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Morpho-physiological variation and phenotypic plasticity in Mexican populations of coconut (*Cocos nucifera* L.)

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Abstract

We studied the pattern of variation of 19 morphological and physiological characteristics of leaves and their phenotypic plasticity in 18 Mexican coconut populations experimentally grown under similar conditions and in the presence of LY. The results showed: (a) the existence of five ecotypes differentiated by characteristic means and plasticity of these characteristics: Atlantic Tall, Pacific Tall 1, Pacific Tall 2, Pacific Tall 3 and Malayan Yellow Dwarf (MYD); (b) the characteristics that best differentiate the five ecotypes were: leaf length, number of leaves produced per unit time, and percentage of proximal rachis in leaf; (c) the ecotypes correspond with population groups previously observed in a study of morphological characterization of fruit *in situ*. Pacific Tall 2 and MYD exhibited high resistance to LY and valuable morphological characteristics making them useful as parents in hybridization programs.

Introduction

The coconut (*Cocos nucifera* L.) was introduced to Mexico by the Spaniards in the 16th century from different parts of the world (Zizumbo-Villarreal 1996). It is widely cultivated in Mexico for oil extraction in about 200,000 ha. At present, coconut plantations are being infected by a phytoplasma disease (Class Mollicutes) lethal yellowing (LY). It is transmitted by *Myndus crudus* Van Duzze (Homoptera: Cixiidae). LY has destroyed the plantations in the states of Quintana Roo, Yucatan and Campeche. *It may soon destroy the entire area in the country* (Oropeza and Zizumbo-Villarreal 1997). The only effective strategy against the disease in other countries has been to replant with resistant varieties. The genetic diversity present in Mexico is unknown, as are the possible levels of resistance to the disease of the different populations.

Breeding programs for coconut generally rely upon crosses between Dwarf and Tall cultivars, using the high heritability and resistance to LY in Dwarf cultivars, better yield due to complementary yield components, and the possible expression of heterosis. The characterization of the coconut germplasm to be used in a breeding program may be based on both the characteristics of the fruit and vegetative parts (IBPGR 1992; Santos et al. 1998). The importance of characterizing the coconut germplasm in the early stages of growth has been emphasized for selection studies (Satyabalan and Mathew 1983). Palm vigor can be estimated from the rate of leaf production, leaf length, trunk diameter, etc. Evaluating these characteristics during the early years of growth accelerates the process of selection (Santos et al. 1998).

The objective of the study was to analyze the morphological and physiological variations in Mexican coconut populations under experimentally controlled conditions and in the presence of LY disease with a view to: (1) describing their patterns of variation and phenotypic plasticity based on their vegetative characteristics, (2) determining the existence, if any, of vegetatively differentiated groups of populations, (3) to compare this with that obtained in the study of fruit morphological characteristics (Zizumbo-Villarreal and Piñero 1998), (4) define the characteristics that best discriminate the groups of populations detected, and (5) analyze the distinctive vegetative characteristics of each ecotype in terms of its relevance to breeding programs.

This would indicate the possibility of genetic differentiation, which in turn would open the possibility of selection of genotypes resistant to LY and finding genotypes with characteristics useful for breeding programs. Genetically differentiated populations are often adapted to different sets of environmental conditions (Sultan 1987). These adaptations operate through genetic variation and phenotypic plasticity of the organisms (Oyama 1994). Phenotypic plasticity is the ability of an organism genotype to alter its physiology and morphology in response to changes in environmental conditions. It is genetically controled, and evolves in some cases in response to specific environmental influences (Bradshaw 1965). A high genetic plasticity of an organism can lead to a better response to agronomic management or restrictive environmental factors.

Several studies on morphological variation patterns have been carried out in coconut in different parts of the world, using diverse multivariate statistical methods (Harries 1978; Ashburner et al. 1997). The variation pattern of fruit found in Mexico suggests the existence of four morphotypes and the presence of genetic differences between them (Zizumbo-Villarreal and Piñero 1998).

Material and methods

Eighteen coconut populations of Mexico were studied, 17 Talls representing the current range of variability in the country, and one of Dwarf, the Malayan Yellow Dwarf (MYD) (Zizumbo-Villarreal et al. 1993). The seed nuts were planted in July 1989 in the nursery, in bags, and transplanted in January 1991 in an experimental plantation on the north coast of Yucatan Peninsula (Figure 1), where LY disease is prevalent.

This was on a sandy strip of coastal dune which separates an internal lagoon system from the sea, in calcareous regosol. The design consisted of four blocks in a north-south direction following a slight topographical slope. A treatment consisted of six palms per population and was established at random. The distance between palms was 9 m.

The number of leaves produced was recorded between January 1993 and August 1995. In August 1994 the first open leaf of each palm was marked, and the next year, in August 1995, at the commencement of the adult stage of the plants (when about 20% of the

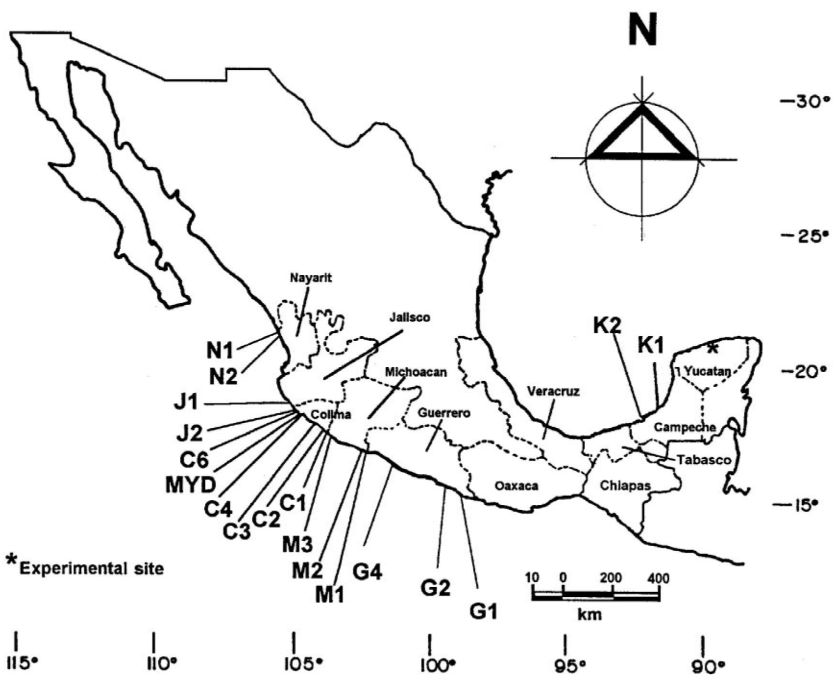

Figure 1. Locations of the 18 Mexican populations sampled and the experimental site in Yucatan, Mexico.

population were flowering), we recorded 10 characteristics on leaves of the same age (Table 1, Figure 2). Using these data, eight ratios between characteristics were calculated (in order to reduce the effects of the size of the plant) (Table 1). An estimate was made of the leaflet density in the blade (number of leaflets/blade length) and of the leaf area per leaf (length of blade/length of leaflet). The characteristics evaluated were those suggested by IBPGR as coconut descriptors (IBPGR 1992).

The numerical and statistical analyses were carried out using the Statistical Analysis System (SAS) version 6.04 (SAS Institute 1988). The normality of the data was tested on the residuals, using the procedure UNIVARIATE. All the characteristics were normal. Alpha significance levels were adjusted using the Bonferroni inequality to account for the simultaneous inferences made for each group of analyses (Miller Jr 1981). To analyze the discontinuities in the pattern of variation of populations and its clustering pattern, two analyses were carried out on the matrix of population means: (1) Principal Component Analysis (PCA) of the correlation matrix using the PRINCOMP procedure and plots of the first three standardized principal components; and 2) Agglomerative Hierarchical Cluster Analysis using the CLUSTER procedure. For this analysis, the elements of the matrix were standardized, and the matrix of similarities was obtained using as an indication of similarity, the square of the Euclidean distance. Clustering was done utilizing the unweighted pair-group method using arithmetic averages (UPGMA). The groups were then represented in a dendrogram that uses the standardized average distance as height.

To test the hypothesis that groups of populations clustered together in PCA plots are significantly different, a one-way ANOVA was carried out for the PCA scores of each one of the four plots of each population (in order to have a replica for those ecotypes with only one population). This ANOVA was done for each principal component. Comparison of means was done using the Bonferroni test for multiple comparisons of means ($\propto = 0.05$).

A Stepwise Discriminant Analysis using STEPDISC procedure was performed to establish which characteristics contributed most to the differentiation of population groups. Variables were chosen to enter or leave the discrimination model if the squared partial correlation for predicting the variable under consideration was $\geq$0.50, from the group classificatory variable, while controlling the effects of the variables already selected for the model.

The differences between populations and between characteristics, regarding their levels of variability or phenotypic plasticity, were analyzed by means of a two-way ANOVA using their coefficient of variation (CV) across the four treatments. A design of random blocks was used (Sokal and Brahuman 1980), each characteristic representing a block. The normality of the CV was tested on the residuals with the procedure UNIVARIATE. Only the CV of the ratios petiole length/blade length and length/width of the leaflet were not normal. Normality was achieved with an arc sine transformation. The tests for separation of means were carried out using the Bonferroni test ($\propto = 0.5$).

Results

Patterns of variation and differences between populations

Means and CV of the 19 characteristics studied are presented in Table 1. The PCA using the matrix of population means explained 88% of the total variation in the first three components (Table 2). The first component explained 51% of the variation, and the characteristics that best contributed to the model (with a coefficient of the function equal to or higher than the absolute value of 0.30) were: blade length, proximal rachis length, and leaf length. The second component explained 25% of the variation and the characteristics that best contributed to the model were: leaflet length, proximal rachis length/distal rachis length, percentage of proximal rachis, percentage of distal rachis, and leaflets length/width. The third component explained 12% of the variation. The most important characteristics were: leaf production, petiole length/blade length, petiole length and percentage of distal rachis (Table 2).

Visual inspection of the plots for the first, second and third component showed five groups of populations or ecotypes: MYD, Atlantic Tall (AT), Pacific Tall 1 (PT1), Pacific Tall 2 (PT2) and Pacific Tall 3 (PT3), (Figure 3). These groups are the same as those shown by the phenogram obtained with UPGMA (Figure 4). In this last figure, we can see that the MYD ecotype and the group of Tall coconut populations give the first hierarchical division, indicating that these groups showed the highest differentiation. The cluster of Tall coconuts was subdivided into two secondary clusters, the populations K1 and K2 or AT ecotype, and the populations distributed on the Pacific coast were further divided into two clusters. The first

Table 1. Means and CV (in parenthesis, percent) of 19 morphological characteristics of the 18 populations studied, population code and place of collection (municipality and state).

Code	Place of collection	Leaf production per year	Petiole length	Proximal rachis length (m)	Distal rachis length (m)	Blade length (m)	Leaf length (m)	Leaflets number	Leaflets length (m)	Leaflets width (m)	Rachis width (m)	Rachis thickness (m)	Petiole blade length	Proximal/ distal rachis length	Petiole length/ width	Leaflets length/ /width	Leaflets density	Leaf area	Proximal rachis percent	Distal rachis percent
K1	Champoton, Campeche	11.8(21)	1.16(14)	1.05(15)	1.66(10)	2.27(10)	3.88(10)	84.9(8)	0.9(16)	0.05(11)	0.05(14)	0.04(19)	0.43(12)	0.64(13)	20(13)	19(17)	31.5(11)	2.46(25)	27.12(10)	42.89(5)
K2	Cd. Carmen, Campeche	12.8(20)	1.13(12)	1.09(22)	1.71(16)	2.8(17)	3.93(15)	90.3(13)	0.92(15)	0.05(10)	0.06(18)	0.04(17)	0.41(13)	0.63(15)	19.4(15)	19.8(16)	32.6(12)	2.62(28)	27.44(11)	42.49(6)
G1	Ayozu, Guerrero	12.5(21)	1.06(21)	1.47(16)	1.77(10)	3.23(11)	4.3(12)	88.5(11)	0.81(16)	0.05(13)	0.06(15)	0.04(17)	0.33(20)	0.83(12)	24.6(8)	15.5(13)	27.5(10)	2.64(23)	34.04(7)	41.38(9)
G2	Copala, Guerrero	13.3(18)	1.19(15)	1.51(13)	1.85(9)	3.36(9)	4.55(8)	94(9)	0.86(12)	0.05(10)	0.06(11)	0.04(22)	0.36(17)	0.82(14)	25.3(11)	15.9(13)	28(7)	2.89(16)	33.21(9)	40.61(7)
G4	Tecpan, Guerrero	13.4(21)	1.24(12)	1.42(16)	1.68(12)	3.1(13)	4.33(11)	93.1(10)	0.78(10)	0.05(11)	0.06(16)	0.04(22)	0.4(13)	0.84(12)	24.5(12)	16(9)	30.2(8)	2.44(18)	32.55(8)	38.83(6)
M1	L. Cardenas, Michoacan	14.0(21)	1.16(12)	1.38(19)	1.76(12)	3.14(13)	4.31(11)	96.8(12)	0.79(17)	0.05(12)	0.06(14)	0.04(18)	0.37(14)	0.79(16)	24.6(12)	15.3(20)	31.1(11)	2.5(23)	31.9(10)	40.92(9)
M2	L. Cardenas, Michoacan	14.8(25)	1.23(14)	1.39(14)	1.77(10)	3.17(10)	4.4(11)	93.4(9)	0.86(11)	0.05(13)	0.06(13)	0.04(21)	0.39(9)	0.79(12)	23.2(11)	16.9(19)	29.6(8)	2.7(17)	31.67(7)	40.35(6)
M3	Coahuayana, Michoacan	15.0(36)	1.19(16)	1.33(19)	1.77(11)	3.1(13)	4.29(13)	96.3(13)	0.8(13)	0.05(11)	0.06(16)	0.04(18)	0.38(12)	0.75(14)	23.1(13)	16.6(17)	31.2(8)	2.5(20)	30.85(9)	41.43(6)
C1	C. Ortega, Colima	14.8(25)	1.38(15)	1.42(20)	1.97(12)	3.38(14)	4.76(13)	98(10)	0.89(17)	0.05(10)	0.06(16)	0.04(20)	0.41(14)	0.72(16)	23.4(12)	17.5(20)	29.3(11)	3.05(28)	29.54(11)	41.48(7)
C2	C. Ortega, Colima	14.5(31)	1.39(14)	1.4(15)	1.9(10)	3.3(10)	4.69(9)	99.5(11)	0.87(11)	0.05(12)	0.06(15)	0.04(19)	0.42(15)	0.74(13)	24.8(14)	17.3(17)	30.2(7)	2.89(18)	29.79(10)	40.65(6)
C3	Tecoman, Colima	16.0(22)	1.33(12)	1.55(14)	1.85(10)	3.4(11)	4.72(10)	102(10)	0.86(12)	0.05(14)	0.06(15)	0.04(22)	0.39(11)	0.84(11)	24.9(13)	18(17)	30.3(9)	2.95(20)	32.67(8)	39.21(5)
C4	Cuyutlan, Colima	14.5(19)	1.24(12)	1.39(20)	1.83(12)	3.22(13)	4.46(11)	96.3(4)	0.86(15)	0.05(10)	0.06(17)	0.04(22)	0.39(14)	0.76(18)	22.4(12)	17.2(19)	29.9(5)	2.78(22)	30.97(12)	41.13(8)
C6	Manzanillo, Colima	13.5(21)	1.17(14)	1.37(19)	1.76(12)	3.13(13)	4.31(12)	97.9(12)	0.84(15)	0.05(13)	0.06(17)	0.04(18)	0.38(12)	0.78(18)	23.2(11)	16.8(19)	31.4(10)	2.64(22)	31.64(10)	41.09(8)
J1	Cihuatlan, Jalisco	13.8(20)	1.23(10)	1.27(13)	1.73(13)	3(11)	4.23(10)	88.4(10)	0.83(16)	0.05(13)	0.05(13)	0.04(16)	0.41(12)	0.74(14)	23.4(11)	16.9(19)	29.6(10)	2.52(24)	30.08(9)	40.73(6)
J2	Cihuatlan, Jalisco	13.7(21)	1.17(16)	1.34(16)	1.76(11)	3.1(12)	4.28(12)	92(9)	0.82(15)	0.05(11)	0.06(13)	0.04(20)	0.38(11)	0.76(12)	23.5(11)	16.7(16)	29.8(9)	2.58(25)	31.29	41.32(5)
N1	San Blas, Nayarit	14.3(20)	1.32(14)	1.41(16)	1.74(15)	3.2(12)	4.51(11)	88.2(11)	0.9(12)	0.05(10)	0.06(11)	0.04(20)	0.42(15)	0.8(13)	24.6(11)	18.1(15)	27.9(14)	2.88(20)	31.2(9)	39.5(7)
N2	San Blas, Nayarit	14.6(20)	1.33(14)	1.45(19)	1.82(11)	3.27(12)	4.6(11)	95.9(11)	0.84(13)	0.05(8)	0.06(11)	0.04(19)	0.41(10)	0.8(19)	24.9(15)	17.4(15)	29.5(10)	2.76(21)	31.36(11)	39.7(9)
MYD	Tecoman, Colima	17(13)	0.96(10)	1.05(13)	1.31(13)	2.36(12)	3.31(11)	80.2(7)	0.73(12)	0.04(9)	0.05(14)	0.03(18)	0.41(9)	0.81(14)	21.7(9)	17.8(10)	34.3(9)	1.74(22)	31.61(7)	39.47(7)

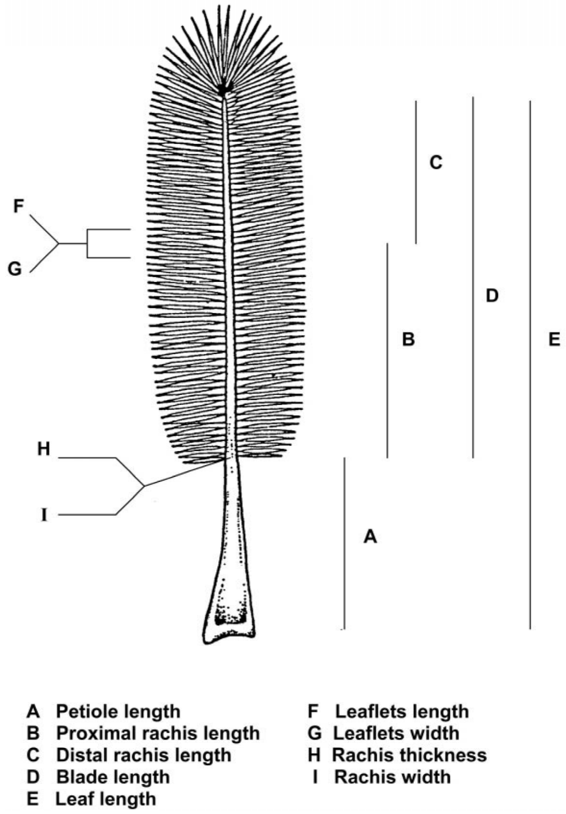

Figure 2. Coconut leaf characteristics studied.

cluster included populations distributed on the Costa Chica of Guerrero (G1 and G2) or PT3 ecotype, and the second cluster included the populations distributed in the states of Colima and Nayarit (C1, C2, C3, N1 and N2) or PT2 ecotype in one subcluster, and those distributed in the states of Guerrero, Michoacan, Colima, and Jalisco (G4, M1, M2, M3, C4, C6, J1 and J2) or PT1 ecotype in the other subcluster.

The one-way ANOVA (Table 3) for the first component scores showed significant differences between populations. The Bonferroni test revealed two groups: (1) MYD population and AT populations, which had significantly lower values, and (2) all the PT populations. The one-way ANOVA for the second component also showed significant differences between populations. This time the Bonferroni test revealed significant differences between AT populations and MYD, which had significantly lower values. There were also significant differences between AT and PT populations, MYD was also significantly different from PT populations except for PT3. The one-way ANOVA for the third component also showed significant differences between populations. There were significant differences among the three PT populations.

Stepwise Discriminant Analysis (Table 4) indicated that the characteristics that contributed best to the differentiation of the five ecotypes were: leaf

Table 2. Eigen vectors of the first three principal components in the 18 populations.

Characteristic	FIRST COMPONENT	SECOND COMPONENT	THIRD COMPONENT
Leaf production	−0.02955	−0.2044	0.475689
Petiole length	0.21434	0.189765	0.375936
Proximal rachis length	0.307128	−0.12589	0.058158
Distal rachis length	0.280047	0.202698	0.010255
Blade length	0.319014	0.035257	0.044009
Leaf length	0.305871	0.085865	0.150773
Leaflets number	0.246823	0.069043	0.162704
Leaflets length	0.092402	0.402689	0.042071
Leaflets width	0.277052	0.045322	−0.23658
Rachis width	0.285615	0.052826	−0.02819
Rachis thickness	0.247083	0.154261	−0.27623
Petiole/blade length	−0.13353	0.225893	0.445684
Proximal/distal rachis length	0.140917	−0.39489	0.077006
Petiole length/petiole width	0.246428	−0.23958	0.119769
Leaflets length/leaflets width	−0.15678	0.309203	0.238438
Leaflets density	−0.25836	0.005753	0.120084
Leaf area	0.273644	0.219057	0.07332
Proximal rachis percentage	0.157049	−0.38436	−0.08517
Distal rachis percentage	−0.08349	0.324606	−0.37432
Variance explained	51%	25%	12%

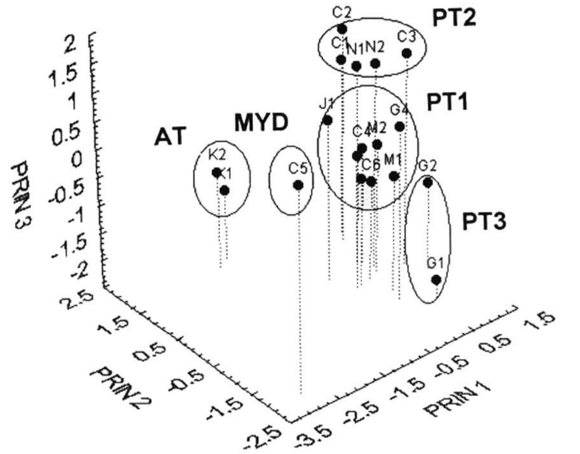

Figure 3. Principal Component Analysis plot of variation of 19 morphological and physiological characteristics of 18 coconut populations.

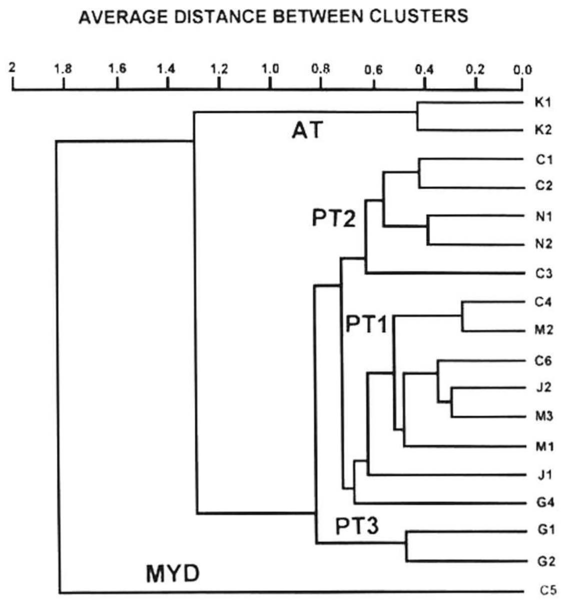

Figure 4. Cluster Analysis dendrogram (UPGMA) of 18 coconut populations. Grouping based on 19 morphological and physiological characteristics. Ecotypes: AT: Atlantic Tall; PT1: Pacific Tall 1; PT2: Pacific Tall 2; PT3: Pacific Tall 3; MYD: Malayan Yellow Dwarf.

length, number of leaves produced, and percentage of proximal rachis.

Phenotypic plasticity

There were significant differences between populations with respect to their profile of variability or plasticity ($F = 4.0$; $P < 0.0001$). MYD had the lowest plasticity with an overall CV (meaning CV across all characters) of 11.5%. Six tall populations, C4, M1, C6, M3, C1 and K2, had a significantly higher plasticity with an overall CV between 14.4% and 15.5%.

There were also significant differences between the CVs of the characteristics across all the populations ($F = 40.0$; $P < 0.0001$). Number of leaves produced, leaf area, and thickness of the rachis had higher plasticity (between 19.2% and 21.9% on an average). The length of the distal rachis, leaflet length/width, rachis width, proximal rachis length/distal rachis length, leaflet length, petiole length, petiole length/blade length, and blade length showed lower plasticity than that of the previous group (between 16.6% and 12%), but higher than that of the characteristics: number of leaflets, density of leaflets, percentage of proximal rachis, and percentage of distal rachis, which showed between 10.6% and 6.9% plasticity. The length/width of petiole, proximal rachis length, leaf length and the width of the leaflet showed no differences from the two previous groups.

Discussion

Patterns of variation and differences between populations

The MYD characteristics of short leaves and blades, as well as their higher rate of growth, as shown by greater rate of leaf production, have proved to be useful in programs for the production of hybrid seed involving Dwarfs × Talls. The short leaves permit a higher density of cultivation and higher rate of pro-

Table 3. One-way ANOVA of the scores of the three first principal components.

Source of variation	df	Sum of squares	Mean square	*F*	*P*
First principal component	4	43.5	10.9	26.5	0.0001
Second principal component	4	44.1	11	27.5	0.0001
Third principal component	4	24.3	6.1	8.7	0.0001

duction of leaves permit production of more bunches per unit time resulting in greater production of nuts/ha. MYD has wide leaflets which may increase blade opposition to wind. This characteristic seems to be compensated by leaves with long petioles and a short blade with a short distal rachis, characteristics which suggest greater strength in the leaf and blade.

AT also possesses short leaves and blades, but rate of leaf production is less as compared to MYD, indicating a slower growth rate. It has longer, slimmer leaflets. The leaf has a lower length of petiole in relation to the blade and a low percentage of proximal rachis in the blade, both characteristics suggesting that leaves and blades have less strength, and therefore more susceptibility to cyclone damage.

Leaf length and rate of leaf production were the two characteristics that discriminated best among the five ecotypes. These characteristics could be useful as markers for the selection of female parents in yield improvement programs.

The third best characteristic for discriminating the ecotypes was the percentage of proximal rachis, a structure which apparently gives greater strength to the leaf blade, and which possibly has compensated for changes in the ratio of petiole to blade that make the leaf more fragile.

Phenotypic plasticity

MYD had the lowest phenotypic plasticity, while six populations registered significantly higher levels than MYD: K2 of AT, M1, M3, C4, C6 of PT1, and C1 of PT2. It would be desirable to conserve these populations in order to use them in genetic improvement programs.

The number of leaves produced was the characteristic that showed the greatest plasticity. Coconut appears to have substantial physiological plasticity to adjust itself to the environment by altering its growth rate. Leaf area/leaf was the second most plastic characteristic, indicating that the development pattern is altered through marked changes in the morphology of the leaf. Leaf area is highly correlated with productivity in the coconut (Narayanan and Gopalakrishnan 1991).

The percentage of proximal rachis and the number and density of leaflets were the least plastic characteristics and therefore had the least environmental influence. Of these three characteristics, the percentage of proximal rachis in the leaf could be useful for identification of ecotypes, as it was one of the three characteristics which best distinguishes differences among them.

Comparison of the classification of the populations based on vegetative and fruit characteristics

The groups of populations (ecotypes) found in this study were very similar to those previously identified by analysis of fruit morphological characteristics (Zizumbo-Villarreal and Piñero 1998). AT has a fruit with high content of mesocarp, low content of immature endosperm, and an elongated and angular shape, and these are characteristics of wild populations. PT1 has large nuts with low mesocarp content, high content of liquid endosperm, and spherical shape, which are characteristic of domesticated populations (Harries 1978). PT2 and PT3 have medium-sized fruits with low percentage of mesocarp, high content of solid endosperm, and a round shape. MYD has small fruits with high percentage of mesocarp and solid endosperm, which are characteristic of domesticated populations (Zizumbo-Villarreal and Piñero 1998).

These results indicate that the use of vegetative characteristics, such as leaf parameters, when they are obtained under similar growth conditions and in plants of similar age, enables the differentiation of population groups in coconut palm with greater precision than the fruit characteristics obtained from areas of production.

Response to LY

Experimental evaluation of these five ecotypes indicates a differential response to LY after ten years of exposure to the disease (Zizumbo-Villarreal et al.

Table 4. Stepwise discriminant analysis. Partial R-square to enter or leave the discrimination model < 0.50.

Step	Characteristic selected	Partial R-square	*F*	*P*
1	Leaf length	0.32	49.3	0.0001
2	Number of leaves produced	0.27	40.1	0.0001
3	Percentage of proximal rachis	0.21	28.8	0.0001

1999). AT had the highest percentage of mortality (79%), significantly higher than those of PT2 (23%) and PT1 (37%), but not of PT3 (56%). At present, the plantations on the coasts of the Caribbean and the Gulf of Mexico, in the states of Quintana Roo, Yuctan, and Campeche, where populations of AT are growing, have been almost totally eliminated by the disease due to the high susceptibility of this ecotype. MYD showed the lowest percentage of mortality (6%). PT2 and MYD showed high resistance to LY and valuable morphological characteristics for possible use as parents in variety improvement programs.

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