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Genecological Differentiation in Provenances of *Brosimum alicastrum* – a Tree of Moist Tropical Forests

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ABSTRACT

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A genecological study of *Brosimum alicastrum* Sw., a dominant tree of the moist tropical forest of Mexico and Central America, was conducted within a limited area in its natural range in nine provenances of Veracruz, Mexico. Seeds were randomly collected from five to eleven individuals from each provenance along a latitudinal gradient. The variation between provenances was analyzed based on seed weight and dry weight of roots, stems, and leaves.

The results obtained by the use of a principal component analysis and linear correlation indicate the existence of ecoclinal variation in seed size (weight and diameter) and in energy allocation variation to the roots of seedlings, both of which are well correlated with several climatic factors. It was also demonstrated that seed size strongly influences initial seedling size, and the relative size of seedling roots which increased in response to habitat dryness and the geographic origin.

The results suggest that *Brosimum alicastrum* employs an adaptative strategy in response to water deficits which occur during the prolonged dry seasons in the initial phase of seedling growth and establishment.

INTRODUCTION

From an ecological standpoint the seed phase has long been recognized as a very crucial stage in the life-history of plants. During this phase strong pressures operates on those seed traits that most directly affect its survival (Harper, 1977; Hickmann, 1979). One of the results is a wide seed morphology which shows many intricate adaptations for dispersal, germination and establishment (Harper et al., 1970). With few exceptions the knowledge on seed size strategies in tropical trees has scarcely been recorded (Janzen, 1977; Howe and Richter, 1982; Foster and Janson, 1985; Foster, 1986).

Brosimum alicastrum, commonly known as 'ramón', 'capomo', 'ojite', 'ojoche', or 'ox', is a major component of Mexico's moist forest and has been studied with different approaches (Puleston, 1968, 1972; Pardo-Tejeda and Sánchez,

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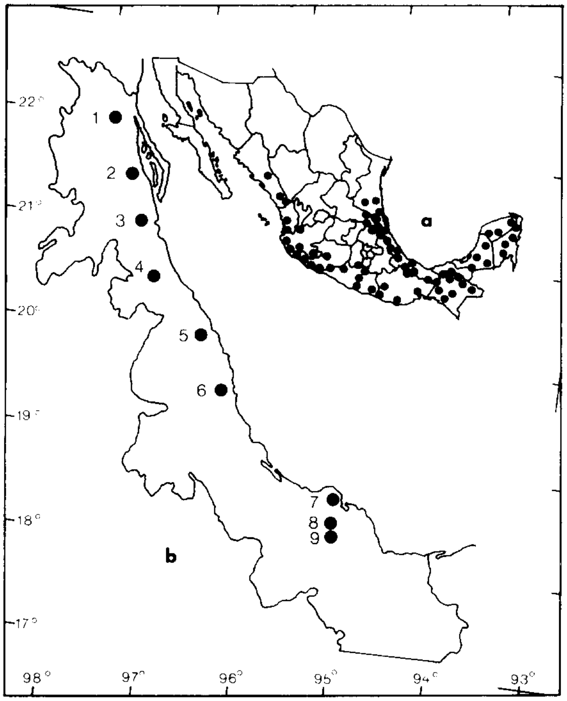

Fig. 1. (a) Geographical distribution of *Brosimum alicastrum* in Mexico (from Pennington and Sarukhán, 1968; Rzedowski, 1978) and (b) location of the nine provenances studied in the state of Veracruz.

1979; Lambert and Arnason, 1982; Peters, 1982, 1983, 1986). *Brosimum alicastrum* is a member of the Moraceae family and is widely distributed in the warm-humid and subhumid regions of Mexico and Central America. The distribution of this species in Mexico (Fig. 1a) is restricted to the coastal plains of the Gulf of Mexico and the Pacific Ocean, along the east and west slopes of the Sierra Madre Oriental and Occidental, within an altitudinal range from 20 to 800 m a.s.l. Its upper latitudinal limit fluctuates between 22°30′ on the Gulf slopes and 24°30′ on the Pacific slopes.

Brosimum alicastrum is a dominant tree in both tropical evergreen forest and tropical deciduous forest (Pennington and Sarukhán, 1968), and can also be found in protected canyons and valleys within the deciduous seasonal forest (Rzedowski, 1978). Dense forests of the tree characteristically occur on steep, rocky calcareous soils (Pennington and Sarukhán, 1969; Puig, 1976), yet the species is not restricted to this type of geological substrate (Rzedowski and McVaugh, 1966). *Brosimum alicastrum* frequently reaches a height of 30 m, with a straight trunk which commonly is over 1 m in diameter. The tree has well-developed buttresses, sympodal branching and a dense pyramidal crown.

Flowering of *B. alicastrum* at Veracruz is in January–February, occasionally to March. This species is very plastic in its sex expression; some of the literature indicates that the species is dioecious (Berg, 1972), but other authors have classified it as monoecious (Standley and Steyermark, 1946; Pennington and Sarukhán, 1968; Puleston, 1968; Croat, 1978) or both (Woodson and Schery, 1960). Observations on reproductive phenology carried out by Peters (1986) in Veracruz indicate that all of these possibilities can occur. *Brosimum alicatrum* is an anemophilous species with obligate outcrossing when the sexes are separate in a given population (Peters, 1986); however, when monoecy is present the outcrossing is less strict. Records of phenological data suggest that fruit production in *B. alicastrum* is initiated by April–May, with a peak fruitfall occurring during the rainy season (Pennington and Sarukhán, 1968; Peters, 1986; National Herbarium of Mexico records).

As a consequence of the wide ecological tolerance that *B. alicastrum* possesses, it was felt that the potential for variation among the morphological, physiological, and biochemical characteristics of the species was extremely high. The objectives of this study, therefore, were to evaluate the magnitude and pattern of intraspecific variation in *B. alicastrum* along a latitudinal gradient, and to identify the principal climatic factors which are correlated with the pattern of variation. This paper presents effects of variation in seed mass on seedling characteristics of *B. alicastrum* and analyzes continuous variation in the mean seed size of nine ecologically different provenances from Veracruz, Mexico.

MATERIALS AND METHODS

Provenances' localization

Based on herbarium collections data of *B. alicastrum*, nine provenances were selected following a latitudinal gradient in Veracruz (Fig. 1b). The criteria of this selection were to assure encountering individual trees in fruitfall phase and to facilitate the fruit collection by hand.

Provenances' climate

From the ecological point of view, both the amount of rainfall during the dry season (with <60 mm month^{-1}) and wide temperature fluctuation between coldest and warmest months are the most significant seasonal parameters in Veracruz (Gómez-Pompa, 1973). Along the latitudinal gradient studied, the total annual rainfall is far less in the north, and monthly rainfall distribution tends to be more uniform in the south. In the north, there is a dry season of 7 months compared to 3–5 months in the south (Fig. 2). The amount of rain during the dry season varies from 175 mm in the north to 120 mm in the south. The relative winter rainfall is the amount of rain that falls during Janu-

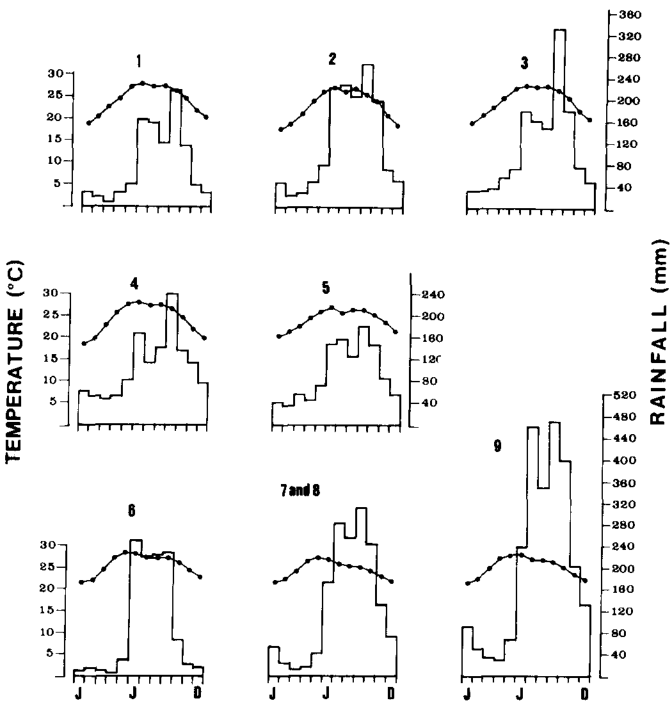

Fig. 2. Annual distribution of rainfall (——) and mean temperature (●—●) for each of nine provenances studied in Veracruz, Mexico. Numbers of each diagram correspond to each provenance (see Table 2 for definition of provenances).

ary–March in relation to total annual rainfall, multiplied by 100 (García, 1970), and represents a measure of the intensity of the dry season. Conversely, fluctuation in mean annual temperature trends to be wider in the north than in the south, being 7–14°C and 5–7°C, respectively. The maximum temperatures occur before the rainy season, which runs from May to October (Fig.2).

Fruit harvest

Brosimum alicastrum fruits were collected within a range between latitudes 18–22°N and longitudes 95–98°W (Fig. 1b). Fruits were collected directly below the crowns of individual trees. The numbers of trees sampled at each provenance varied between 5–11, depending on the density and distribution of the individuals in each. Fruits of a total of 72 trees were collected. After removal of the fresh pericarp, the mean seed size per individual tree was determined based on the diameter and wet weight of 90 seeds. To assess germination, under uniform laboratory conditions, seeds were placed in 20-cm plastic dishes on sterilized cotton, and maintained at 28°C, continuously moistened by periodic additions of distilled water. The date of emergence of the radicle and

TABLE 1

Identification of 14 variables included in statistical analysis of *Brosimum alicastrum* provenances study

Variable	Definition
X_1	Latitude (°N)
X_2	Longitude (°W)
X_3	Altitude (m.a.s.l.)
X_4	Total annual rainfall (mm)
X_5	Mean annual temperature (°C)
X_6	Relative winter rainfall (%)
X_7	Fluctuation in mean annual temperature (°C)
X_8	Seed weight (g)
X_9	Seed diameter (cm)
X_{10}	Root biomass (g dry weight)
X_{11}	Stem biomass (g dry weight)
X_{12}	Total seedling biomass (g)
X_{13}	Percent root weight (g)
X_{14}	Percent stem weight (g)

hypocotyl of each seed was recorded. Germination rates and percent germination were calculated using 15 seeds per individual tree. After germination, seeds were immediately transplanted in 12.7-cm plastic pots containing vermiculite to promote homogeneous water retention and aeration, as well as to facilitate the extraction of seedling roots as the time of harvesting. The seedlings were watered at 4-day intervals.

Data collection

The height, length and width of leaves, and length of 'drip tips' were measured on each seedling. Twenty-eight days after transplanting, concurrent with the first leaf of all seedlings fully expanded, all seedings were harvested. Each plant was separated into roots, stems, and leaves and dried to constant weight at 95°C.

The variables analyzed can be arranged in two groups: The first (Table 1, X_1–X_7) represents the physical characteristics of each seed provenance, geographic location, and climatic variables, taken from each provenance as identified in Table 2. The second group represents the characteristics of the progeny, including morphological variables of the seed and seedling (Table 1, X_8–X_{14}).

Statistical procedures

The relationships between progeny characteristics and their respective physical environmental factors were assessed by means of linear correlation

TABLE 2

Geographic location and climatic factors of nine *Brosimum alicastrum* provenances tested (see Table 1 for definition of variables)

Provenance	X_1	X_2	X_3	X_4	X_5	X_6	X_7
1 Topila	22°07′	97°58′	25	945.3	24.3	5.45	9.4
2 Mamey	21°32′	97°38′	10	1565.8	23.6	6.09	9.4
3 Tuxpan	21°05′	97°35′	10	1347.8	24.9	7.80	8.5
4 Los Alpes	20°25′	97°15′	110	1283.9	24.3	12.78	9.4
5 La Florida	19°56′	96°37′	250	1158.2	24.3	11.84	6.5
6 El Viejon	19°42′	96°24′	20	1093.3	25.6	3.21	6.7
7 P. Escondida	18°36′	96°24′	60	2543.2	25.4	7.21	6.4
8 Sta. Rosa	18°17′	95°08′	540	1627.8	24.7	5.79	5.8
9 Los Mangos	18°15′	95°08′	320	1627.8	24.7	5.79	5.8

and principal component analysis, using the factor procedure of SAS (1982). Considering that only a part of the total range of *B. alicastrum* was included, and that provenances were sampled along a latitudinal gradient, a high and significant correlation coefficient is regarded as an indication of clinal variation. The factor procedure retains a number of components on the basis of the eigenvalue-greater-than-1 rule. Based on the recommendations of Morgen-

TABLE 3

Principal component analysis between selected characteristics of *Brosimum alicastrum*, geographic location and climatic factors (see Table 1 for definition of variables)

Axis	1	2	3
Eigenvalue	8.31	2.15	1.85
Total variance (%)	59.39	74.78	88.01
Variables	Loadings		
X_1	0.884*	−0.218	−0.373
X_2	0.911*	−0.153	−0.327
X_3	−0.465	0.220	0.745*
X_4	−0.650	0.438	−0.234
X_5	−0.731	−0.216	−0.252
X_6	0.427	0.820*	0.193
X_7	0.792	0.060	−0.550*
X_8	0.970*	−0.064	0.054
X_9	0.978*	−0.032	0.019
X_{10}	0.803	−0.315	0.474*
X_{11}	0.932*	0.065	0.332
X_{12}	0.855*	−0.090	0.454
X_{13}	−0.199	−0.879*	0.127
X_{14}	0.731	0.482	0.182

TABLE 4

Variation in mean seed size of *Brosimum alicastrum* provenances tested

Provenance	Latitude (°N)	Seed size		
		Diameter (cm)	Fresh weight (g)	Dry weight (g)
1 Topila	22°07′	1.956	3.432	0.905
2 Mamey	21°32′	1.909	3.285	0.857
3 Tuxpan	21°05′	1.811	2.751	0.802
4 Los Alpes	20°25′	1.836	2.917	0.795
5 La Florida	19°56′	1.945	3.500	0.937
6 El Viejón	19°42′	1.702	2.435	0.897
7 P. Escondida	18°36′	1.636	2.086	0.730
8 Sta. Rosa	18°17′	1.617	1.883	0.667
9 Los Mangos	18°15′	1.620	2.089	0.677

stern (1969), components were represented as axes and two to four highest loadings of each axis, indicated by the asterisk, were used in interpretations of results.

RESULTS

The results of principal component analysis (Table 3) show that three eigenvalues together account for 88.01% of the standardized variance. Thus the first three principal components provide an adequate summary of the data. The first component has some large positive loadings with an especially high correlation with both seed diameter ($r=0.978$) and seed weight ($r=0.970$),

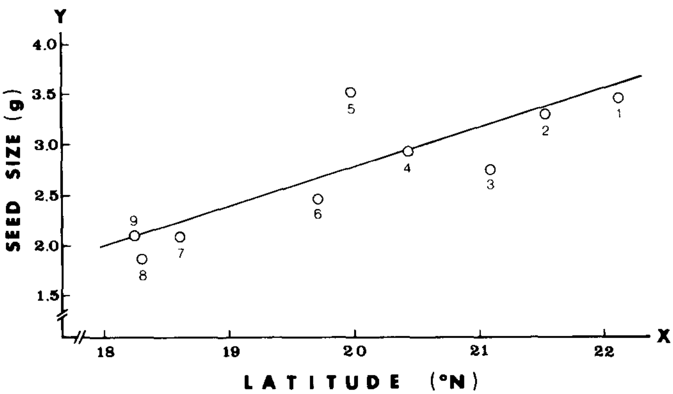

Fig. 3. Clinal variation of mean seed size of *Brosimum alicastrum* along the latitudinal gradient in Veracruz, Mexico ($Y=-4.62+0.37X$; $r=0.84$, $P<0.005$).

TABLE 5

Linear correlation coefficients of *Brosimum alicastrum* based upon pooled data from 72 single-tree progenies from nine provenances along latitudinal gradient at Veracruz, Mexico

	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}	X_{11}	X_{12}	X_{13}	X_{14}
X_1	1.00													
X_2	0.98*	1.00												
X_3	−0.69$^+$	−0.66$^+$	1.00											
X_4	−0.58	−0.66$^+$	0.12	1.00										
X_5	−0.53	−0.53	−0.03	0.30	1.00									
X_6	0.09	0.20	0.06	−0.06	−0.37	1.00								
X_7	0.91*	0.91*	−0.66$^+$	−0.39	−0.57	0.23	1.00							
X_8	0.84′	0.85′	−0.48	−0.60	−0.66$^+$	0.39	0.69$^+$	1.00						
X_9	0.87′	0.88′	−0.47	−0.61	−0.68$^+$	0.40	0.74$^+$	0.99*	1.00					
X_{10}	0.59	0.61	−0.16	−0.70$^+$	−0.61	0.18	0.32	0.85′	0.81°	1.00				
X_{11}	0.67$^+$	0.72$^+$	−0.22	−0.62	−0.76$^+$	0.52	0.53	0.93*	0.92*	0.91*	1.00			
X_{12}	0.61	0.64	−0.15	−0.64	−0.66$^+$	0.39	0.38	0.88′	0.86′	0.97*	0.97*	1.00		
X_{13}	−0.07	−0.14	0.01	−0.27	0.19	−0.78$^+$	−0.25	−0.13	−0.19	0.16	−0.20	−0.10	1.00	
X_{14}	0.56	0.62	−0.32	−0.30	−0.69$^+$	0.69$^+$	0.76$^+$	0.63	0.64	0.31	0.64	0.42	−0.42	1.00

See Table 1 for definition of variables; superscripts indicate levels of significance: * = 0.001, ′ = 0.005, $^\circ$ = 0.01, $^+$ = 0.05.

so as with total seedling biomass ($r=0.932$) and geographic origin of provenances ($r=0.884$ and 0.912). The second and third components are both a contrast of relative root size ($r=-0.879$) against the relative winter rainfall ($r=0.820$), and altitude ($r=0.745$) against the fluctuation in mean annual temperature ($r=0.550$), respectively.

In Table 4 is shown the variation in mean seed size (i.e. wet and dry weight and diameter) which tended to vary continuously along the latitudinal gradient, with the largest seeds being found at the northern limit of the natural range of distribution of *B. alicastrum* on the coastal plain of the Gulf of Mexico.

There are strong correlations between latitude and mean seed size (Fig. 3) as well as between seed size and total seedling biomass (Table 5). This gradation in variables implies a cline (Huxley, 1938; Gregor, 1944, 1946; Langlet, 1971). Clinal variation in mean seed size of *B. alicastrum* directly affects the total seedling biomass; that is, the longer the seed the heavier the seedling. Also, there is a negative correlation between relative winter rainfall and percent root weight (Table 5), indicating that the percent root weight tends to increase as relative winter rainfall decreases. There is also a cline in relation to physical factors along the latitudinal gradient. There is a negative correlation between altitude and fluctuation in mean annual temperature, as well as between the fluctuation in mean annual temperature and mean seed size, so as with latitude (Table 5). Furthermore, there is a negative correlation between relative winter rainfall and percent root weight (Table 5).

DISCUSSION

It is evident that the mean seed size of *B. alicastrum* varies with geographic origin and climatic factors. Within the latitudinal gradient, the fluctuations in mean annual temperature and length of the dry season at each provenance are larger and therefore more drastic in the northern provenances, becoming smaller at lower latitudes. Thus these climatic factors can act as ecological filters which select for different seed size; so variation in mean seed size of *B. alicastrum* illustrates a strategy for this species.

The larger seeds are located at the distributional limit on the Gulf of Mexico plateau. Seedlings developed from these seeds should have better possibilities of establishment under drought conditions, which are more common at higher latitudes. Having bigger seeds can reduce the effects of moisture stress, while high germination rates reduce the time during which the seedling can be susceptible both to predation (Vázquez-Yanes, 1976; Foster, 1986) and/or to fungal pathogens (Augspurger, 1983; Augspurger and Kelly, 1984). These findings suggest that seed size variation of *B. alicastrum* along this latitudinal gradient on Veracruz is environmental in origin.

Several studies (Smith and Fretwell, 1974; Smith, 1975; Werner, 1979; Schaal, 1984) have shown that the larger the seed, the more successful germination and the higher the probability of seedling survival. Baker (1972) also reported an increasing seed weight in respond to increasing risk of drought exposure after germination.

The dry-matter allocation pattern to the roots of *B. alicastrum* seedlings can also be viewed as an adaptive trait. Seedlings with high relative root size appear to be associated with an increasingly xeric habitat found in the northern provenances studied; that is, the relative root size increases as the length of the drought period increases. The risk to seedling survival and establishment under soil moisture deficit can be partly solved through the development of a more extensive root system.

CONCLUSIONS

From the evidence presented in this paper, *B. alicastrum* seed size varies ecoclinally throughout a large part of its natural range on Veracruz, with the mean seed size increasing in higher latitudes. This pattern of variation correlates consistently with several other climatic parameters, the fluctuation in mean annual temperature being the most important, according to principal components analysis.

Seed size was strongly correlated with the development of *B. alicastrum* seedlings. Seed size influences root, shoot and total seedling biomass. In addition, the developmental parameters of the seedling confirm the existence of an ecoclinal variation, as there are consistently good correlations with climatic parameters such as relative winter rainfall and relative root size (Table 5).

Finally, the results from this study suggest that the variation pattern shown in *B. alicastrum* in the state of Veracruz represents an adaptive strategy in response to latitudinal climatic fluctuations.

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