

## FLOWER MORPHOMETRY OF *RHIZOPHORA MANGLE* (RHIZOPHORACEAE): GEOGRAPHICAL VARIATION IN MEXICAN POPULATIONS<sup>1</sup>

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We explored the patterns of intra- and interpopulation variation in flower morphology of the red mangrove, *Rhizophora mangle*. Twelve populations in Mexico were studied: five from the Gulf of Mexico and the Caribbean Sea, and seven from the Pacific Coast. Six metric floral attributes were measured from a sample of 1370 flowers. Significant differences among populations were found for all six attributes. Because floral attributes were all correlated, scores derived from principal factor analysis were used to describe the variation in flower morphology. Two factors explained essentially all of the variance in flower morphology. Corolla and calyx size had a strong effect on factor 1, while gynoecium size had the higher effect on factor 2. Nested analyses of variance on the scores from both factors revealed significant differences among coasts, among populations within coasts, and among plants within populations. Nonetheless, this variation cannot be explained as a result of clinal variation, as indicated by a series of regression analyses. Cluster analysis (UPGMA) showed that a population from the Pacific coast was clustered together with those of the Atlantic, and the arrangement of populations within each coast showed no evident geographical pattern. We propose that frequent events of extinction and recolonization by a few individuals, followed by selfing, may produce differentiation among populations of red mangrove.

**Key words:** flower morphology; Mexico; population differentiation; Rhizophoraceae; *Rhizophora mangle*.

Species with wide geographical distributions offer the opportunity to explore the dynamics of the evolutionary processes that occur among and within populations (Mayr, 1963; Dobzhansky, 1970). The large environmental heterogeneity characteristic of broad geographical ranges may promote differentiation among local populations facing contrasting physical and biotic conditions. The end result for each population would depend on the relative importance of gene flow among populations and the evolutionary processes operating at a local scale (Wright, 1931, 1932, 1988; Slatkin, 1987, 1994). The study of morphological differentiation among populations is a first step in determining the identity and relative importance of the evolutionary forces promoting or preventing differentiation. The lack of phenotypic differentiation among populations could be the result of (1) a recent origin of the populations, (2) high rates of gene flow, or (3) natural selection favoring similar phenotypes in each population. In contrast, population differentiation may be promoted by either natural selection or genetic drift. Intense natural selection may favor different phenotypes in each population in response to differences in selective regimes among localities. On the other hand, if populations were founded by a few individuals, or if their population sizes were small, differentiation could be the

result of genetic drift (Wright, 1931, 1932, 1988; Mayr, 1963; Dobzhansky, 1970; Slatkin, 1987, 1994).

In this study we describe the geographical patterns of phenotypic variation of the floral attributes of the red mangrove, *Rhizophora mangle*, in Mexico. We then use this information in order to infer the underlying evolutionary mechanisms leading to the present patterns of phenotypic variation.

### MATERIALS AND METHODS

**The plant species**—*Rhizophora mangle* L. (Rhizophoraceae) is a perennial tree whose habitat is restricted to intertidal zones and coastal lagoons. It is found from Mexico to northern Ecuador on the Pacific Coast, and ranges from Mexico to Brazil on the western Atlantic Coast (Tomlinson, 1994). This species is also found in the west coast of Africa, from Angola to Mauritania (Tomlinson, 1994). In America, *R. mangle* has its northernmost latitudinal limit at 24° N on the Gulf of Mexico, and at 29° N on the coasts of Baja California (Rzedowski, 1978). Although this species has a marked habitat specificity, it occurs on several geomorphologically distinct landscapes. These habitats are associated with differences in water salinity, water temperature, hydrology, and general climate (see Table 1), which, in turn, bring about variation in morphological structure of trees, dominance, and leaf and fruit size (Lugo and Snedaker, 1974; López-Portillo and Ezcurra, 1989; Flores-Verdugo et al., 1992; Rico-Gray and Palacios-Ríos, 1996). With the exception of the large populations of *R. mangle* located in the states of Sinaloa and Nayarit, the populations of the Pacific coast of Mexico are smaller and more scattered than the populations in the Gulf of Mexico and the Caribbean Sea (Rzedowski, 1978). *R. mangle* flowers throughout the year, although a peak occurs at the end of the summer (Rico-Gray, 1979). Flowers are perfect, self-compatible, and the main pollen vector is wind (Primack and Tomlinson, 1980; Tomlinson, 1994). The pollen:ovule ratio is high, in agreement with the expectation for wind-pollinated species (Cruden, 1977). The morphology (Fig. 1) of the

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TABLE 1. Studied localities of *Rhizophora mangle* in Mexico. Sample sizes per population (trees) and the average number of flowers analyzed per tree are also given. (T and PP correspond to average annual temperature and precipitation, respectively.)

Locality	State	Latitude	Longitude	Number of plants	Average number of flowers/plant	T (°C)	PP (mm)
<b>Pacific Coast</b>							
1 Bahía Kino	Sonora	28°47'	111°54'	13	4	22.1	179.6
2 Topolobampo	Sinaloa	25°36'	109°8'	14	7	24.3	244.1
3 Novillero	Nayarit	22°30'	105°37'	15	7	24.5	1030
4 San Blas	Nayarit	21°33'	105°18'	13	12	25.2	1436
5 Coyuca	Guerrero	16°57'	100°02'	14	7	27.5	1360
6 Chacahua	Oaxaca	15°58'	97°35'	15	7	28.0	905.5
7 Chantuto	Chiapas	15°12'	92°52'	15	8	26.5	1578.4
<b>Atlantic Coast</b>							
8 Tamiahua	Veracruz	21°23'	97°26'	15	8	24.8	1352.4
9 Sontecomapan	Veracruz	18°32'	95°01'	14	8	24.3	2016.9
10 Centla	Tabasco	18°36'	92°27'	17	8	26.6	1560.2
11 Celestún	Yucatán	20°57'	90°21'	20	6	26.4	725.5
12 Ría Lagartos	Yucatán	21°35'	88°4'	20	8	25.6	550.1

flowers allows for self-pollination, which results in high levels of selfing (Lowenfeld and Klekowski, 1992).

The dispersal of *R. mangle* occurs by means of buoyant seedlings, which remain viable for long periods (Rabinowitz, 1978; Tomlinson, 1994). Although these characteristics offer the potential for long-distance dispersal (Primack and Tomlinson, 1980), most of the seedlings establish near the mother plant (Rabinowitz, 1978).

In short, the wide geographical distribution of *R. mangle*, which embraces a heterogeneous set of ecological conditions, its pollination biology, which seems to favor high levels of selfing, and its dispersal biology, which allows for long-distance dispersal, make this species an ideal subject for the study of population differentiation and the processes leading to it.

**Sampling procedures**—Twelve Mexican populations of *Rhizophora mangle*, seven from the Pacific coast and five from the Gulf of Mexico and Caribbean Sea, were selected for this study (Table 1). This sample encompasses the complete range of distribution of this species in Mexico, and comprises a latitudinal expanse of 13°40'. In each population 20 flowering individuals were sampled and a mode of eight flowers per individual tree were collected (Table 1). The number of plants per population and of flowers per individual varied due to the different availability of reproductive individuals among populations. Each flower was filmed using a portable camcorder (Canon LP1, Canon Inc., Tokyo, Japan) and the images were recorded on 8-mm tapes. Two images were

taken for each flower, one from above the corolla and another one from an axial cross section (terminology after Weberling, 1989; Fig. 1) (i.e., a median longitudinal section, as commonly referred to). Digitized images were measured using the program MorphoSys (Meacham and Duncan, 1990). These measurements were done on the amplified images of the flowers (~15×), and this amplification was managed to adjust the resolution of the program (one pixel) to 0.01 cm. The accuracy of this method was evaluated by measuring 48 pieces of paper of known dimensions. The difference between the average estimation and the real value was 0.03 cm (SE = 0.009). Additionally, the repeatability of this method was estimated through the comparison of two consecutive independent measures performed on the same pieces of paper ( $N = 48$ ). The average difference between each pair of measurements amounted to 0.002 cm (SE = 0.007), and did not statistically differ from zero ( $t = 0.33$ ,  $P > 0.5$ ). Therefore, we are confident that this method is accurate and repeatable.

Six measurements were made on each flower, four from above the corolla and two from the axial cross section (Fig. 1). Due to a malfunction of the camcorder, the two measurements from the axial cross section were not obtained for one of the populations (Novillero, Nayarit).

**Statistical analyses**—Variation among populations in floral characteristics was analyzed using both univariate and multivariate methods. In order to reduce the number of variables, a principal factor analysis (PROC FACT; SAS, 1988) was carried out on the six original flower attributes. Principal factors were obtained through a maximum-likelihood algorithm because this method gives better estimates than plain principal factor analysis (PROC FACT; SAS, 1988). The number of factors to be retained was determined by means of  $\chi^2$  tests. Finally, once the number of principal factors was determined, factor scores were derived with the Score procedure in SAS (SAS, 1988). Because factor scores are linear combinations of the original variables, they may be used as integrated descriptors of the general morphology of the flowers (Kleinbaum, Kupper, and Muller, 1988; Marcus, 1990; Reyment and Jöreskog, 1993). In order to partition the total variance in flower morphology into its geographic components, a nested analysis of variance (Sokal and Rohlf, 1981) was performed on the scores of the first two principal factors (PROC GLM; SAS, 1988). Factor scores were partitioned in terms of: the differences (1) between the Pacific and Atlantic coasts, (2) among populations within coasts, (3) among individuals within populations, and (4) among flowers within individuals (this level was used as the error term; Sokal and Rohlf, 1981). Populations and individual trees within populations were assigned as random variables

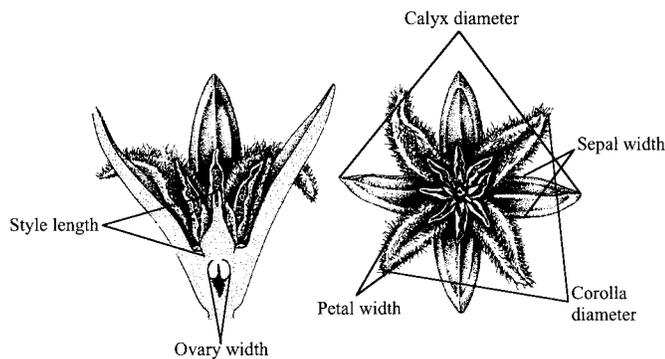


Fig. 1. Flowers of *Rhizophora mangle* showing the six floral characteristics measured: longitudinal and frontal views. (Redrawn from Tomlinson, 1994.)

TABLE 2. Descriptive statistics of floral characteristics measured in 12 populations of *R. mangle* in Mexico. (Coefficient of variation =  $(SD/\bar{X}) \times 100$ .)

Variable	Average (cm)	N (flowers)	Standard deviation	Coefficient of variation
Corolla diameter	1.81	1370	0.43	23.51
Calyx diameter	1.54	1370	0.46	30.06
Petal width	0.26	1370	0.05	19.43
Sepal width	0.41	1370	0.08	19.22
Style length	0.71	1357	0.21	29.40
Ovary width	0.22	1253	0.05	24.27

in the analysis. The percentages of variance accounted for by each hierarchical level, the variance components, were obtained through the calculation of the intraclass correlation coefficients ( $r$ ; Sokal and Rohlf, 1981) with the nested procedure in SAS (SAS, 1988). At any given hierarchical level, the intraclass correlation coefficient represents the sum of the variance components at this and higher levels, standardized by the total variance (Bell, 1989). Thus, variance components can be readily calculated from the intraclass correlation coefficients.

In order to explore whether or not flower variation in *R. mangle* behaves as a cline (a gradient of continuous variation along a geographic range, Huxley, 1942; Mayr, 1963; Ridley, 1993), we regressed the flower's scores derived from principal factor analysis vs. the latitude of each population (PROC GLM; SAS, 1988). Since significant differences between the coasts were detected (see below), two regression analyses per coast (one for each of the two principal factors) were performed. In these analyses we used the flower's scores averaged per individual. Because each population contains several nonindependent observations (corresponding to each individual within a population), we used a regression model with replicates (Sokal and Rohlf, 1981). This method avoids the overestimation of the degrees of freedom brought about by the several measures of individual trees for each population and allows for the estimation of both the categorical (i.e., the variation among populations) and continuous (i.e., the latitudinal position of the populations) effects attributable to populations differences.

Finally, the geographic pattern of differentiation among populations in floral morphology was explored by means of cluster analysis using an unweighted pair-group method with arithmetic averaging (UPGMA; Sokal and Michener, 1958), and Euclidean distances as the criterion for clustering (Statistica; Statsoft, 1994).

## RESULTS

Pooling all sites, the floral attributes analyzed in this study showed coefficients of variation ( $SD/\bar{X} \times 100$ ) that range from 19 to 30% (Table 2). The more variable characters, calyx diameter and style length, were 1.6 times more variable than petal and sepal width, the attributes with the lowest coefficients of variation (Table 2). In spite of the relative low variation observed, one-way analyses of variance revealed statistically significant differences in mean values among populations for each floral trait (Fig. 2). With the exception of the Tamiahua population, which showed the highest mean values for all floral traits (Fig. 2), the patterns of covariation among floral attributes are inconsistent throughout the populations (i.e., a given population may have a low value for one attribute but high for others) (Fig. 2).

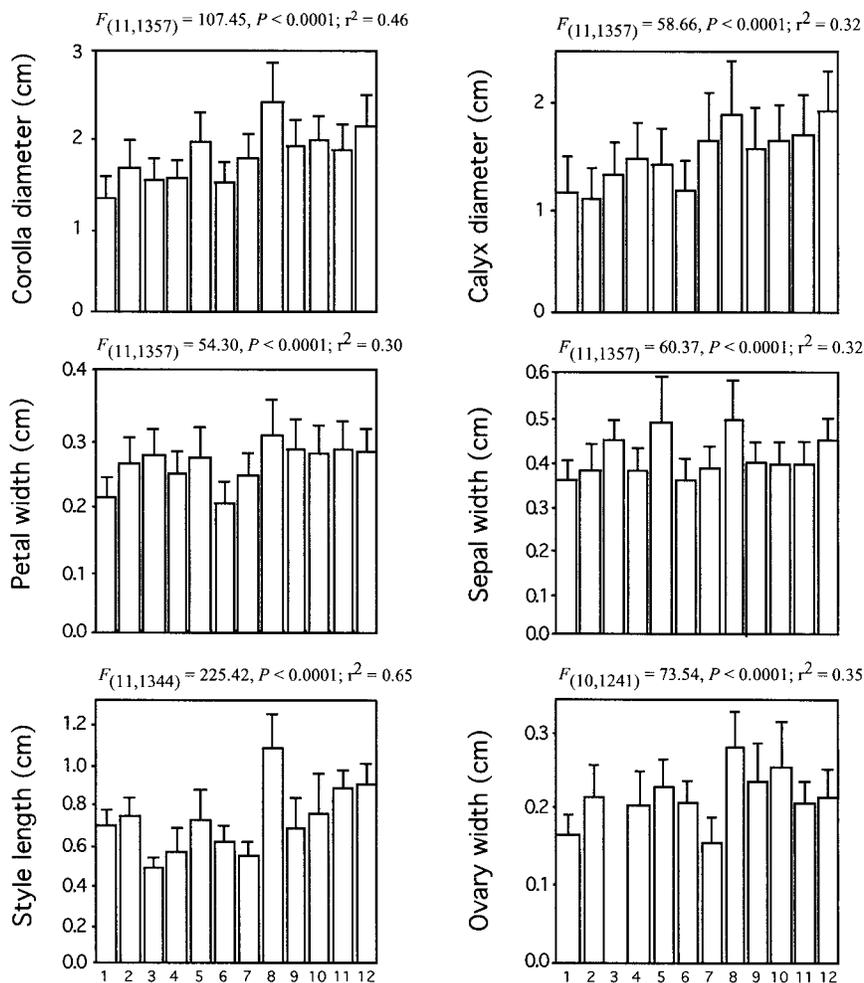
Floral attributes were all positively correlated, and correlation coefficients among all floral traits were statistically significant (Table 3). The higher correlations occurred among characters related to corolla and calyx size ( $r = 0.48$ – $0.71$ ), whereas lower correlations occurred be-

tween either ovary width or style length and the remaining characters ( $r = 0.18$ – $0.5$ ; Table 3).

As expected, results from principal factor analysis are consistent with those found through correlation analyses (Table 4). There were two large positive eigenvalues (factors) that together accounted for 100% of the common variance in flower morphology. Factor analysis based on iterative methods, as the one used here, commonly produce some negative eigenvalues. When this method converges properly, the sum of the eigenvalues corresponding to rejected factors should be 0 (SAS, 1988). The sum of the third to sixth eigenvalues equaled 0 [0.0615 + 0.0019 + (-0.0131) + (-0.0503)]. As a consequence, two factors were enough to explain the common variance in flower morphology ( $\chi^2_2 = 4.01$ ,  $P = 0.404$ , for the null hypothesis that two factors are sufficient). The first factor accounted for 88.9% of the variance, while the second factor accounted for the remaining 11.1%. All factor loadings were positive, emphasizing the fact that much of the flower variation is associated with size. Because the higher loadings on factor 1 corresponded to corolla and calyx size (Table 4), this factor may be considered as summarizing the size of perianth. In contrast, ovary width and style length had the higher loadings on factor 2, so this factor may be interpreted as the size of the gynoecium (Table 4).

Nested analyses of variance performed on the scores of factors 1 and 2 revealed that all levels considered (among coasts [Pacific and Atlantic], populations within coasts, and trees within populations) explained a statistically significant proportion of the total variation in the flower morphology of *R. mangle* (Table 5). Differences between coasts (Pacific vs. Atlantic) explained the greatest proportion of variance in factor 1 (28.18%), followed by individual trees within populations (18.33%), and then by differences among populations within coasts (17.46%). The differences between the coasts explained 25.63% of the variance in factor 2, which is almost equal to the magnitude of explained variance in factor 1 by this level. In contrast, populations (i.e., localities) within coasts explained 1.64 times more variance in factor 2 than in the case of factor 1 (28.73 and 17.46%, respectively). Differences among individuals within populations accounted for only 11% of the variance in factor 2. It is remarkable that, for both factors, approximately one-third of the variation in flower morphology is accounted for by the differences among flowers within individuals (cf. Table 5). Thus, although there is considerable phenotypic variation among individuals within populations for natural selection to act (cf. Table 5), a substantial amount of the total variation in flower morphology is accounted for by the error term (flowers within individuals), and thus, can be attributable to developmental instability (cf. Møller, 1996).

Regression analyses with replicates (see Materials and Methods) showed that flower morphology significantly differs among populations of *R. mangle* (Table 6). Nonetheless, this variation does not behave as continuous (clinal) variation throughout the latitudinal range of distribution of this species in Mexico. This was true for both factors at both coasts (Table 6). In all cases the effect of the deviations from regression term was significant, suggesting the existence of a large amount of random vari-



### Populations

Fig. 2. Average values ( $\pm 1$  SE) for the six floral characters of *Rhizophora mangle* measured in 12 populations from Mexico. Results of one-way ANOVAs are indicated ( $F$  and  $P$ ). The numbers of each population correspond to the names given in Table 1.

ation around the regression line (see Sokal and Rohlf, 1981).

The observed lack of variation in flower morphology of *R. mangle* in relation to a latitudinal (clinal) gradient rules out the possibility that this variation arises as a re-

sponse to continuous variation of environmental factors such as temperature. There are at least two other alternative explanations for this pattern of variation: (1) populations of *R. mangle* have become differentiated as a result of a heterogeneous (and nonclinal) regimen of selection, which has led each population to its local optima;

TABLE 3. Pearson correlation coefficients ( $r$ ) among six floral characteristics measured in 12 populations of *Rhizophora mangle* from Mexico. All correlations were significant with  $P < 0.0001$  (Student's  $t$  test).

Variable	Corolla diameter	Calyx diameter	Petal width	Sepal width	Style length	Ovary width
Corolla diameter	1.0	0.71	0.62	0.60	0.54	0.39
Calyx diameter		1.0	0.53	0.49	0.35	0.18
Petal width			1.0	0.50	0.34	0.33
Sepal width				1.0	0.34	0.33
Style length					1.0	0.50
Ovary width						1.0

TABLE 4. Factor loadings of the six floral morphological attributes measured in *Rhizophora mangle* on the two first principal factors derived from factor analysis (values were multiplied  $\times 100$  for comparative purposes and rounded to the nearest digit).

Variable	Factor 1	Factor 2
Corolla diameter	86	36
Calyx diameter	80	10
Petal width	66	30
Sepal width	63	32
Style length	14	75
Ovary width	35	60
Percentage of total variance	88.9%	11.1%

TABLE 5. Variance partitioning (nested ANOVA) to evaluate geographic differentiation in the descriptors of flower morphology in populations of *Rhizophora mangle* from Mexico. Variance partition on the scores from factor 1 (A) and factor 2 (B) that were derived from principal factor analysis of six floral characters. For details see Materials and Methods.

Source of variation	Variance component (%)	F	P
<b>A) Factor 1</b>			
Coast	28.18	11.40	0.0081
Locality (Coast)	17.46	12.30	0.0001
Trees (Locality, Coast)	18.33	4.75	0.0001
Flowers (Locality, Coast, Tree)	36.03		
Total	100		
<b>B) Factor 2</b>			
Coast	25.63	5.20	0.0487
Locality (Coast)	28.73	30.15	0.0001
Trees (Locality, Coast)	10.94	3.33	0.0001
Flowers (Locality, Coast, Tree)	34.70		
Total	100		

and/or (2) differentiation is a consequence of genetic drift produced by the lack of gene flow among populations, and by founder events. It could be expected for geographically adjacent populations to have similar environmental conditions and, possibly, similar abiotic selective pressures (Núñez-Farfán et al., 1996a; see also Mayr, 1963; Endler, 1977). Such a selective hypothesis would predict that closer populations should tend to share similar morphology. Thus, we would expect a negative relationship between flower similarity among populations and the distance separating them. In contrast, the genetic drift hypothesis does not predict any relationship. In order to evaluate the preceding hypotheses we performed a cluster analysis (UPGMA), which groups the populations in terms of their flower similarity. This analysis (Fig. 3) does not support the selective (nonclinal) hypothesis: although populations from each coast tend to be clumped, a Pacific population, Coyuca, is clustered within the Atlantic coast group. Moreover, two very clustered populations within the latter group (Sontecomapan and Celestún) are very separated geographically. Additionally, the northernmost population from the Atlantic coast (Tamiagua) and the southernmost population from the Pacific coast (Chantuto) showed the highest dissimilarity. Thus, the morphological similarities among populations did not show any relationship with the geographic distance that separates them (Fig. 3).

DISCUSSION

In this study, we found that Mexican populations of *R. mangle* have significant levels of phenotypic differentiation as indicated by their flower morphology. Differentiation was evident from both univariate comparisons of floral attributes among populations and multivariate comparisons based on the scores derived from principal factor analysis. The total variation in the flower morphology of *R. mangle* can be expressed in terms of two principal factors: one representing an axis of variation in the size of perianth and another one highly influenced by the size of the gynoecium. Additionally, our results indicate that

TABLE 6. Regression analyses with replicates (ANOVAs) of floral morphology (scores from principal factor analysis) of *Rhizophora mangle* on the populations' latitude. Separate analyses for populations from the Pacific coast (A), and Atlantic coast (B) from Mexico are presented.

Source of variation	df	Sum of squares	Mean squares	F	P
<b>A) Pacific coast</b>					
Factor 1					
Locality	5	119.80	23.96	50.64	0.0001
Latitude	1	33.05	33.05	1.52	N.S.
Deviations from regression	4	86.75	21.68	45.87	0.0001
Error	609	287.89	0.47		
Total	614	407.68			
Factor 2					
Locality	5	117.67	23.53	90.34	0.0001
Latitude	1	8.30	8.30	0.30	N.S.
Deviations from regression	4	109.36	27.37	105.01	0.0001
Error	609	158.64	0.26		
Total	614	276.31			
<b>B) Atlantic coast</b>					
Factor 1					
Locality	4	74.35	18.59	31.02	0.0001
Latitude	1	43.97	43.97	4.34	N.S.
Deviations from regression	3	30.38	10.13	16.90	0.0001
Error	632	378.75	0.60		
Total	636	453.11			
Factor 2					
Locality	4	115.37	28.84	66.74	0.0001
Latitude	1	67.40	6.74	0.18	N.S.
Deviations from regression	3	108.63	36.21	83.80	0.0001
Error	632	273.11	0.43		
Total	636	388.48			

although floral traits of *R. mangle* varied allometrically, each population contains only a fraction of the total variation of flower morphology observed over all samples.

When the variation in flower morphology was partitioned between coasts, among populations, and among

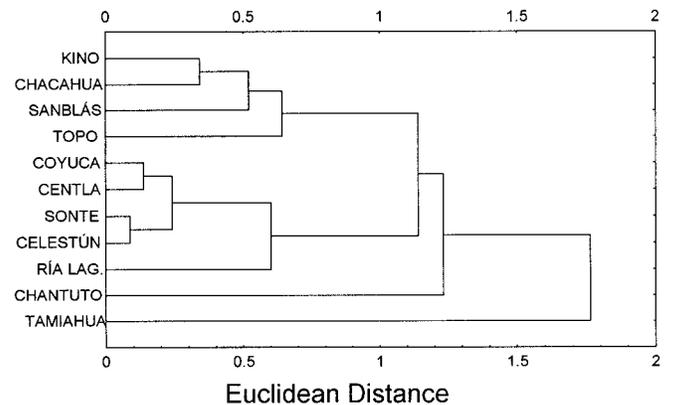


Fig. 3. Phenogram (UPGMA) of 11 populations of *Rhizophora mangle* from Mexico based on Euclidean distances of floral morphology (population from Novillero, Nayarit was excluded since data for ovary width were not available).

individual plants, all levels showed statistically significant differences. We consider that differentiation in flower morphology has a strong historic component, since the difference among the Pacific and Atlantic coasts accounted for 30% of the variation in size (factor 1). In addition, there was an almost twofold difference in the amount of explained variance by this level in comparison with the other two levels (populations within coasts or trees within populations). It is possible that the major differentiation occurred after the connection between the two oceans closed. Geological evidence shows that the uplift of the Panamanian Isthmus occurred ~3.5 million years ago (Tomlinson, 1994; Collins, Budd, and Coates, 1996), isolating animal and plant populations and favoring independent evolution (Mayr, 1963; Ridley, 1993; Collins, Budd, and Coates, 1996). After the closure of the interoceanic channel, the process of colonization and extinction of local populations on each coast has been dynamic and complex. For example, it has been suggested that as a consequence of a reduction of 4°–5°C in the mean temperature during the Pleistocene (12 000–20 000 yr ago), the northern limit of distribution of mangroves was contracted from 29° N to 21° N on the Pacific coast and from 23° N to 19° N on the Atlantic ocean (Sarukhán, 1977; Rzedowski, 1978; Toledo, 1982). Hence, most of the contemporary northerly distribution of *R. mangle* in Mexico is the result of recent recolonization from southern populations that presumably were less affected by the Pleistocene temperature reduction. Thus, the amount of total variation in the size of perianth accounted for by the differences among populations within coasts (almost 18%, factor 1) may be considered as the result of recent evolution in local populations, driven either by natural selection or by genetic drift. In addition, differences in the flower morphology among individuals within populations (18% of the total variation) may be the expression of genetic variation and/or phenotypic plasticity. However, this aspect needs further study.

In contrast, although variation in factor 2 (mainly gynoecium size) had also a geographic component, which was again accounted for by the differences between the coasts (~25%), populations within coasts explained 29% of the variance in flower morphology. As a consequence of the closure of the interoceanic channel, the differences between coasts are likely to have preceded the origin of differentiation among populations within coasts. Therefore, the above result suggests that although a significant proportion of the variance accounted for by factor 2 was originated at least 3.5 million years ago (the differences between coasts), a comparable amount of variation in flower morphology has evolved since the closure of the interoceanic channel (populations within coasts).

Nested analysis of variance also indicated that 18 and 11% (factors 1 and 2, respectively) of the variance in flower morphology were due to significant variation among plants within populations. The presence of significant differences in flower morphology among individuals within a population, if genetically based, may allow further changes through natural selection (Fisher, 1958; Armbruster, 1996).

The high levels of population differentiation in the floral attributes of *R. mangle* observed in this study may be a consequence of two processes. On the one hand, natural

selection for a local optimum can create differentiation among populations (Wright, 1932). On the other, genetic drift may generate random differentiation independent of local conditions. Although it has been shown that natural selection acting along a latitudinal gradient may result in a cline formation in floral morphology (Endler, 1977; Galen, 1989; Steiner and Whitehead, 1990), our results indicate that floral morphology does not vary in a clinal (latitudinal) way. Thus, it seems that natural selection is not responsible for the observed pattern of differentiation among populations of *R. mangle* or, at least, that selective pressures do not act in accordance with a latitudinal gradient. This result contrasts with the findings of Duke (1990) and Rico-Gray and Palacios-Ríos (1996), who found a clinal trend in the phenology of *Avicennia marina* and in the leaf size of *R. mangle*, respectively.

As stated above, the possibility remains that population differentiation is the result of the action of natural selection if the optimum flower morphology varies among populations. Because similar adaptations are expected to evolve as a response to similar selective pressures, and because closer populations are more likely to share similar environments (and probably similar selective pressures), we would expect to find similar flower morphologies between closer populations. This assumption is also maintained by the observation that gene flow among populations should be inversely related to the distance separating them (Slatkin, 1993). Cluster analysis failed to detect similarities in floral morphology among geographically related populations. Hence, our results do not support the selective (nonclinal) hypothesis of population differentiation. Population differentiation in flower morphology is expected when the pollinator guild of animal-pollinated species varies among populations (Galen, 1989; Steiner and Whitehead, 1990). However, for wind-pollinated species like *R. mangle*, the animal component of the geographic variance is absent, and thus a prime selective factor promoting differentiation is absent in this kind of species.

Overall, our data support the hypothesis that population differentiation in the floral characters of *R. mangle* may be the result of genetic drift. Our results also suggest an ancient component of differentiation due to the uplift of the Panamanian Isthmus. This closure was the first phenomenon isolating the populations from both coasts of Mexico, and was followed by repeated events of extinction and recolonization as a result of temperature changes during the Pleistocene. Although the propagules of *R. mangle* possess the capacity for long-distance dispersal, both local extinction and subsequent colonization of new populations by a few individuals (the founder effect) may have been a common event (Primack and Tomlinson, 1980; Tomlinson, 1994). This, in addition to a potentially high regime of selfing in red mangrove, as has been found in other localities (Lowenfeld and Klekowski, 1992; Tomlinson, 1994), may affect genetic diversity and promote population differentiation due to genetic drift.

Phenotypic diversity in *R. mangle* is not contained within a single local population, but it is apportioned in several populations due to differentiation among them. This is also what we have found in the case of genetic diversity (Núñez-Farfán et al., 1996b). In this sense, each

local population may be regarded as unique and the loss of any of them would result in loss of genetic and morphological diversity. Some Mexican mangrove communities are currently experiencing deforestation rates as high as 19% per year (Núñez-Farfán et al., 1996a). This highlights the major threat these unique local populations are undergoing presently. The results described in this report might merit consideration in future conservation and management plans of mangrove communities.

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