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# Response of three mangroves to salinity in two geoforms

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## Abstract

**1** The variation in the physiognomy of the mangroves *Avicennia germinans* L., *Rhizophora mangle* L. and *Laguncularia racemosa* (L.) Gaertn., as related to salinity in two different geomorphic habitats (mudflats and interdistributary basins) was investigated.

**2** Due to the high intercorrelation between variables, principal component analysis was used to examine data on (a) water salinity on two sampling dates and in two geoforms and (b) diameter at breast height, height and per cent cover of each of the three species. The first component of each of these four data sets summarized 77, 64, 90 and 93% of the total variance in the intervening variables.

**3** The projections of the intervening variables on their respective principal component was calculated, and response curves of species against environmental component scores were fitted by generalized linear models. The resulting curves were bell-shaped, except for *A. germinans*.

**4** The highest diversity and the maximum height and diameter for the three species is at low salinities and in interdistributary basins but the cover of *A. germinans* is higher in the mudflat and under high salinities. The range of response to environmental change is wider in *A. germinans*.

**5** There was a negative association between the cover of *A. germinans* and that of the other two species, and the slope of the regression line suggests a substitution of one unit of cover of *A. germinans* by one unit of cover of any of the other two species in the interdistributary basins as salinity decreases.

**6** The results suggest that while abiotic environmental conditions may account for the absence of *L. racemosa* and *R. mangle* in the mudflats, biological interactions are more important in the formation of the mixed forests in the interdistributary basins.

*Key-words:* Geoforms, gradients, mangroves, salinity

## Introduction

Variation in mangrove physiognomy and species composition associated with temperature and rainfall was reported by Lot-Helgueras, Vázquez-Yanes & Menéndez (1975) for the Gulf of Mexico and by Cintrón, Lugo & Morris (1978) for Puerto Rico and adjacent islands, where tree height was negatively correlated with salinity. Ball (1980) demonstrated that an increase in salinity caused by the construction of dikes during an urban development project could influence secondary succession in mangroves. On the other hand, Thom (1967, 1982) stated that 'substratum, ground-water level, soil drainage, and salinity were observed to be dependent on the geomorphic variable', suggesting a tight relationship between geoforms and mangrove species distribution. Rodríguez (1987) treated Thom's point of view as an alternative in explaining mangrove zonation, in contrast to traditional gradient analysis where, according to Rodríguez, zonation is the result of physiological responses to gradients in salinity and tidal levels.

No detailed studies on physiognomic changes in mangrove vegetation have been made in relation to physical factors at a more local scale. This study is intended as a contribution in this respect. In a previous study (López-Portillo & Ezcurra, 1989) we reported the relationship between relief and plant distribution. The present study establishes the relationship between height, diameter at breast height (dbh) and cover of three mangrove species (*Avicennia germinans* L., *Rhizophora mangle* L. and *Laguncularia racemosa* [L.] Gaertn.) along a compound gradient represented by salinity and variation in the geomorphic habitat (geoform).

## Materials and methods

### Study area

The study was made at the Mecoacán lagoon (Fig. 1), which covers an area of approximately 300 km<sup>2</sup>. The lagoon is part of the Grijalva-Mezcalapa deltaic system and originated during the Recent Gulf Fluvial (West, Psuty & Thom, 1976). Sediments are derived from Cretaceous granitic and Tertiary sedimentary rocks from the Sierra Madre de Chiapas. The climate is lowland tropical monsoon; mean temperature is 25°C, and annual precipitation is between 1500 and 2000 mm, with higher rainfall between June and December. The tidal range varies from 35 to 50 cm, water level being occasionally higher when north fronts (locally called *nortes*) reach the area. On these occasions the inlet becomes closed by the strong winds and the water level in the lagoon can reach up to one metre above sea level (Thom, 1967; West, Psuty & Thom, 1976).

Fig. 1 is based on information derived from Thom (1967), aerial photographs (1:30 000), a base map (DETENAL 1979) and our own field notes and sampling stations. Mangrove vegetation involves three basic types: mixed mangrove stands (fluvial environments), *Avicennia germinans* mangals (mudflat environments) and *Rhizophora mangle* mangals (wooded shoreline). Other communities are: halophyllous vegetation (with *Batis maritima*

L., *Salicornia bigelovii* Torr., *Borrchia frutescens* [L.] DC., *Spartina spartinae* [Trin.] Merr. and *Distichlis spicata* [L.] Greene, among others), marshes (where *Thalia geniculata* L. is common) and bogs (usually dominated by *Dalbergia brownii* [Jacq.] Urban). Around the halophytic environment, on higher land, coconut and cacao are cultivated.

### Sampling

Nineteen sampling stations were placed around the lagoon (Fig. 1). Sites were chosen systematically as the most well-preserved (i.e. where no anthropogenous tree felling was observed) and with flooding levels between 10 and 40 cm above the soil level. Stations within each sampling site consisted of 10 × 10 m squares usually located about 50 m from the lagoon or river fringe. In each station, species cover was measured by point-quadrat estimation using a self-levelling pentaprism (Montaña & Ezcurra, 1980) and the height and dbh of the five tallest trees in monospecific mangals were measured. If less than five trees were found within the sampling squares (in which tree density varied from two to seven individuals), other trees outside them were considered. The two tallest trees per species were measured when more than one mangrove species was present.

Water height with respect to soil surface, and

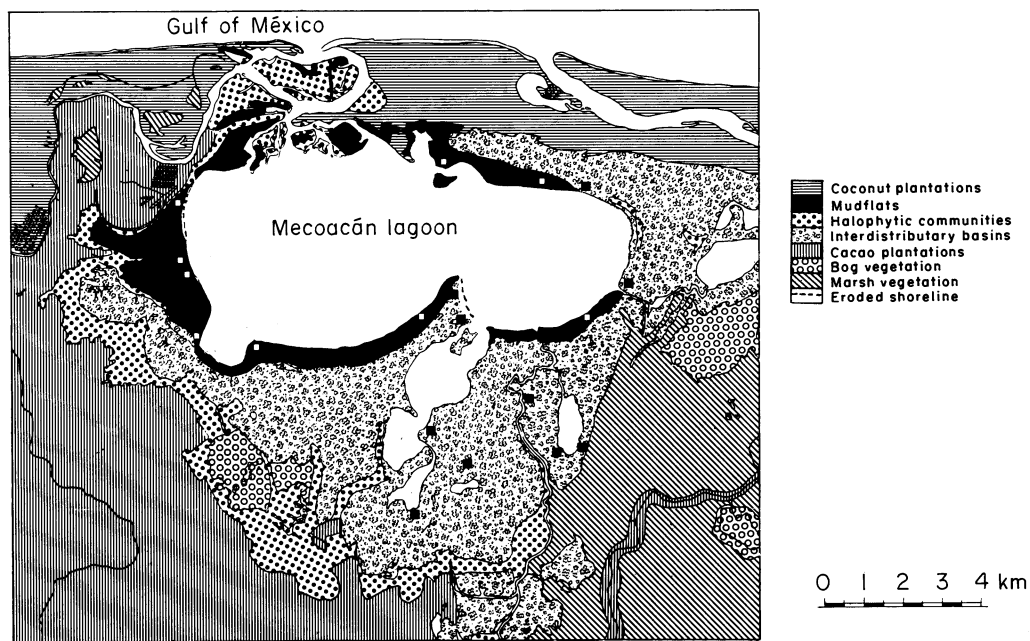


Fig. 1. Plant communities around the Mecoacán lagoon. Squares indicate sampling stations made on mudflats (open squares) or interdistributary basins (closed squares). The area in this figure is between 18° 18'–27'N and 93° 2'–13'W.

oxygen at a soil depth of 5 cm using the Hoffer colorimetric method (Jackson, 1976) were measured at the centre of every station on 17 April 1980, a month in which water levels are well below the mean of the lagoon. Anaerobic conditions prevailed in all the stations. Average water level (used here as an indicator of relief) was 23 cm above soil level. Also, soil and water samples were collected in the centre of each station on three occasions (December 1979, February and May 1980) and their electrical conductivity (on a saturation paste for soils) was measured in the laboratory. Electrical conductivities (EC) in mS can be transformed to per cent dissolved salts (PDS) by using the equation  $PDS = 0.0639 \times EC$  ( $r = 0.999$ ;  $P < 0.0001$ ), which was calibrated for the Mecoacán Lagoon ( $n = 26$ ).

Sampling was done in two geomorphic habitats: interdistributary basins and mudflats. According to Thom (1967), the interdistributary basins (a fluvial habitat) 'are broad, low lying areas formed between distributaries' and within these depressions, land surfaces are characterized by autochthonous organic matter. From the depth of peat in the basins located between abandoned distributaries, Thom concluded that these areas are subsiding in relation to the level of the Gulf of Mexico, and that plants are thus growing in soils produced by their own activity. The mudflat (a lagoon habitat) 'is the product of an influx of fluvially introduced, fine inorganic sediments along a shoreline' (i.e. suspended clay and silt which flocculate as salinity increases, Bloom, 1978). 'As these sediments accumulate, mudflats build out into the lagoon, resulting in the blanketing and isolation of former strandline deposits. Therefore, this environment represents areas of excessive fine sediment which reduces wave action' (Thom, 1967).

#### *Statistical analysis of response functions*

The response of species variation to environmental changes was analysed by means of generalized linear models (GLM, Nelder & Wedderburn, 1972; McCullagh & Nelder, 1983), a general class of linear models which are fitted by maximum likelihood procedures. These models have been used by Austin, Cunningham & Good (1983), Austin, Cunningham & Flemming (1984) and by Ezcurra, Equihua & López-Portillo (1987) to describe the distribution of plant species as a function of independent environmental variables. GLMs explain the variation of an observed dependent

variable as a combination of a systematic component (the linear model) and a random component (the error function). Both components are linked together by a link function which has to be defined from a set of possible links (e.g. identity, inverse, logarithmic and logit links). Link functions can be used to impose restrictions on the predicted values. For example, logarithmic link will make all predicted values positive. The deviance of a fitted model measures the discrepancy between the data and the fitted values and can be compared against the deviance of the null hypothesis (or total deviance), which is that species variation is independent of environmental changes. For normal error, the deviance will be distributed as a sum of squared residues and the fit can be analysed by an ANOVA. For binomial and Poisson errors, the fit will be approximately distributed as Chi-square and can be tested accordingly.

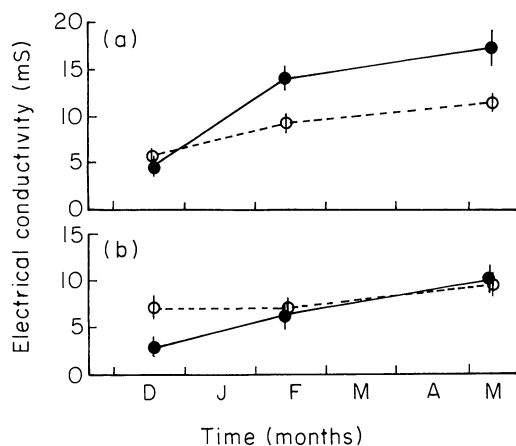
## **Results**

### *Electrical conductivity*

Mean water electrical conductivity for all sampling stations was 3.8, 10.0 and 13.4 mS for December, February and May respectively, indicating a tendency to increase in salinity towards the dry season. The lowest levels of the lagoon occur in May and the highest in January. Mean electrical conductivity of the soil was 6.4, 8.2 and 10.6 mS for the same dates, showing a greater soil buffering capacity for salinity. This buffering effect is also indicated by the slopes of the linear regressions between water and soil conductivity, which decrease as the dry, low water level season proceeds (slope values were 0.57, 0.30 and 0.26 for December, February and May, respectively).

### *Data analysis*

Fig. 2 shows the changes in electrical conductivity as a function of sampling dates and geoforms. Conductivities in the mudflats vary more in time than in the interdistributary basins and water conductivities vary more than soil conductivities. In the mudflat (Fig. 2a) differences between soil and water conductivity tend to increase as the dry season progresses and water conductivity is higher than in the interdistributary basin. The greatest differences between soil and water conductivities in the interdistributary basin were found in December, when water salinity decreased (Fig. 2b).



**Fig. 2.** Changes in electrical conductivity of water (continuous lines) and soil (broken lines) as a function of sampling dates and geoforms. (a) Mudflat; (b) interdistributary basin. Vertical lines indicate  $\pm 1$  SE.

A factorial analysis of variance on the conductivity values showed significant differences between sampling dates ( $F = 31.72$ ; 2, 104 d.f.) and between geoforms ( $F = 20.22$ ; 1, 104 d.f.). No significant differences were found between soil and water substrates. However, the interactions between geoforms and substrates, geoforms and sampling dates and substrates and sampling dates were all significant ( $F$  values are 10.64, 3.98 and 5.33 for 1, 104; 2, 104 and 2, 104 d.f. respectively).

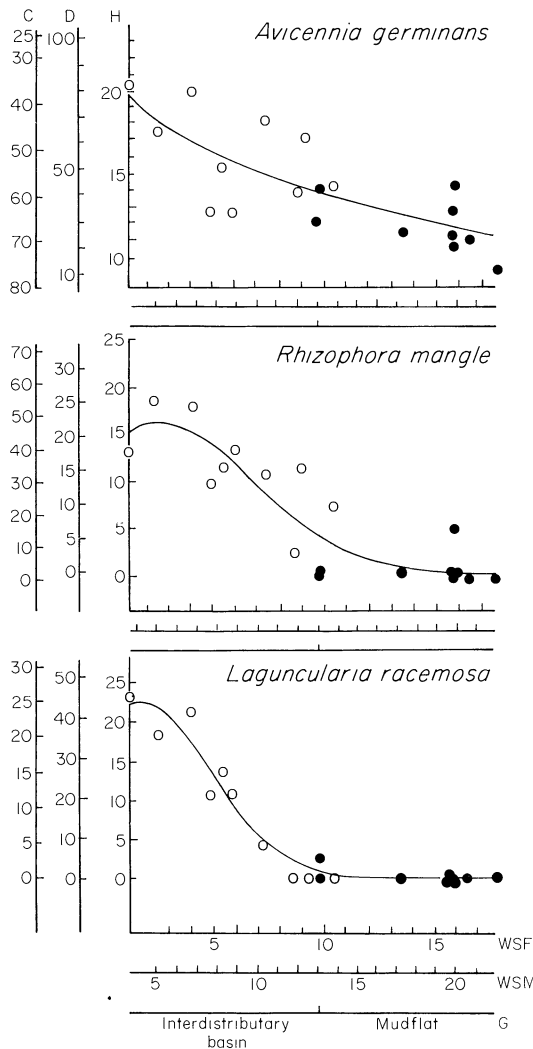
Due to highly significant linear correlation between variables, principal component analysis (PCA) was used to synthesize the environmental variables on one hand and the biotic variables describing each species on the other. For each species, cover, dbh and height were summarized into a single principal component. The problem of non-linear species response ('arch effect', Gauch, 1982), common in ecological ordinations, was not present in these analyses as the variables considered in each PCA belonged to the same species and were strongly correlated. In the case of the environmental data, water salinity in the 2 dry months (February and May) and geoform (a categorical variable defined as 0 or 1, since sampling was done in only two geoforms) were taken as the variables to correlate against plant variation (soil conductivities, and water conductivities in December, were found to be poor predictors of plant variation). The environmental component summarized 77% of the total variance, while the biotic components (which includes height, dbh and cover of each species) summarized 64, 90 and 93% of the total variance in the data sets from *A. germinans*, *R. mangle* and *L. racemosa*, respectively.

As the components are difficult to interpret directly, the projections of the intervening variables on each principal component were calculated. Based on these projections Fig. 3 was developed, which represents the relationship between plant components and the salinity-geoform gradient. However, each axis shows the projected values of the intervening variables instead of the principal component itself. The projected variables (Fig. 3) vary in direction and scale, but they all make a statistically significant contribution ( $r$  in Table 1) to the first principal axis. The projected values are a least-squares linear approximation of the original data (Gabriel, 1978).

Response surfaces were fitted to the species principal component scores as a function of the environmental scores by means of generalized linear models. The error function was declared to be normal, and the link function used was the logarithmic transformation, after shifting the origin of the dependent variables in order to avoid taking logarithms of negative numbers. Table 2 shows the resulting exponential models and the basic statistics obtained from them. It is important to note that the coefficient of the quadratic term ( $c$ ) was negative and significantly different from zero for *R. mangle* and *L. racemosa*, a fact that indicates that the response surfaces of these species to the abiotic variables under study are bell-shaped. However, *A. germinans* did not show a significant quadratic term, indicating a less pronounced response to these variables. It can be seen that: (1)

**Table 1.** Eigenvalues ( $\lambda$ ) of the first principal component for the four data sets. The component scores ( $x$ ) of the intervening variables, and their correlation coefficients with the first principal axis ( $r = \sqrt{\lambda x}$ ) are indicated.

	$x$	$r$
Environmental component ( $\lambda = 2.32$ )		
Water salinity (February)	0.61	0.92
Water salinity (May)	0.58	0.88
Geoform	-0.55	-0.84
<i>Avicennia</i> component ( $\lambda = 1.92$ )		
Height	0.65	0.90
Diameter	0.66	0.91
Cover	-0.39	-0.54
<i>Rhizophora</i> component ( $\lambda = 2.70$ )		
Height	0.60	0.98
Diameter	0.57	0.94
Cover	0.56	0.92
<i>Laguncularia</i> component ( $\lambda = 2.81$ )		
Height	0.59	0.99
Diameter	0.57	0.96
Cover	0.57	0.96



**Fig. 3.** Response curves of three compound axes summarizing the biotic characteristics of *Avicennia germinans*, *Rhizophora mangle*, and *Laguncularia racemosa*, as a function of a compound axis summarizing the environmental factors. For the ordinates: C, cover (%); D, dbh (cm); H, height (m); for the abscissa: WSF, water conductivity in February (mS); WSM, water conductivity in May (mS); G, geoform. Full circles and empty circles indicate interdistributary and mudflat sampling stations respectively.

The maximum values for all the biotic characteristics of *R. mangle* and *L. racemosa* are around conductivities of two to five mS, although *R. mangle* shows a higher amplitude of response; (2) the model for *A. germinans* predicts that trees are taller and thicker towards the lowest sampled salinity and shows an even higher amplitude of response; (3) there is no important presence of *R. mangle* or *L. racemosa* in the range occupied by the mudflat environments; and (4) the direction of increase in cover of *A. germinans* is opposite to that of the other two species.

Correlation coefficients were negative and significant ( $P < 0.01$ ) when comparing the cover of *A. germinans* (A) with that of *R. mangle* (R) and *L. racemosa* (L) in mudflats and interdistributary basins (correlation coefficients are: A vs R  $r = -0.85$ , A vs L  $r = -0.61$  and A vs R + L  $r = -0.81$ ;  $n = 19$ ). *R. mangle* and *L. racemosa* showed a positive correlation coefficient between themselves ( $r = 0.70$ ;  $n = 19$ ). The correlation between *A. germinans* cover and *R. mangle* plus *L. racemosa* cover considering only the interdistributary basins (in which the three species coexist) was  $-0.56$  ( $n = 10$ ). The slope of the bivariate regression line (Sokal & Rohlf, 1981) was not significantly different from one ( $P < 0.05$ ; Fig. 4), which indicates that in the interdistributary basin, as salinity decreases, each unit of cover of *R. mangle* or *L. racemosa* that is lost is replaced by approximately one unit of cover of *A. germinans*.

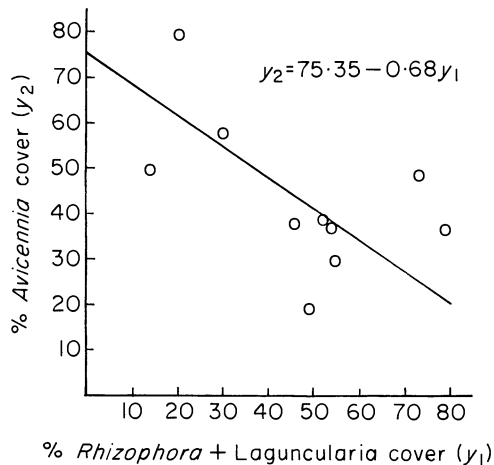
The plant diversity of the mangrove forest (measured as the inverse of Simpson's index,  $N_2 = 1/\sum p_i^2$ ) showed a qualitatively similar bell-shaped response as those of the individual plant species components. Maximum diversity occurs at low salinities in the interdistributary basins, and decreases rapidly towards the saline mudflats. Above 10–13 mS the mixed mangrove forests become monospecific stands of *A. germinans*.

## Discussion

All of the stations sampled were under anaerobic conditions. However, the three species under study show adaptations to anaerobic substrates (pneumatophores and lenticels in *Avicennia* and *Laguncularia*, lenticels in the stilt roots and trunk in *Rhizophora*). It has been shown that mangrove species can oxidize the root environment and thus modify the micro-environment in which nitrogen and phosphorus, which are not available under reducing conditions, can be taken up (Boto, Safigna & Clough, 1985). However, this phenomenon is more evident in some species than others and may explain the absence of *L. racemosa* and *R. mangle* within the mudflat. For example, Thibodeau & Nickerson (1986) show that *Avicennia germinans* lives in more anaerobic substrates than *Rhizophora mangle* and our results indicate that *A. germinans* shows a higher amplitude of response to changes in salinity and geoform. On the other hand, organic matter abundance was as high as 10% in the mudflat near the lagoon inlet (López-Portillo & Ezcurra, 1989) and is probably higher in the interdistributary basin, due to its biogenic origin (Thom, 1967). This evidence and

**Table 2.** Coefficient values and standard errors of the species response functions obtained by generalized linear models ( $y_c = \exp[a + bx + cx^2]$ ) and the corresponding determination coefficients ( $r^2$ ). These parameters are given in principal component units.

	<i>A. germinans</i>	<i>R. mangle</i>	<i>L. racemosa</i>
Coefficient			
<i>a</i>	-0.80 (0.15)	-1.59 (0.41)	-3.56 (0.64)
<i>b</i>	-1.42 (0.45)	-6.12 (2.28)	-13.18 (2.96)
<i>c</i>	-0.07 (0.94)	-6.15 (3.05)	-11.90 (3.24)
$r^2$	0.59	0.74	0.95

**Fig. 4.** Relationship between the joint cover of *Rhizophora* + *Laguncularia*, plotted against the cover of *Avicennia* ( $r = -0.56$ ;  $P < 0.01$ ). The line was fitted by bivariate regression. The slope of the line was not significantly different from one.

the dimensions of individuals, suggest that nutrient availability is not the limiting factor in itself.

The strong association between salinity and geoform (mudflats are more saline than interdistributary basins) indicates that both the distance from the saline source and the depositional environment in which mangroves live are important and statistically ablated environmental factors influencing mangrove establishment and growth. The results unite two points of view which have been traditionally considered in isolation: (1) the effect of salinity and (2) the influence of the geomorphic habitat on the distribution of mangrove communities. These views have been defined by Rodríguez (1987) as 'gradient analysis' and as 'physiographic ecology', respectively. The response surfaces of the three species indicate that salinity, either as salinity *per se* or as osmotic potential (Naidoo, 1985), and geoform, as an

overall indicator of contrasting environmental conditions, are playing an important role in mangrove distribution and abundance. The two geoforms have different salinity and water regimes (as indicated by the significant interaction terms in the ANOVA displayed in Fig. 2). Also, soil texture may have a salinity buffering effect (which may be higher in the interdistributary basin), since fine particles and organic matter act as chelators during cation exchange (McMillan, 1975).

There is a marked contrast between the behaviour of variables measured at an individual level (dbh and tree height) with respect to cover, a variable reflecting global ecological conditions. Final diameter and height (i.e. after establishment of the dominant individuals) of the three mangrove species can be considered as the result of a physiological response to environmental conditions, described here as changes in salinity and geoform. For all three species, these variables tended to increase in value towards the less saline environments. However, cover seems to be the result of another set of variables defined at an ecological, as opposed to a physiological, level. There seems to be no other explanation for the high *A. germinans* cover values observed in the more saline and physiologically unfavourable environments. The physiological success of *A. germinans* (as shown by the values of diameter and height) within the interdistributary basins suggests that its low cover in this geoform is the result of the interaction with *R. mangle* and *L. racemosa*. This argument is reinforced by the negative association between the cover of *A. germinans* and that of the other two species under study. It may be concluded that although the actual situation is a result of historical causes (i.e. species colonization and competition in different habitats, rising water level, sediment deposition and soil subsidence and compaction) interspecific interactions change with salinity and position within geoforms and thus influence the actual aspect of the mangrove communities.

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