A DIRECTIONAL CLINE IN **MOURIRI GUIANENSIS** (MELASTOMATACEAE)

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Abstract

Morphological variation in **Mouriri guianensis** is described and analyzed throughout its range in Brazil and adjacent regions. Features that vary are ovary size, locule and ovule number, shape and smoothness of the leaf blade and petiole length. The largest ovaries with the most ovules occur in west central Amazonia; intermediate sizes and numbers are widespread but reach the coast only between Marajó and Ceará; and the smallest ovaries with the fewest locules and ovules are coastal or nearcoastal from Delta Amacuro in Venezuela to Marajó. Small ovaries also occur in coastal Alagoas and at Rio de Janeiro. Ovaries with the fewest locules and ovules are believed to be the most specialized, the result of evolution toward decreased waste of ovules, since the fruits of all members are few-seeded. Leaf characters correlate statistically with ovule numbers. Possible origen of the distribution pattern of the species is compared in terms of present rainfall patterns and in terms of Pleistocene climatic change with associated forest refuges. It is concluded that both phenomena were probably influential. High specialization appears to have accompanied isolation, for reasons that are unclear. Because the plants from Delta Amacuro to Marajó are the most specialized they may once have been more isolated than now.

INTRODUCTION

Mouriri guianensis is a small sometimes shrub-like tree of the neotropics. Its distribution lies across Brazil and extends to Venezuela on the north and to Rio de Janeiro on the south (Fig. 10). Certain characteristics of the plants are highly variable over this range; the variation is examined here to see to what extent it may correlate with the geographic distribution. An unusual feature of the present example is that the direction of specialization of the most important variable, the ovary, can be clearly identified. The overall pattern of distribution was briefly described previously (Morley, 1975, 1976); the present paper is a detailed report.

MATERIAL AND METHODS

The study was carried out with pressed specimens borrowed from many herbaria, to whose curators I am grateful. The most instructive characters are those of the unripened ovary, and therefore only flowering material was of value in most cases. It was necessary that specimens have a considerable excess of flowers for the dissections to be made without harm but fortunately only a few collections had to be omitted for this reason. In a few critical fruiting collections leaf measurements alone were recorded. The omission of most fruiting collections from Fig. 10 does not materially affect the distribution shown, partly because most collections of the species are of flowering plants, partly because by good fortune most of the fruiting collections are from localities where flowering material has also been taken or from places nearby. No important range extensions are omitted. Coverage of the collections I believe to be adequate for the purposes of this paper, but there are many gaps which will probably be filled in the future.

The relevant floral features are those of ovary size and shape (Fig. 3-9) and the inner components that affect those characters. The diameter of the dried

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ovary can be used as one parameter; however, outside measurements of the tapering and often distorted ovaries are not always reliable. The ovary size is a reflection of the number of ovules within, and to a lesser extent of the number and thickness of the partitions. Consequently the numbers of locules and ovules have been mapped as the major variables of the ovary.

Material permitting, three to five flowers were dissected for each of the 71 collections examined and occasionally more. Limitations of material precluded larger samples. In most cases the range of variation encountered in a given collection was not great with these small sample numbers, leading me to believe that the results are reasonably representative. The consistency of counts of different collections from the same locality and the consistency of the patterns shown in Fig. 10 support the opinion that the results are adequate for use.

The leaves also vary with geography. Blade shape is the most consistent variable that is readily measured, and the width of the basal angle is the most consistent character of the shape. As the angle becomes narrower, the leaves tend to become more elliptic and less ovate, but this does not always hold. The possibility that the leaves on a particular specimen do not represent a norm for that plant is a problem that cannot be avoided.

Leaf variation on the same specimen is often considerable. The leaf-bearing twigs grow in spurts or flushes, with resting periods between. The lowest leaves of each growth flush tend to have the widest included basal angles, the upper the narrowest (Figs. 1,, 2). The difference may be very slight. When there is but a single pair of leaves on a twig, its leaves are most often like those of the lowest leaves or sometimes the middle leaves of twigs with several pairs. The average angle is used here to express this leaf character. When the leaves are folded lengthwise no reliable angle can be obtained. When all are loose in a pocket an average angle can of course be obtained but there is no certainty that the lowest and uppermost forms are present. Averages range from 79° to 160°; the smallest and largest individual angles measured were 61° and 180°. The basal angle is shown in Fig. 10 as a continuous variable.

Petiole lenght is also variable and has been mapped. The length ranges from 1 to 5 mm, and the averages of the collections vary from 1.5 to 4 mm. In this instance a two-state presentation seemed all that could be justified; a bar on the diagram in Fig. 10 indicates a petiole average greater than 2.5 mm.

The prominence of the lateral nerves in dried leaves is also greater in some areas than others and is mapped, although sometimes highly variable and difficult to measure consistently, only a visual estimate being practical. The dried leaf surface was rated on a scale of 1–5, from veiny to smooth, using a standard veiny collection (Morley 1164) and a smooth surface as reference points. In this case also only a two-state presentation is given in Fig. 10. A bar on the diagram indicates a smoothness rating of greater than 3.

The shoots of these plants are of two types, leader shoots and dorsiventral ones, and leaves of the two are dissimilar. The relatively few leaders, which grow upward with great vigor, bear unusually short leaves which are often cordate at base, while the much more common dorsiventral shoots produce the typical leaves of the plant. Only the typical leaves are referred to in this paper.

RESULTS

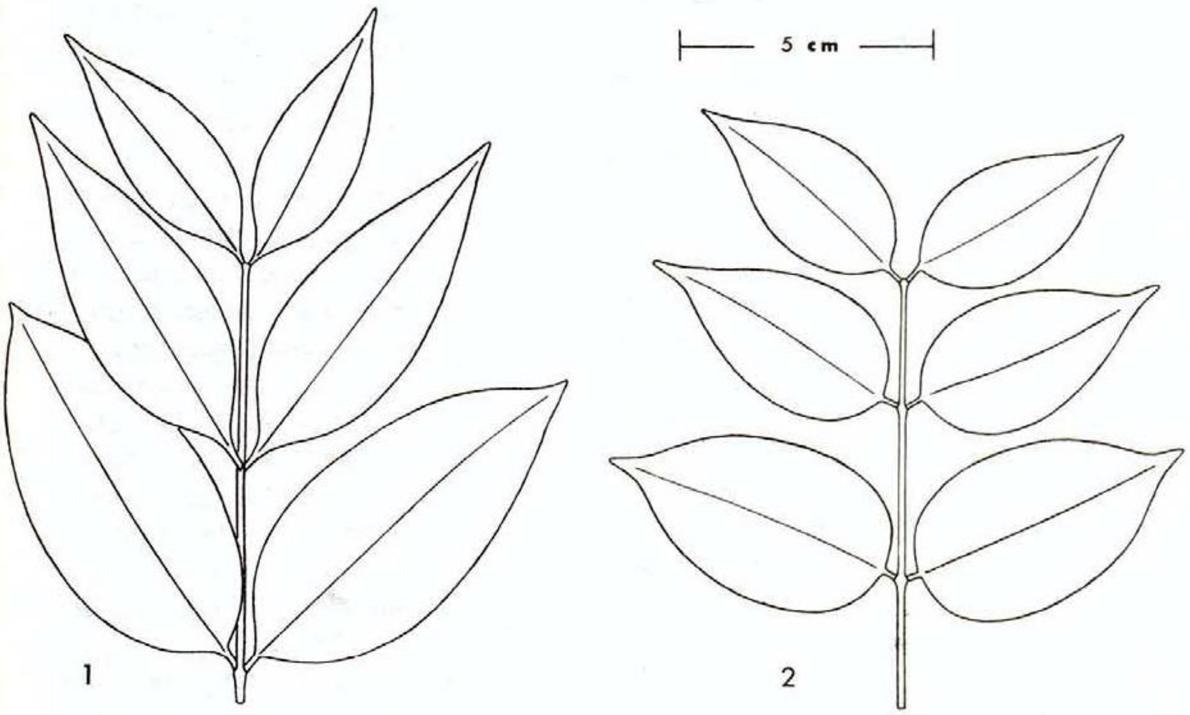
Examination of the distribution map (Fig. 10) shows the following points of significance:

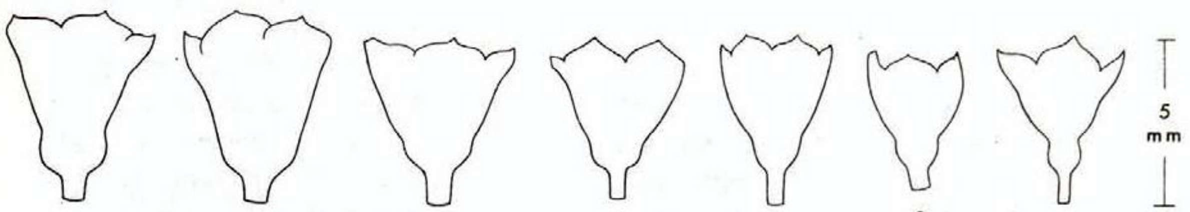
1. Locule number.

   A. This varies from 5 (rarely 6) to one. Plants with 5 and 4 locules are very widespread.
   B. The smallest locule numbers occur from coastal Delta Amacuro to the south side of Marajó. All those ovaries with 2.5 or fewer locules occur here, and none here have more than 3 except for the collection at the northeast tip of Marajó.
   C. The coastal and near-coastal collections in Alagoas and Rio de Janeiro have relatively low locule numbers. The 2.6 that occurs on the upper Rio Branco is exceptional, by far the smallest number in the interior.

2. Ovule number.

   A. This correlates with locule number, with some variation. Five





3 4 5 6 7 8 9

Figs. 1, 2. Leafy twigs illustrating variation in shape of leaf blade from plant to plant and from lower to upper leaves in a growth flush. Tracings. 1. Moore 437. 2. Broadway 275. Figs. 3–9. Inferior ovary and calyx of different flowers illustrating variation in size and shape of the ovary in dried flowers. Camera lucida. 3. Ule 5915. 4. Level 118. 5. Kubitzki 75–79. 6. Weddell 2494. 7. Froes 2008. 8. Oliveira 2082. 9. Soubirou s.n.

locules are usually associated with 15 or more ovules, never less than 11. The smallest ovule numbers occur only in ovaries with 1 or 2 locules.

B. The greatest number of ovules occurs in west central Amazonia. The largest number counted was 33, for the plant with an average of 29.3. The numbers decrease to the north, east, and south from here. An area of moderately high numbers occurs along the Amazon in Pará

C. High-intermediate ovule numbers of about 20 occur in western Venezuela, southwest Amazonia, two places northwest of Brasilia, and at one site in inner Maranhão. None are on or near the coast.

D. Low-intermediate numbers of about 12-15 are widespread, and extend to the coast between Marajó and Ceará. This is the only part of the coast occupied by plants of intermediate numbers.

E. A group of six similar collections is found in west-central Mato Grosso. The similarity in locule and ovule numbers is emphasized by generally similar leaf characters.

F. The low ovule numbers of 7-9 are all coastal or near-coastal, occurring between Delta Amacuro and Marajó. In this respect they coincide with the low locule numbers mentioned above and with the small sizes mentioned below. No ovule numbers here are greater than 11.3 except for the collection at the northeast tip of Marajó. The 10's and 11's are all from the Paramaribo area. The smallest individual number counted was 6, for the Surinam collection with an average of 7.3.

G. The only other occurrences of 10's and 11's below 11.5 are also coastal or nearly so, one in Alagoas and two at Rio de Janeiro. The exceptional collection from the upper Rio Branco with 11.6 ovules (referred to in point 1D) is the inland collection closest in number to any of these: five of its flowers yielded ovule counts from 10 to 13.

3. Ovary diameter: the fewer the ovules and locules, the smaller the ovary. Size differences are slight but rather consistent. Thus the largest ovaries are found in western Amazonia and the smallest ones on or near the coast from Georgetown to Amapá. All ovaries less than 1.2 mm in diameter occur in the latter area, none are 1.3 mm or greater, and only two measured 1.2 and 1.25 mm. The coastal collection in Delta Amacuro has a small locule and ovule number but measured 1.3 mm as did the collection on the south side of Marajó. No inland collections had dry ovaries measuring less than 1.2 mm.

4. Leaf characters: these are highly variable, but some correlations with distribution do exist. Nearly all the coastal plants, from Delta Amacuro to Rio de Janeiro, have broad to moderately broad basal angles, short petioles and veiny leaves, while plants of the interior tend to have the opposite conditions. An abstract factor to express these conditions can be made for each collection by multiplying the average petiole length by the inverse of the blade angle by the leaf surface rating by 100. The coastal plants have relatively low factors and the inland ones rela-

tively high factors; when the two are compared as groups the difference is highly significant (F test, P = < .001). The same result is reached using only the blade angles. The coastal plants from Delta Amacuro to Amapá have slightly lower factors than those from Marajó to Ceará but this difference is not statistically significant. When the leaf factors are tested for correlation with ovule numbers the result is also highly significant (P = < .001), the high factors correlating with high ovule numbers. Throughout most of the interior the leaf characters are quite variable, but two centers of long petioles, low basal angles, and smooth surfaces can be seen in Fig. 10, one along the lower Amazon and the other in Mato Grosso.

5. Very few collections have been made in the central Amazon basin except along the Amazon itself. Whether this presents a true picture or results from incomplete collecting is unknown.

In order to determine if the species might be composed of two or more taxonomic groups, frequency histograms were made of the single most reliable character ovule number (Fig. 11). One diagram (A) uses only the average numbers plotted in Fig. 10, while the other (B) uses all individual counts. In A one sees a grouping of flowers with 7–9 ovules which is so distinct that one might think it indicates a taxonomic unit (see point 2F above). However, in B it is seen that the gap between 9 and 11 ovules is bridged by many individual flower from plants with average numbers other than 10. This suggests at least that the gap is not as sharp as the averages make it appear, There is another factor that partly explains the groupings seen in A. The ovules tend to be the same number on each placenta; usually there is a single placenta in a locule. The total for the ovary will be the product of locule number times the average number of ovules per locule (Table I). The total numbers of 20 and 20, 16 and 15, 12 and 12, and 9 and 8 are closer to each other than to adjoining numbers and would create peaks in a histogram much like those actually found in Figs. 11A and 11B. The 20–20 peak shows only in 11B. In 11A, only the peak at 14 is out of place. Consequently, although the few-ovuled coastal plants have developed more or less recognizable features, they do not appear sufficiently distinct as groups to warrant taxonomic status.

From a purely morphological point of view it is noteworthy that the placentation in certain collections with high ovule numbers (Appun 1711, Krukoff 6613, Level 118, Prance & Silva 59321, Ule 5915) resembles in part that of several species of **Mouriri** in which the ovules are borne on all sides of each placenta. In the collections named the ovules are often arranged in a full circle at the apex of the placenta, but spread apart to pass on each side of it part way toward the base.

DISCUSSION

The overall distribution pattern is one in which flowers with the largest ovaries and the most ovules occur in west central Amazonia while the smallest ovaries with the fewest locules and ovules are coastal or near-coastal from Delta Amacuro to the south side of Marajó, with two other localities of small ovaries in coastal Alagoas and at Rio de Janeiro.

Considering what is known of the phylogeny of the genus (Morley, 1953, 1976) there can be no doubt that the 5–loculed condition is primitive for the species and that the lower numbers of locules and ovules represent progressive reduction. The more primitive members of the subgenus **Mouriri**, to which **M.**

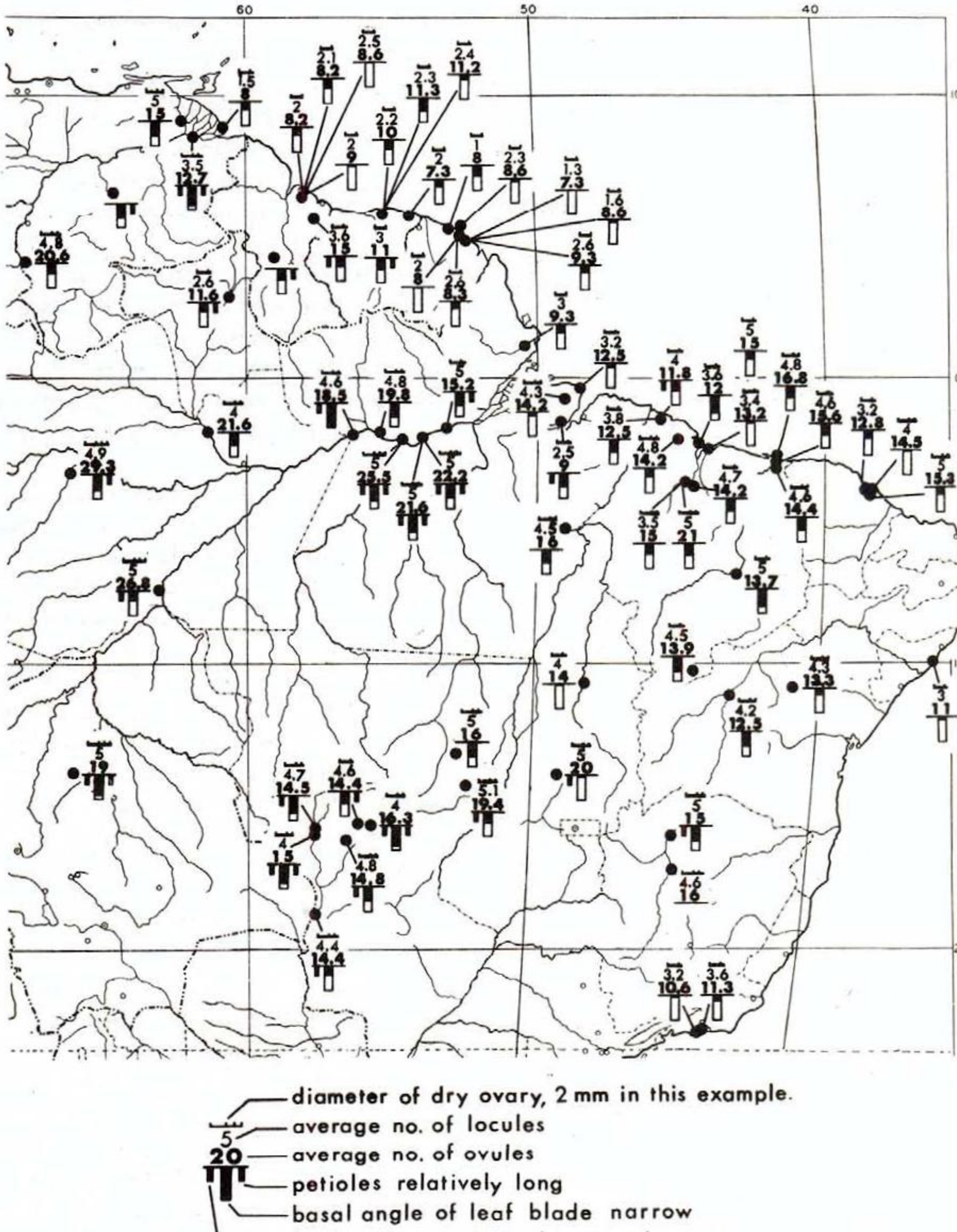


Fig. 10. Distribution of **M. guianensis** showing geographic variation of selected flower and leaf characters. See legend. A bar is shown when the petioles are more than 2.5 mm long, and when the leaf surface is smoother than the median on a smoothness scale. Included angles of leaf bases range from 79° (narrow) to 160° (wide). See Materials and methods.

guianensis belongs, have 15–30 ovules per ovary and it therefore appears reasonable to suppose these numbers to be primitive for **M. guianensis.** Therefore according to the present distribution the most primitive members of the species are those of western Amazonia and the most specialized ones are the coastal and near-coastal ones with small ovaries and few locules and ovules. The species appears to have originated in the west and migrated north, east and south from there.

An adaptive value can be rationalized for the more specialized forms. All known fruits of the species are small and contain one or two or at most three seeds. Small few-seeded fruits are found in the most widespread species of the tribe Memecyleae and appear to be advantageous for bird dispersal (Morley, 1975 p. 19). Since so few seeds are produced, many ovules must abort when a large number is present before fertilization. One might therefore expect a reduction series in ovule number to occur in the interests of greater efficiency.

However, it is not clear why this reduction should have been accelerated more in some areas than in others. One can only speculate that unknown competitive forces were greater in the areas of reduction. Because those areas are all relatively small at present and may have been smaller in the past it is possible that de-

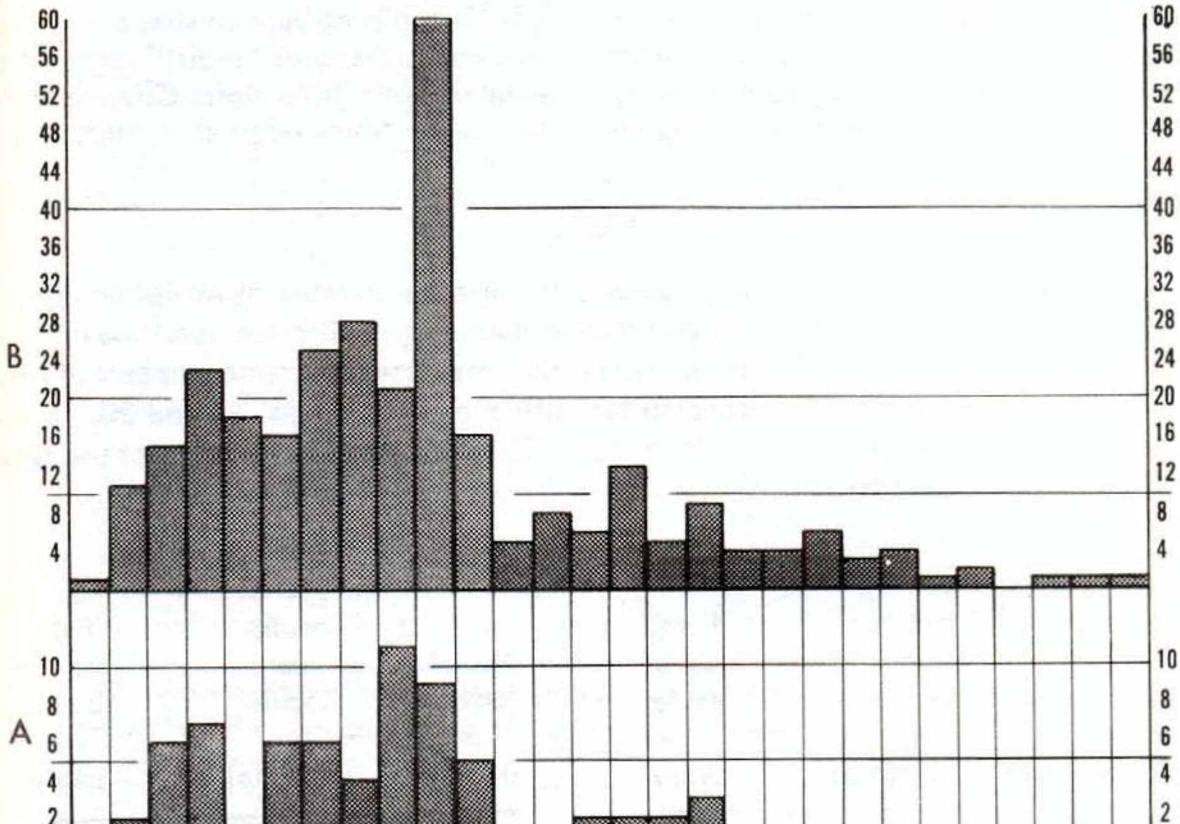


Fig. 11. Frequency histograms of ovule numbers in **M. guianensis.** A. Frequencies of the averages from Fig. 10 as read to the nearest whole number, e. g. a number from 13.6 to 14.5 is counted as 14. B. Frequencies of all individual counts mede. The same number of counts could not always be made for each collection; see Materials and methods, and Results.

creased population size with its modified evolutionary forces may have been one factor in promoting the reduction. Differing dispersal agents and other altered environmental conditions might also have played a part.

The association of leaf characters with ovule numbers (point 4 above) suggests that leaves with long petioles, narrow basal angles, and smooth surfaces may be primitive for the species.

In seeking an explanation of the distribution pattern of the species, we should first consider whether it might have developed under present environmental conditions. If so, the distribution of the variables in the species should match present environmental zones reasonably well. Rainfall is the factor most easily compared, although even for it the information available is incomplete (Fig. 12). If one excludes the plants of Alagoas and Rio de Janeiro, there is some correlation of distribution with precipitation to the extent that the largest ovaries and the smallest ones both occur in areas of high rainfall, one inland, the other coastal. The intermediate sizes and numbers occupy a wide range of rainfall zones but the ones that reach the coast, from Pará to Ceará, are mostly in a region of lower rainfall. The Alagoas collection correlates with an isolated pocket of relatively high rainfall and a very short dry season (Prance, 1978). Only the Rio de Janeiro site appears to have no relation to a zone of higher precipitation and here the dry season is not very pronounced, probably a relevant factor. Both the Alagoas and Rio de Janeiro sites are in a narrow coastal strip of "moist" forest which extends north from Santa Catarina to Rio Grande do Norte (Mori **et al**, 1981).

Table I

Locule and ovule numbers in **M. guianensis** The average number of ovules per locule may vary from flower to flower and from collection to collection, resulting in different total numbers of ovules in ovaries that may have the same numbers of locules. Some total numbers are closer to each other than to others: 20 and 20, 16 and 15, 12 and 12, 9 and 8. These groupings may partly account for some of the peaks seen in Fig. 11. See Results.

No. of locules (or placentas)	Average no. of ovules per locule (or placenta)	Total no. of ovules per ovary
5	6	30
5	5	25
5	4	20
5	3	15
4	5	20
4	4	16
4	3	12
3	4	12
3	3	9
2 or 1	4	8
2 or 1	3	6

(1 locule always contains 2 placentas)

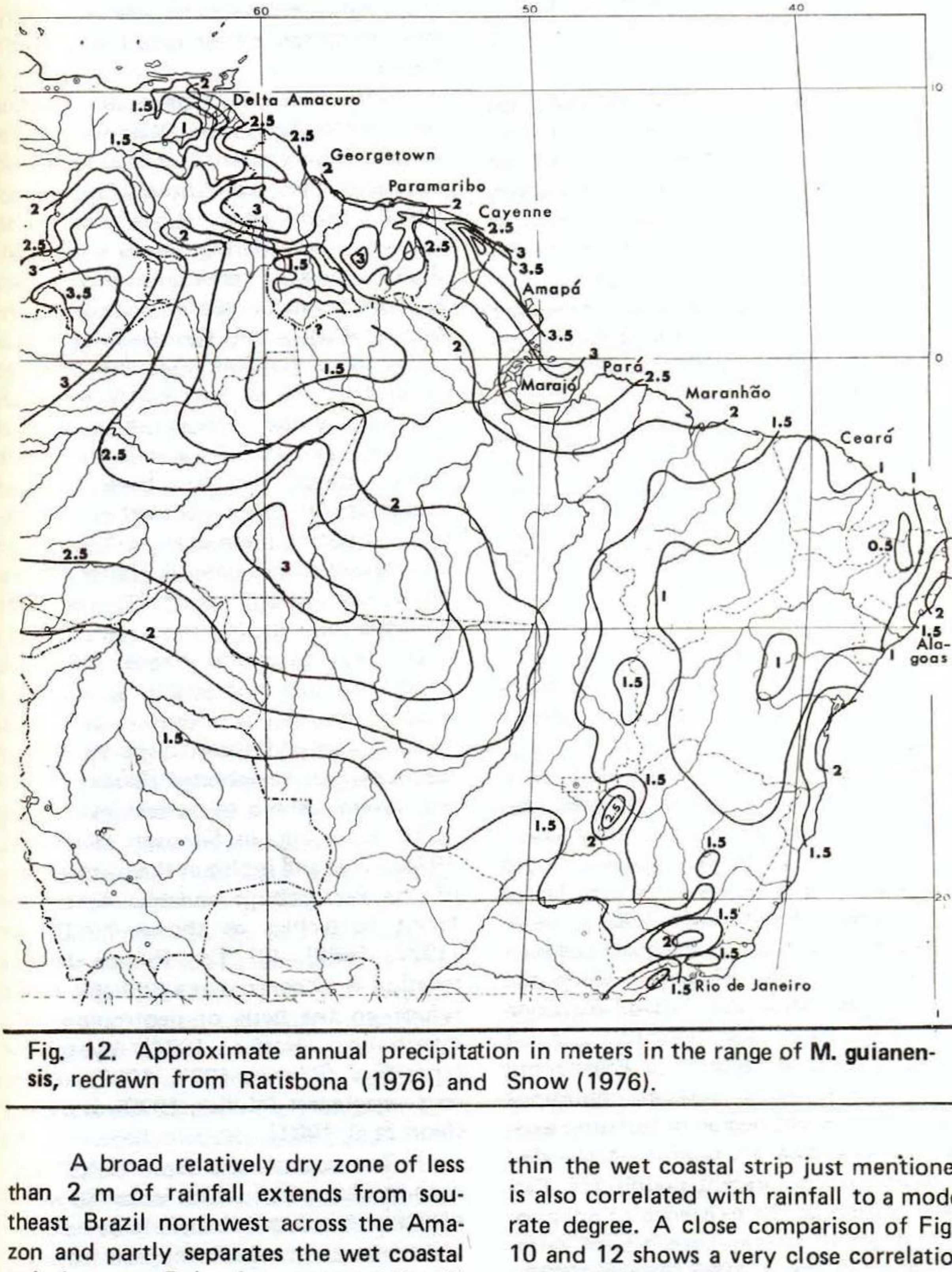


Fig. 12. Approximate annual precipitation in meters in the range of **M. guianensis**, redrawn from Ratisbona (1976) and Snow (1976).

A broad relatively dry zone of less than 2 m of rainfall extends from southeast Brazil northwest across the Amazon and partly separates the wet coastal strip between Delta Amacuro and Marajó from the wet interior. The bulk of this dry arm northwest of the Amazon is shown by Brown (1982) as having a pronounced dry season of from 3–5 months.

The distribution of the plants within the wet coastal strip just mentioned is also correlated with rainfall to a moderate degree. A close comparison of Figs. 10 and 12 shows a very close correlation at the Delta, while southeast along the coast the collection from sites with 2.5 m of rain or more tend to have fewer locules and ovules than those from slightly drier areas. Thus it can be said that there is a definite but imperfect relation between present rainfall patterns and distribution of the different forms of **Mouriri guianensis.**

The very high water table of most of Delta Amacuro might lead one to suspect a relation between this condition and the plants with few ovules. However, in French Guiana similar plants grow at the edges of savannas which are relatively dry according to Granville (1982).

Nor does the available information on soils and other environmental factors appear to coincide with the distribution of the species.

The fact that the plants along the coast have leaves with relatively short petioles, broad basal angles, and veiny surfaces (point 4 above) suggests a relation between these forms and maritime influences; the adaptive value of such forms if any is unknown.

If the species diversified under present conditions, one would hypothesize its history about as follows: moderate reduction of the ovary tended to occur as the plants spread north, east, and south from the point of origin in the west, perhaps in relation to environmental gradients, but this is not clear. Isolation does not appear to have been a major factor in this development. Plants with moderate reduction carried to the coast between Marajó and Ceará. However, when the plants penetrated the broad dry zone mentioned above and reached the coast between Delta Amacuro and Amapá and became adapted to coastal conditions there, a sufficient degree of isolation existed in this case to permit accelerated evolution under present conditions. Partial isolation or the existence of environmental gradients may permit such differentiation (Benson, 1982, Endler, 1982). Long distance dispersal would have brought the plants to Alagoas and Rio de Janeiro, where they were well isolated and where accelerated evolution appears to have taken place. Being bird-dispersed, the plants presumably have high mobility. Bird migration routes could have been a factor.

However, the degree of reduction seen in the plants from Delta Amacuro to Amapá is very sharp and may have been produced under conditions of greater isolation than now appear to exist, especially considering that a similar but slightly lesser reduction took place apparently under nearly complete isolation at Alagoas and Rio de Janeiro. Therefore it is possible that the observed differences are at least partly the result of past climatic changes which involved to some extent the various Pleistocene forest refuges that have been proposed as centers of forest contraction and expansion during these changes. The subject is reviewed by Simpson & Haffer (1978). Some correlations exist: (1) the plant with the most ovules, in western Amazonia, is close to one of Prances (1982) refuges although not within it. (2) The Alagoas location is within or very close to the proposed forest dispersal centers for numerous vertebrates (Muller, 1973) and several genera of butterflies (Lamas, 1973, n. v., ill. in Simpson & Haffer, 1978). This site is also at the southern tip of the Pernambuco endemic center for forest butterflies as shown by Brown (1977, 1982). (3) The Rio de Janeiro location is recognized as a probable forest refuge on the basis of neotropical bird distribution (Haffer, 1974), nymphalid butterflies (Brown, 1977, 1982), numerous vertebrates (Muller, 1973), and trees (Mori **et al**, 1981).

The coastal strip from Delta Amacuro to Amapá in which occur so many plants with reduced flowers finds no close counterpart in the proposed refuges. However, Muller (1973) and Ab'Saber (1982) indicate a large inland arboreal dispersal center nearby that extends from just south of the Orinoco delta through most of Amapá, avoiding the coast except just northwest of Georgetown. Prance shows two smaller refuges farther inland in the same general area, and Brown shows a part of Amapá as a refuge.

If climatic change involving refuges was a major factor in the modification of the species, then its history might have been as follows: during a Pleistocene dry period the broad relatively dry zone of less than 2 m rainfall that extends from southeast Brazil across the Amazon to the northwest became drier and expanded, dividing the population into four groups of different sizes-the plants to the west, those crowded along the northeast coast From Delta Amacuro to Amapá, and those in Alagoas and Rio de Janeiro. The plants trapped along the northeast coast followed the moist zones; if the present rainfall pattern is relevant they would have been squeezed into a small area in eastern French Guiana and nearby Amapá with possibly a second group in Guyana. During the Flandrian transgression they would have been forced inland, very likely to the approximate areas proposed as refuges by Ab'Saber, Brown, and Prance. The transgression would also have driven plants from the area of the Atlantic embayment that might otherwise have persisted along the main watercourses. For reasons that are unclear but which may have been related to small population size, the coastal plants evolved rapidly in the direction of smaller ovaries with fewer ovules; reproductive barriers seem not to have been formed judging by the series of transitional forms, but this has not been tested. The plants on the west remained relatively unchanged.

When climatic conditions shifted toward those of today, the plants spread into all suitable habitats, occupying much of the territory between the four restricted zones including the coast between Marajó and Ceará. Plants within the four zones tended to keep their original characteristics, but the migrants developed more or less intermediate traits, possibly due to hybridization.

The Alagoas and Rio de Janeiro colonies remain isolated, but some of the plants of the northeast coast are now close to plants of the interior and it is here that any hybridization and thus "secondary contact" would have taken place.

In fact it does not appear necessary to choose one of the above hypotheses to the exclusion of the other. It seems probable that both were operative. The evidence for climatic change is strong, but the changes would have been of varying degrees and would have produced different effects in different places depending on variables such as rainfall, soil, water table, and wind patterns. In some areas present isolation is already so complete that lessened precipitation probably would not increase appreciably the likelihood of differentiation occurring. In other areas a moderate decrease in rainfall would accentuate existing differences and accelerate differentiations already proceeding at a slower pace under conditions of partial isolation or environmental gradients or both. Plants might persist along watercourses and in sheltered places during dry times. Thus the populations might diminish but not necessarily disappear in the driest zones during dry periods and then multiply during wetter periods. Changes of this level appear sufficient to account for much and perhaps all of the differentiation found in **M. guianensis.** Perhaps in some areas or for other organisms full and drastic climatic shifts would be necessary to bring about differentiation.

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Resumo

Variação morfológica em **Mouriri guianensis** é descrita e analisada em relação a sua distribuição no Brasil e regiões adjacentes. Carac-

terísticas que variam são tamanho do ovário, número de lóculos e de óvulos, forma e lisura da folha seca, e comprimento do pecíolo. Os maiores ovários com o maior número de óvulos ocorrem no centro-oeste amazônico; tamanhos e números intermediários estão distribuídos largamente mas alcançam a costa marítima somente entre a ilha de Marajó e Ceará; e os menores ovários com os menores números de lóculos e óvulos encontram-se na costa ou próximo da costa entre o Delta Amacuro na Venezuela e Marajó. Pequenos ovários também ocorrem nas costas de Alagoas e Rio de Janeiro. Acredita-se que ovários com o menor número de óvulos e lóculos são os mais especializados, resultado da evolução em direção à diminuição da perda de óvulos, já que os frutos de todos os membros possuem poucas sementes. Folhas com relativamente longos pecíolos, ângulos basais estreitos, e superfície lisa correlacionam-se com número grande de óvulos e podem ser primitivos para a espécie. Folhas deste tipo tipificam as plantas do interior enquanto plantas costeiras tendem a ter folhas com condições opostas. A evidência é insuficiente para subdividir a espécie em dois ou mais grupos taxonômicos. A possível origem do padrão observado da distribuição da espécie é discutido em termos (1) dos padrões da precipitação atual, e(2) das mudanças climáticas do Pleistoceno e refúgios florestais associados. Conclui-se que ambos os fenômenos tenham provavelmente influenciado. Alta especialização parece ter acompanhado isolamento, por razões que não estão claras. Visto que as plantas encontradas entre o Delta Amacuro e Marajó são mais especializadas, elas talvez tenham estado mais isoladas no passado do que observa-se hoje em dia.

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