situ* 17.5%, *ex situ* 15.8%). These results may be due to the effect of agronomic practices of control of competition by planting density, and the elimination of weeds, both of which reduces the environmental variation in the areas of coconut cultivation in Mexico.

The grouping patterns found both in *ex situ* and *in situ* conditions, using PCA analysis and cluster analysis, were similar to those found using morphological and physiological leaf characteristics under *ex situ* conditions (Zizumbo-Villarreal and Colunga-GarcíaMarín 2001). In the last study, the groups conformed in general to the same populations, however, the populations G1 and G2 formed an independent group. These results indicate a strong consistency in the grouping patterns under both conditions; they also suggest the possibility of genetic infiltration between populations in close proximity to each other, as could be the case in the populations C6, J1 and J2 that grow in the valley of Cihuatlán on the boundaries of Colima and Jalisco.

The groupings reported both in the present study and in the study carried out under *in situ* conditions were also similar to those reported by genetic characterization using isoenzymes. In both studies, the ecotype Atlantic Tall was phylogenetically related to the West African Tall, while the Pacific groups were related to the coconuts from the Pacific islands, and the population of Dwarf coconut C5 was related to the Malayan Dwarf varieties (Zizumbo-Villarreal and Piñero 1998; Zizumbo-Villarreal et al. 2002).

In addition, the study made on the distribution of genetic diversity of the coconut on a world wide scale using microsatellite markers (Baudouin and Lebrun 2002), which included populations K1, M1 and C1 revealed that the population K1 of the morphotype Atlantic Tall is phylogenetically related to the populations of East and West Africa, while the population C1 of the morphotype Pacific Tall 2 is related to populations of Melanesia in the South Pacific. Additionally, the population

M1 of the morphotype Pacific Tall 1 was shown to be related to the populations of the Philippines. Therefore, the fruit morphological data obtained *in situ*, the morphological and physiological data of fruit and leaf obtained *ex situ*, and the phylogenetic studies using isoenzymes and microsatellites, all corroborate historical records regarding the introduction of the coconut to Mexico during the 16th and 17th centuries, as analyzed by Zizumbo-Villarreal (1996). They further support the hypothesis on the evolution and diffusion of the coconut proposed by Harries (1978) based on the morphological characterization of fruit.

We can conclude that both morphological characterization of the fruit *in situ* and characterization *ex situ* are equally valuable for the estimation of the genetic variation of the coconut and for the establishment of collecting strategies because under both growing conditions: (1) the discontinuities in variation and grouping patterns were similar, (2) the characteristics differentiating groups were basically the same, although there were some differences, and (3) the variability profiles in the same populations were similar. In addition, we observed consistency with the variation and grouping patterns reported when morpho-physiological characteristics of the leaf in *ex situ* conditions were used and with other studies where biochemical and molecular characteristics were used. It is important to emphasize that with the morphological characterization of fruit under *in situ* conditions, evolutionary inferences were made that were consistent with studies based on isoenzymes and microsatellites. The ease of application in remote areas and low cost makes the morphological characterization of fruit *in situ* a useful methodology in tropical countries with low technological and economic resources for genetic diversity studies, and also for the establishment of germplasm collecting strategies and in the design of strategies for the conservation and use of coconut germplasm, thereby strengthening the programs of conservation *ex situ*. The characterization *in situ* facilitates the rapid identification of populations and relevant genotypes which can be used immediately and which can be easily monitored over long periods of time, with the aid of permanent labels with bar codes, satellite locators and adequate computer programs, given the long life of these trees. This is important due to the high monetary cost and the extensive areas required in order to establish *ex situ* collections.

The high heritability values found in mass and percentage of water in the fruit suggest that conscious and consistent human selection of these characters could have led to a differentiation of populations with these characteristics. Furthermore, the strong positive correlation found for these characteristics with the mass and roundness of the fruit and seed suggest that selection focused on heavy round fruit, characteristics which are easily distinguishable, could have led to the obtainment of populations with a greater quantity of water in the fruit. On the other hand, the strong negative correlation of these characters with the percentage of mesocarp indicates that domestication process also led to populations with low fiber content in the fruit.

Solid endosperm also presented a strong positive correlation with the mass of fruit, seed and water, and with the roundness of the fruit and seed. This result suggests that human selection of these characters could also have had a positive effect on the quantity of meat during the domesticating process. The high heritability of solid endosperm has been taken advantage of in improvement programs, and important increases have been obtained (Bourdeix 1999). The percentage of mesocarp or fiber in the fruit also showed a high heritability value, however, it showed a negative correlation with the percentage

of water, meat and with the roundness of the seed, indicating that human selection for water and meat could have had a negative effect on the percentage of fiber during the domesticating process. Round or spherical fruit, with high water content and low fiber content comprise part of the domestication syndrome in the species (Harries 1978, 1990).

Given the degree of competition on the world market for vegetable oils, the cultivation of the coconut is being oriented toward productive diversification. There is increasing interest in the production of water as a natural serum, the production of fresh endosperm for the elaboration of simulated milk products and the obtainment of fibers and activated carbon (Ranasinghe 1999). The high heritability values found in these characteristics indicate that their selection in improvement programs could be successful, although selection aimed at increasing fiber does have a negative effect on increases in water and meat.

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Appendix 1

Code, name of population, location (municipality, state, latitude, longitude), altitude (Alt.), annual mean temperature (T), and annual mean precipitation (P) of 16 coconut populations sampled from Mexico.

| Code | Population | Municipality | State | Latitude | Longitude | Alt. ^a (m) | T ^a (°C) | P ^a (mm) |
|------|---------------|--------------|-----------|----------|-----------|-----------------------|---------------------|---------------------|
| K1 | Champoton | Champoton | Campeche | 19°20' | 90°43' | 3 | 26.4 | 1132 |
| K3 | Sabancuy | Escarcega | Campeche | 19°00' | 91°00' | 3 | 27.1 | 1889 |
| G1 | Marquelia | Azoyu | Guerrero | 16°45' | 98°35' | 20 | 25 | 800.9 |
| G2 | El Carrizo | Copala | Guerrero | 16°50' | 98°35' | 20 | 25 | 801 |
| G4 | Tecpan | Tecpan | Guerrero | 17°31' | 101°13' | 30 | 27.4 | 1235 |
| M1 | El Caiman | L. Cardenas | Michoacan | 18°15' | 101°55' | 20 | 29.2 | 733 |
| M2 | El Manglar | L. Cardenas | Michoacan | 18°15' | 101°55' | 20 | 29.2 | 733 |
| M3 | Coahuayana | Coahuayana | Michoacan | 18°19' | 103°30' | 10 | 27.5 | 884.4 |
| C1 | Callejones | C. Ortega | Colima | 18°56' | 103°58' | 28 | 27.6 | 710 |
| C3 | Tecoman | Tecoman | Colima | 18°54' | 103°52' | 40 | 26.5 | 660.4 |
| C4 | Cuyutlan | Cuyutlan | Colima | 18°55' | 104°05' | 20 | 26.5 | 1121 |
| C6 | Centinela | Manzanillo | Colima | 19°10' | 104°30' | 20 | 26.5 | 1048 |
| J1 | Cihuatlan | Cihuatlan | Jalisco | 19°15' | 104°35' | 5 | 26.7 | 1048 |
| J2 | B. de Navidad | Cihuatlan | Jalisco | 19°15' | 104°45' | 5 | 26.7 | 1048 |
| N1 | San Blas | San Blas | Nayarit | 21°33' | 105°17' | 2 | 24.7 | 1396 |
| C5 | Enano Malayo | Tecoman | Colima | 18°54' | 103°52' | 40 | 26.5 | 660.4 |

^a García (1973).

Appendix 2

Number of plants (N), mean and coefficient of variation (CV) of 17 characters of fruit in 16 coconut populations from Mexico growing under *ex situ* and *in situ* conditions. Data *in situ*. From Zizumbo-Villarreal and Piñero (1998).

| Code | Growing condition | N | Fruit mass (g) | | Mesocarp mass (g) | | Endocarp mass (g) | | Seed mass (g) | | Water mass (g) | | Meat mass (g) | | Fruit length (cm) | |
|------|-------------------|----|----------------|------|-------------------|------|-------------------|------|---------------|------|----------------|------|---------------|------|-------------------|------|
| | | | Mean | CV | Mean | CV | Mean | CV | Mean | CV | Mean | CV | Mean | CV | Mean | CV |
| K1 | <i>Ex situ</i> | 28 | 1528.8 | 19.5 | 822.9 | 32.3 | 206.5 | 15.7 | 499.3 | 24.7 | 158.1 | 44.6 | 341.2 | 19.8 | 24.4 | 13.5 |
| | <i>In situ</i> | 25 | 1632.0 | 20.8 | 852.5 | 27.4 | 223.8 | 16.2 | 555.6 | 20.3 | 185.0 | 33.8 | 370.7 | 16.4 | 22.9 | 7.5 |
| K3 | <i>Ex situ</i> | 28 | 1429.8 | 16.8 | 695.3 | 26.2 | 202.6 | 12.8 | 532.0 | 20.7 | 190.5 | 32.5 | 341.5 | 17.4 | 23.1 | 9.2 |
| | <i>In situ</i> | 15 | 1543.1 | 22.1 | 794.7 | 24.8 | 225.8 | 19.3 | 522.6 | 24.0 | 170.1 | 39.7 | 252.5 | 19.3 | 23.5 | 8.8 |
| G1 | <i>Ex situ</i> | 28 | 1892.8 | 14.8 | 610.0 | 24.4 | 262.3 | 16.0 | 1020.5 | 14.4 | 454.0 | 20.1 | 566.5 | 13.1 | 24.0 | 7.4 |
| | <i>In situ</i> | 12 | 2183.9 | 21.7 | 980.5 | 19.2 | 284.6 | 21.5 | 918.8 | 30.5 | 392.4 | 39.1 | 526.4 | 25.3 | 26.0 | 7.9 |
| G2 | <i>Ex situ</i> | 28 | 1674.7 | 15.9 | 581.1 | 30.0 | 226.7 | 16.8 | 866.8 | 17.6 | 389.1 | 25.7 | 477.7 | 14.5 | 22.9 | 10.8 |
| | <i>In situ</i> | 25 | 1369.0 | 16.6 | 468.3 | 26.3 | 229.8 | 25.8 | 670.9 | 23.2 | 269.0 | 33.8 | 401.9 | 18.7 | 20.9 | 8.7 |
| G4 | <i>Ex situ</i> | 28 | 1742.0 | 22.7 | 593.9 | 28.4 | 233.1 | 19.8 | 915.0 | 27.4 | 406.7 | 35.8 | 508.3 | 23.3 | 24.6 | 7.5 |
| | <i>In situ</i> | 21 | 1463.3 | 22.9 | 565.2 | 33.6 | 208.1 | 21.0 | 689.9 | 30.2 | 292.7 | 48.4 | 397.3 | 21.6 | 22.9 | 9.5 |
| M1 | <i>Ex situ</i> | 28 | 1744.8 | 20.8 | 618.4 | 25.1 | 227.9 | 19.4 | 898.5 | 25.3 | 428.0 | 32.5 | 470.5 | 22.8 | 22.4 | 12.3 |
| | <i>In situ</i> | 37 | 2055.2 | 17.0 | 798.3 | 25.4 | 297.3 | 18.0 | 959.7 | 21.7 | 431.7 | 30.3 | 527.9 | 16.1 | 24.1 | 7.9 |
| M2 | <i>Ex situ</i> | 28 | 1801.0 | 18.1 | 689.2 | 25.7 | 179.0 | 35.3 | 932.8 | 22.9 | 441.9 | 29.1 | 490.9 | 18.7 | 22.7 | 7.7 |
| | <i>In situ</i> | 18 | 2114.0 | 19.6 | 909.2 | 25.1 | 268.3 | 21.6 | 936.6 | 26.6 | 422.7 | 32.6 | 513.9 | 22.9 | 24.4 | 8.3 |
| M3 | <i>Ex situ</i> | 28 | 1638.9 | 14.2 | 509.8 | 27.9 | 224.5 | 17.0 | 904.7 | 17.6 | 385.9 | 22.5 | 518.8 | 17.8 | 22.0 | 10.3 |
| | <i>In situ</i> | 21 | 1427.2 | 15.0 | 542.5 | 18.5 | 225.2 | 17.9 | 659.5 | 21.8 | 270.4 | 31.6 | 389.1 | 16.6 | 23.4 | 9.6 |
| C1 | <i>Ex situ</i> | 28 | 1551.8 | 14.2 | 514.1 | 22.8 | 210.6 | 12.5 | 827.1 | 16.0 | 330.4 | 24.8 | 496.8 | 14.4 | 23.2 | 9.4 |
| | <i>In situ</i> | 38 | 1214.2 | 16.0 | 416.7 | 19.2 | 193.0 | 16.1 | 603.8 | 22.5 | 232.7 | 31.0 | 371.1 | 18.6 | 22.0 | 11.7 |
| C2 | <i>Ex situ</i> | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd |
| | <i>In situ</i> | 18 | 1329.0 | 16.6 | 543.9 | 25.8 | 188.5 | 19.7 | 596.6 | 23.2 | 222.3 | 42.6 | 374.3 | 12.8 | 23.5 | 7.8 |
| C3 | <i>Ex situ</i> | 28 | 1462.2 | 16.0 | 524.0 | 22.7 | 193.1 | 18.4 | 745.1 | 19.1 | 316.1 | 24.5 | 429.0 | 16.2 | 21.7 | 9.4 |
| | <i>In situ</i> | 20 | 1668.2 | 16.5 | 655.7 | 19.5 | 230.6 | 16.6 | 781.9 | 22.4 | 316.5 | 26.0 | 465.4 | 21.8 | 24.7 | 11.4 |
| C4 | <i>Ex situ</i> | 28 | 1713.0 | 11.1 | 635.5 | 24.0 | 232.8 | 12.2 | 844.7 | 15.0 | 378.8 | 19.5 | 465.9 | 15.3 | 23.4 | 10.4 |
| | <i>In situ</i> | 18 | 1350.0 | 17.8 | 478.7 | 32.3 | 205.5 | 16.3 | 665.8 | 20.4 | 269.3 | 30.0 | 396.6 | 18.0 | 21.8 | 8.5 |
| C6 | <i>Ex situ</i> | 28 | 1619.6 | 17.1 | 596.8 | 28.4 | 192.6 | 20.5 | 830.2 | 24.8 | 375.1 | 33.7 | 455.1 | 19.3 | 22.1 | 8.9 |
| | <i>In situ</i> | 19 | 1828.6 | 15.4 | 683.1 | 22.2 | 246.8 | 13.2 | 898.7 | 24.0 | 402.6 | 34.1 | 496.1 | 17.0 | 24.1 | 6.1 |
| J1 | <i>Ex situ</i> | 28 | 1686.1 | 15.0 | 615.9 | 28.2 | 229.9 | 17.8 | 840.4 | 19.0 | 370.9 | 26.7 | 469.5 | 16.3 | 23.3 | 7.5 |
| | <i>In situ</i> | 20 | 1589.5 | 22.5 | 665.6 | 40.2 | 223.9 | 32.9 | 745.4 | 30.7 | 301.9 | 44.7 | 443.5 | 23.1 | 23.3 | 8.4 |
| J2 | <i>Ex situ</i> | 28 | 1842.6 | 16.8 | 654.1 | 24.4 | 241.6 | 17.7 | 947.0 | 22.6 | 446.1 | 28.1 | 500.9 | 20.5 | 23.1 | 8.2 |
| | <i>In situ</i> | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd |
| N1 | <i>Ex situ</i> | 28 | 1516.8 | 19.1 | 560.3 | 24.8 | 214.1 | 17.2 | 742.9 | 22.5 | 319.9 | 29.3 | 422.5 | 19.5 | 22.2 | 11.2 |
| | <i>In situ</i> | 22 | 1118.2 | 19.2 | 385.5 | 31.8 | 175.9 | 23.9 | 556.8 | 21.2 | 188.6 | 23.5 | 368.3 | 24.7 | 21.1 | 7.9 |
| N2 | <i>Ex situ</i> | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd |
| | <i>In situ</i> | 22 | 1174.2 | 19.5 | 514.0 | 24.5 | 188.7 | 19.7 | 471.3 | 26.0 | 161.5 | 43.1 | 309.8 | 20.0 | 20.7 | 5.7 |
| C5 | <i>Ex situ</i> | 28 | 794.4 | 21.4 | 321.1 | 32.2 | 98.3 | 24.2 | 375.0 | 25.5 | 124.9 | 44.0 | 250.0 | 22.1 | 18.9 | 7.6 |
| | <i>In situ</i> | 20 | 746.1 | 15.3 | 243.6 | 17.1 | 117.7 | 9.7 | 384.7 | 20.9 | 123.8 | 48.3 | 260.9 | 11.9 | 18.6 | 2.8 |

Appendix 2. Continued.

| Fruit width (cm) | Endocarp length (cm) | | Endocarp width (cm) | | Mesocarp thickness (cm) | | Mesocarp (%) | | Endocarp (%) | | Water (%) | | Meat (%) | | Length/width fruit | | Length/width endocarp | | | |
|---------------------|-------------------------|------|------------------------|------|----------------------------|------|-----------------|------|-----------------|------|--------------|------|-------------|------|-----------------------|-----|--------------------------|------|------|----|
| | Mean | CV | Mean | CV | Mean | CV | Mean | CV | Mean | CV | Mean | CV | Mean | CV | Mean | CV | Mean | CV | | |
| 18.9 | 16.4 | 12.9 | 7.5 | 10.7 | 7.7 | 11.5 | 25.9 | 0.53 | 17.6 | 0.14 | 18.1 | 0.10 | 40.0 | 0.22 | 21.9 | 1.3 | 19.3 | 1.2 | 8.9 | |
| 17.7 | 10.5 | 12.8 | 6.0 | 11.2 | 7.1 | 6.5 | 23.3 | 0.51 | 9.2 | 0.13 | 13.8 | 0.11 | 19.9 | 0.23 | 14.0 | 1.3 | 9.1 | 1.1 | 8.0 | |
| 16.8 | 9.5 | 12.6 | 6.2 | 10.7 | 7.8 | 10.5 | 16.3 | 0.48 | 14.8 | 0.14 | 13.7 | 0.13 | 28.4 | 0.24 | 16.8 | 1.4 | 7.6 | 1.2 | 8.2 | |
| 17.5 | 9.8 | 13.4 | 11.8 | 10.7 | 9.1 | 6.8 | 21.2 | 0.51 | 7.6 | 0.14 | 14.3 | 0.10 | 23.4 | 0.23 | 9.3 | 1.3 | 9.8 | 1.3 | 6.3 | |
| 20.0 | 7.3 | 13.3 | 6.5 | 13.9 | 5.9 | 10.7 | 12.5 | 0.32 | 14.9 | 0.14 | 9.5 | 0.24 | 12.1 | 0.30 | 12.0 | 1.2 | 7.5 | 0.96 | 7.0 | |
| 21.4 | 8.5 | 13.5 | 8.9 | 14.6 | 16.7 | 6.9 | 29.4 | 0.45 | 12.1 | 0.13 | 11.0 | 0.17 | 20.9 | 0.24 | 13.0 | 1.2 | 8.3 | 0.94 | 13.6 | |
| 18.5 | 9.1 | 12.6 | 9.6 | 12.9 | 7.8 | 10.3 | 15.9 | 0.34 | 20.1 | 0.14 | 13.5 | 0.23 | 18.3 | 0.29 | 13.9 | 1.3 | 11.6 | 1 | 11.8 | |
| 17.9 | 7.1 | 11.8 | 6.1 | 12.6 | 8.8 | 5.3 | 21.3 | 0.34 | 21.4 | 0.16 | 21.0 | 0.19 | 24.8 | 0.29 | 10.8 | 1.2 | 9.2 | 0.94 | 8.4 | |
| 19.6 | 10.3 | 12.9 | 9.0 | 13.2 | 8.8 | 11.7 | 10.0 | 0.34 | 14.8 | 0.14 | 12.0 | 0.23 | 16.4 | 0.29 | 11.3 | 1.3 | 8.7 | 0.98 | 7.7 | |
| 18.4 | 12.9 | 11.6 | 7.4 | 12.4 | 9.9 | 5.9 | 30.3 | 0.38 | 21.2 | 0.14 | 13.6 | 0.19 | 34.7 | 0.27 | 12.5 | 1.3 | 7.1 | 0.94 | 5.8 | |
| 19.3 | 9.9 | 12.6 | 10.7 | 13.3 | 9.2 | 9.8 | 19.3 | 0.36 | 16.6 | 0.13 | 12.4 | 0.24 | 18.6 | 0.27 | 12.4 | 1.2 | 11.3 | 0.95 | 10.9 | |
| 20.9 | 7.6 | 14.2 | 6.5 | 14.1 | 7.0 | 6.7 | 21.5 | 0.38 | 17.0 | 0.14 | 15.5 | 0.20 | 20.0 | 0.25 | 12.5 | 1.2 | 8.2 | 1 | 9.2 | |
| 18.9 | 7.6 | 12.6 | 8.5 | 13.5 | 8.1 | 10.1 | 13.9 | 0.38 | 18.5 | 0.10 | 33.1 | 0.24 | 17.0 | 0.27 | 11.8 | 1.2 | 8.6 | 0.94 | 9.7 | |
| 20.7 | 9.2 | 14.2 | 9.9 | 13.6 | 9.3 | 7.1 | 20.3 | 0.43 | 17.5 | 0.12 | 12.2 | 0.19 | 19.8 | 0.24 | 13.2 | 1.2 | 5.9 | 1 | 8.8 | |
| 18.6 | 6.6 | 12.4 | 6.1 | 13.6 | 6.7 | 9.6 | 18.5 | 0.31 | 23.9 | 0.14 | 9.4 | 0.24 | 19.8 | 0.32 | 13.4 | 1.2 | 11.7 | 0.91 | 8.6 | |
| 17.8 | 9.2 | 12.6 | 6.5 | 12.2 | 9.8 | 5.5 | 23.9 | 0.38 | 16.1 | 0.15 | 12.2 | 0.18 | 20.0 | 0.27 | 11.0 | 1.3 | 11.6 | 1 | 11.4 | |
| 18.1 | 9.4 | 12.9 | 8.5 | 13.0 | 6.0 | 10.3 | 13.3 | 0.33 | 15.9 | 0.14 | 9.2 | 0.21 | 16.4 | 0.32 | 12.7 | 1.3 | 8.3 | 1 | 8.6 | |
| 17.1 | 7.0 | 12.4 | 9.3 | 12.2 | 7.2 | 5.2 | 20.0 | 0.34 | 15.5 | 0.16 | 9.2 | 0.18 | 19.6 | 0.30 | 9.7 | 1.3 | 11.8 | 1 | 8.8 | |
| nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd |
| 18.3 | 10.0 | 12.3 | 8.9 | 11.6 | 9.0 | 6.7 | 29.5 | 0.40 | 17.1 | 0.14 | 16.6 | 0.16 | 33.3 | 0.28 | 11.2 | 1.3 | 12.2 | 1.1 | 14.7 | |
| 17.8 | 9.2 | 12.1 | 7.4 | 12.3 | 7.5 | 9.6 | 16.2 | 0.36 | 15.2 | 0.13 | 14.5 | 0.22 | 16.1 | 0.29 | 8.2 | 1.2 | 12.7 | 1 | 11.5 | |
| 19.4 | 14.5 | 13.0 | 9.7 | 12.9 | 10.2 | 6.5 | 34.6 | 0.39 | 14.2 | 0.13 | 10.0 | 0.18 | 16.3 | 0.27 | 11.3 | 1.3 | 19.7 | 1 | 16.1 | |
| 18.7 | 7.2 | 12.6 | 6.4 | 12.9 | 6.3 | 10.9 | 21.4 | 0.37 | 19.5 | 0.14 | 9.3 | 0.22 | 19.1 | 0.27 | 12.6 | 1.3 | 10.8 | 0.98 | 8.7 | |
| 18.5 | 8.1 | 12.1 | 10.8 | 12.0 | 9.0 | 6.5 | 17.8 | 0.35 | 23.2 | 0.15 | 9.9 | 0.19 | 27.9 | 0.29 | 12.0 | 1.2 | 11.2 | 1 | 8.1 | |
| 18.0 | 7.1 | 12.5 | 7.1 | 12.5 | 10.2 | 9.6 | 18.0 | 0.37 | 24.5 | 0.12 | 13.2 | 0.23 | 24.5 | 0.28 | 12.9 | 1.2 | 9.1 | 1 | 11.0 | |
| 19.7 | 5.8 | 13.1 | 7.1 | 13.6 | 7.2 | 6.1 | 19.7 | 0.37 | 18.7 | 0.13 | 12.1 | 0.21 | 23.3 | 0.27 | 11.3 | 1.2 | 6.8 | 0.96 | 6.5 | |
| 19.9 | 9.2 | 12.7 | 7.7 | 13.0 | 7.3 | 10.6 | 11.9 | 0.36 | 20.9 | 0.14 | 14.4 | 0.22 | 18.7 | 0.28 | 13.9 | 1.2 | 9.8 | 0.97 | 5.5 | |
| 19.6 | 8.8 | 12.8 | 5.9 | 13.1 | 11.6 | 6.4 | 23.8 | 0.42 | 32.8 | 0.13 | 23.4 | 0.18 | 26.6 | 0.28 | 16.9 | 1.2 | 9.2 | 0.98 | 12.3 | |
| 20.1 | 8.7 | 12.7 | 7.3 | 13.5 | 8.6 | 10.4 | 15.8 | 0.36 | 19.7 | 0.13 | 11.5 | 0.24 | 16.5 | 0.27 | 14.3 | 1.2 | 7.2 | 0.95 | 7.3 | |
| nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd |
| 18.1 | 8.9 | 12.1 | 7.1 | 12.4 | 8.4 | 10.1 | 23.7 | 0.37 | 13.8 | 0.14 | 9.3 | 0.21 | 16.3 | 0.28 | 10.4 | 1.2 | 11.5 | 0.96 | 7.5 | |
| 17.0 | 9.0 | 11.8 | 7.1 | 11.5 | 11.8 | 5.5 | 20.6 | 0.34 | 21.2 | 0.15 | 18.6 | 0.26 | 18.7 | 0.32 | 18.2 | 1.2 | 8.9 | 1 | 11.3 | |
| nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd |
| 17.1 | 7.9 | 11.6 | 4.5 | 11.2 | 9.7 | 5.9 | 26.8 | 0.43 | 16.0 | 0.16 | 10.3 | 0.13 | 30.3 | 0.26 | 16.7 | 1.2 | 9.0 | 1 | 10.6 | |
| 14.6 | 15.8 | 10.2 | 6.6 | 10.0 | 8.4 | 8.7 | 12.8 | 0.40 | 20.4 | 0.12 | 17.6 | 0.15 | 28.3 | 0.32 | 19.3 | 1.3 | 10.2 | 1 | 7.4 | |
| 15.6 | 9.2 | 10.1 | 5.4 | 10.3 | 5.5 | 5.2 | 30.9 | 0.32 | 11.2 | 0.15 | 11.3 | 0.16 | 36.2 | 0.35 | 7.3 | 1.2 | 7.6 | 0.97 | 5.7 | |

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