

## Geometry, biomass allocation and leaf life-span of *Avicennia germinans* (L.) L. (Avicenniaceae) along a salinity gradient in Salinas, Puntarenas, Costa Rica

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**Abstract:** A population of *Avicennia germinans* (reproductive plants from 9 cm to 6 m height) growing along a salinity gradient (35 to 85 %) was studied at Salinas, Puntarenas, Pacific coast of Costa Rica. Trees from higher salinity areas were characterized by: smaller size, larger width to height ratio, smaller leaves, earlier and more profuse branching, allocation of a higher proportion of biomass to roots, and longer life expectancy of leaves.

The general shape of plants and their parts is genetically determined. These shapes, however, can be modified in responses to particular environmental conditions (Chapin and Chapin 1981; Hallé, Oldeman y Tomilson 1978; Horne 1971, Longstreth and Novel 1979, Nestler 1977, Richars 1976)

Those genetic or environmental differences, selected under different conditions, have an adaptative value through aspects such as the quantity of light that the plant can intercept (Horne 1971, Loomis 1965); thermal control (Gnoerr and Guy 1965, Turrell and Austin 1965, Vogel 1969); water and nutrient intake (Nye and Tinker, 1979, Robinson and Robinson 1985).

Plant biomass allocation can be modified by stress and disturbance. Stress results form conditions that restrict production *e.g.*, shortage of light, water, nutrients or any other suboptimal environmental condition. Disturbance is associated with the total or partial destruction of the plant biomass (Grime 1977). Plants tolerant to stress tend to modify their biomass allocation in their compartments (roots, shoots, leaves and reproductive material) depending on the envi-

ronmental conditions. This differential distribution has a selective value, and contributes to the reproductive success and survival of the species.

*Typha latifolia* allocates a high proportion of biomass to roots in low nutrient conditions (Grace and Wetzel 1981). After a fire *Rhus glabra* allocated a greater proportion of biomass to leaves and woody tissue utilized for vertical growth than unburned shoots (Knaps 1986). In *Lolium perenne* and *Trifolium repens*, the growth of roots relative to foliage growth is increased by deficiencies of available moisture, nitrogen and phosphorus in the soil (Davidson 1969). Dandelions and *Helianthus* spp. from disturbed environments allocate a higher proportion of biomass into reproductive tissue (Gadgil and Solbrig 1972, Gaines *et al.* 1974).

Since leaves are photosynthetic organs, their life-spans can be considered as part of the strategy of a species to maximize carbon gain under the environmental conditions of its habitat (Chabot and Hicks 1982, Kikusawa 1984).

Some authors have mentioned that the life-span of leaves depends on the environmental conditions. Leaves tend to live longer in high stress sites such as the understory of a forest (Bazzaz and Picket 1980, Grime 1977) and poor nutrient sites (Al-Mufti *et al.* 1977, Chapin *et al.* 1980).

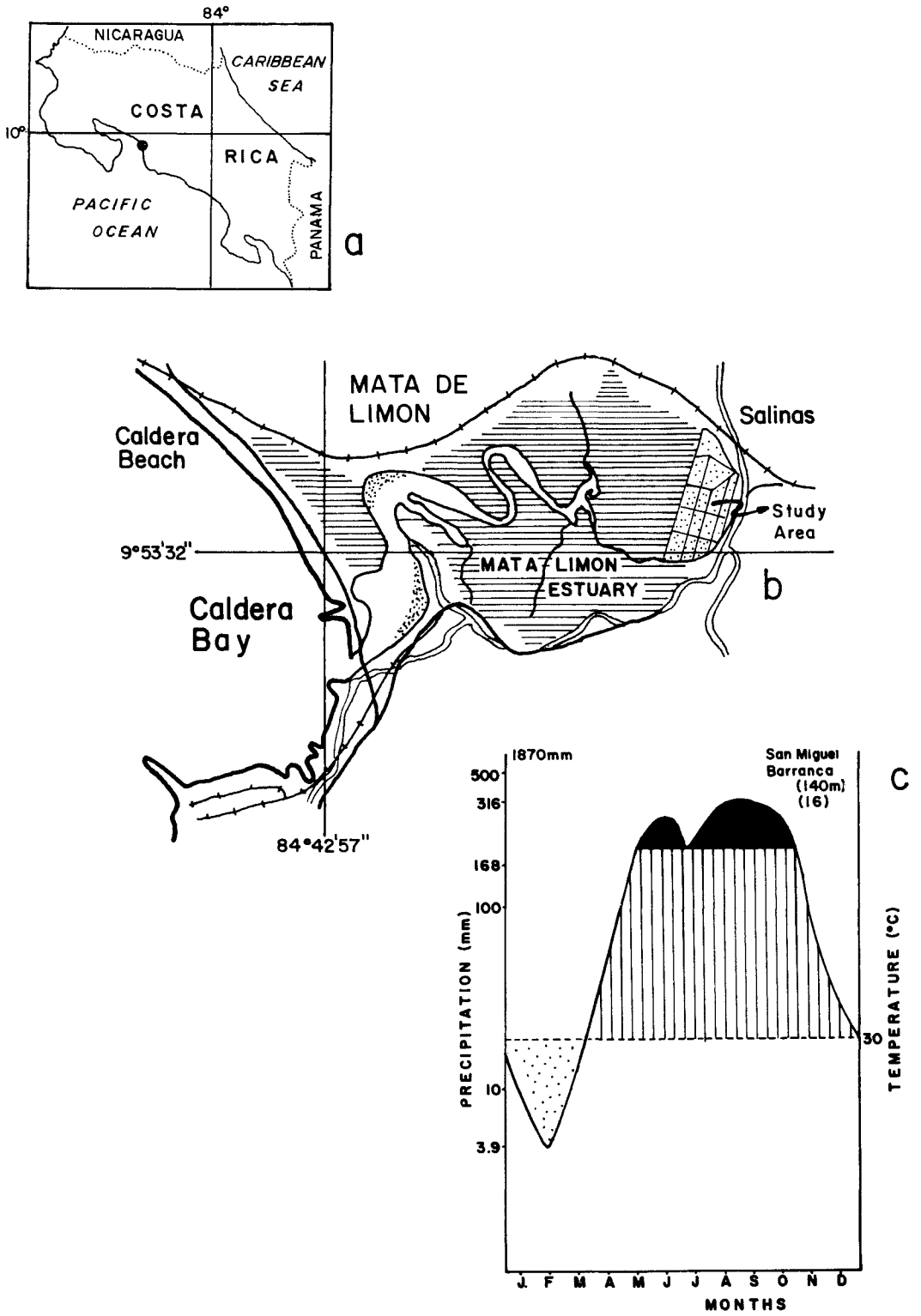


Fig. 1. Location and climatic conditions of the study area.

This study examines the effect of a salinity gradient on the geometry, biomass allocation, and leaf life-span of *Avicennia germinans* (L.) L. in a mangrove community established on an abandoned salt pond.

## MATERIAL AND METHODS

**Site:** Observations on geometry, biomass allocation, leaf life-span and growth pattern of seedling of *Avicennia germinans* (L.) L. were made in a mangrove community established in an old salt pond that was abandoned about 15 years ago, at Salinas, Puntarenas, Costa Rica (Fig. 1a). Plant height in the stand increase from the open areas in the center of the sand flat (where the salinity is higher:  $\bar{x}$ : 80 %), to the places of low salinity on the borders of the old salt production ponds ( $\bar{x}$ : 40 %). See Soto and Jiménez 1982, Jiménez and Soto 1985, Soto and Corrales 1986 and Muñoz 1986, for a more comprehensive description of the site and conditions. The area is included in the moist transition of the tropical dry forest life zone (Tosi 1969). It presents a rainy season from May to early November (Fig. 1c).

**Geometry:** To study the geometry of the plants along the salinity gradient, a transect of 200 m was run from the center of the sand flat to the borders of the old salt pond.

To quantify variations in shape of the plants, height and width of a hundred plants, randomly selected along the transect, were measured according, to the criteria of Horne (1971).

To study if the differences were genetically or environmental controlled; in 1985, 120 fruits from trees under 1 m high were planted; 60 near their parents (controls) in the high salinity area and 60 under trees 12 m high in the shaded and low salinity area as treatments.

In additions 120 fruits from the 12 m high trees were planted; 60 under their parents (controls) and 60 near the plants less than 1 m high. Growth rate, mortality and branching pattern of the seedlings that became established were observed every two weeks (the first month) and on a monthly basis for two years. In 1986, 240 fruits from the tall trees and 240 from the dwarf ones were planted under the same design of 1985, and the same date were collected.

**Biomass allocation:** Forty five reproductive plants, from 9 cm to 8 m tall were harvested

along the salinity gradient, in a systematic way. Each plant was separated in roots, leaves and branches, and trunk. The material was dried at 70°C. Interstitial salinity was measured in at least five holes in each sector, where the plants were harvested, using an Americal Optical Co. refractometer, model No. 10423.

**Leaf Life-Span:** Observations of leaf life-span were made on 15 trees grouped in three height categories; less than 1 m; 1 to 2.5 m and 5 to 7 m. In each tree six new leaves, less than 10 mm long were tagged and measured every two weeks the first month and every four weeks afterwards, to study growth rate and leaf life-span.

**Statistical analysis:** Differences in size (leaves), height (seedlings), growth rate and survivorship were analysed using Kruskal-Wallis one way analysis of variance.

The degree of association in biomass allocation between the different compartments (leaves, branches and roots) was tested by Spearman's Rho rank correlation.

## RESULTS

**Geometry:** Dwarf trees of *Avicennia germinans* have crowns proportionally wider than tallest trees. The coefficient height-to-width is larger for taller trees (Table, 1). Branching angles (of lateral branches in relation to the central axis) is wider in dwarf plants growing in open areas of high salinity ( $\bar{x}$ : 85 %). Tall trees growing in dense stands and low salinity ( $\bar{x}$ : 40 %) show narrow angles (Table, 1).

Seedlings planted in open areas with high salinity and high light intensity have earlier and more profuse branching (Table, 2).

Of 15 seedlings from dwarf parents that became established in 1985 and 50 in 1986, 46.6 % and 36.0 % respectively, produced from 1 to 6 lateral branches at an age of two months. On the contrary, out of 39 and 22 seedlings from dwarf parents that became established in the shaded and low salinity area in the same years, only 2.6 % and 6 % respectively, produced a lateral branch, and none of them have produced a second branch after two years (Table, 2).

Seedling from parents 12 m high growing in both areas showed the lowest frequency of branching, with only one individual established in the open place producing one lateral branch at an age of two months. None of the others

TABLE 1

*Height to width ratios and angle of branching of Avicennia germinans plants growing along a salinity gradient*

Height range (cm)	Number of samples	Average high/wide	Standard deviation	Average angle of branching	Standard deviation
12-20	18	0.70	.33	68.6	7.9
21-30	16	0.54	.19	74.6	14.8
31-40	11	0.56	.26	76.2	11.9
41-50	9	0.38	.11	83.0	6.0
31-100	12	0.62	.35	79.1	12.8
101-200	6	2.14	2.27	87.2	3.4
201-400	7	2.04	1.11	0.0	0.0
401-800	11	3.19	1.27	8.0	12.7
801-1200	7	2.59	.99	0.0	0.0

TABLE 2

*Branching patterns of seedlings of Avicennia germinans growing under different environmental conditions, Salinas, Puntarenas, Costa Rica. (N: Number of seedlings; % Percentage of seedlings with one to six branches)*

Conditions	1985		1986	
	N	%	N	%
1. Seedlings from dwarf plants growing near their parents	15	46.6	50	36.0
2. Seedling from dwarf parents under 10 m trees.	39	2.6	22	6.0
3. Seedlings from 10 m trees growing under their parents	18	1.1	24	0.0
4. Seedlings from 10 m trees growing in the area of dwarf plants	16	0.0	27	0.0

have produced lateral branches after two years (Table, 2).

Seedlings from dwarf and 12 m trees planted in the open and high salinity area show no significant differences in the average height they reach at different ages. Differences in height, however, were highly significant for the rest of the treatments ( $P < .001$ ). (Table, 3; Fig. 2).

There were no significant differences in growth rate between treatments. Survivorship was different only between seedlings from dwarf

parents growing under 12 m trees and seedlings from 12 m trees under their parents ( $P < .006$ ). (Table, 3). Survivorship curves fit fairly well Pearl's (1928) type II (Fig. 2).

**Biomass allocation:** Shorter plants of *Avicennia germinans* in general allocate a high proportion of biomass to roots. This proportion is larger in dwarf trees with wider crowns. This is very evident in trees such as numbers 34 and 37, in which the crowns are extremely wide in rela-

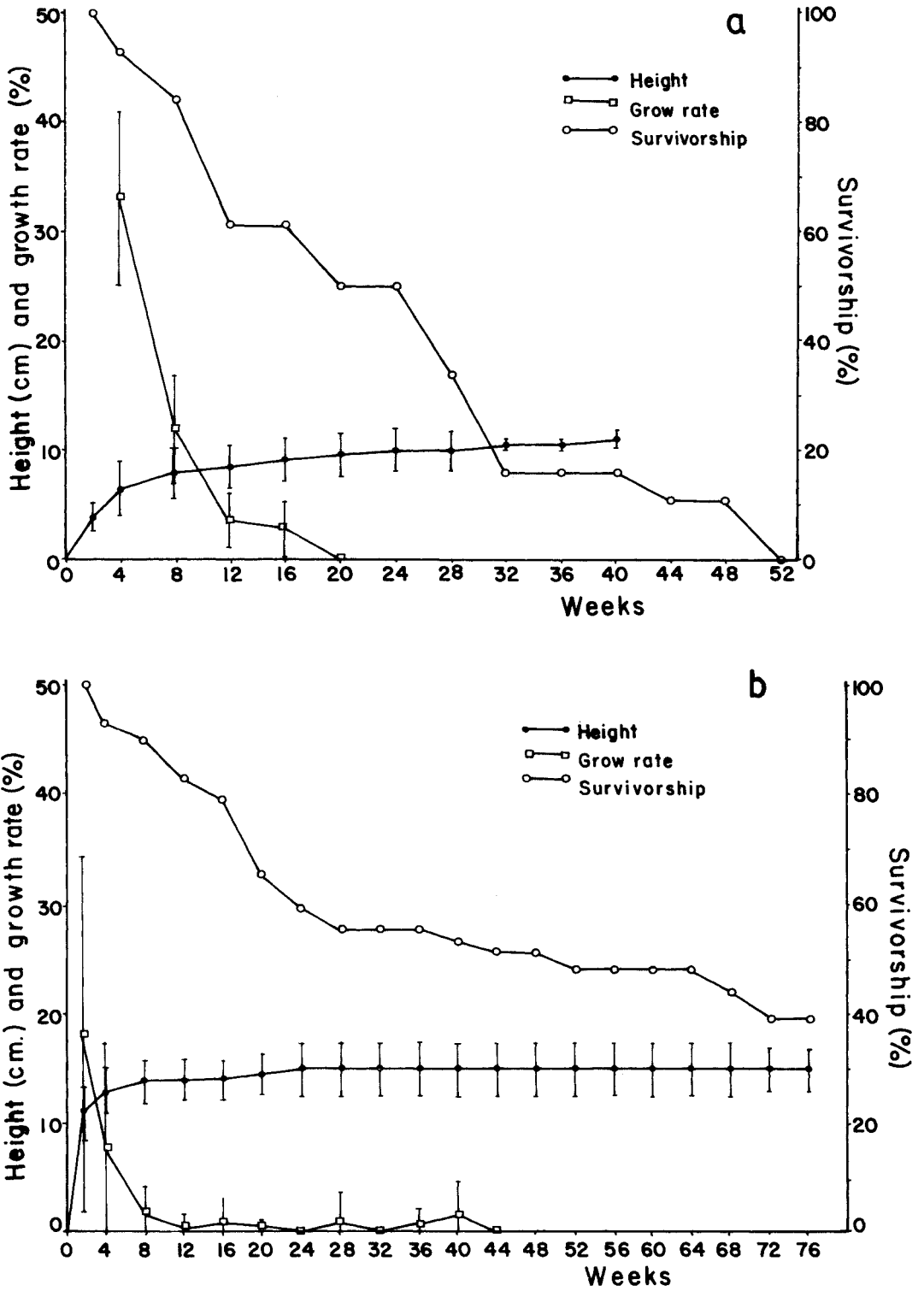


Fig. 2. Height, growth rate and mortality of seedlings of *Avicennia germinans* planted under different environmental conditions a: seedlings from dwarf trees planted near their parents, b: seedlings from dwarf trees planted under 12 m trees.

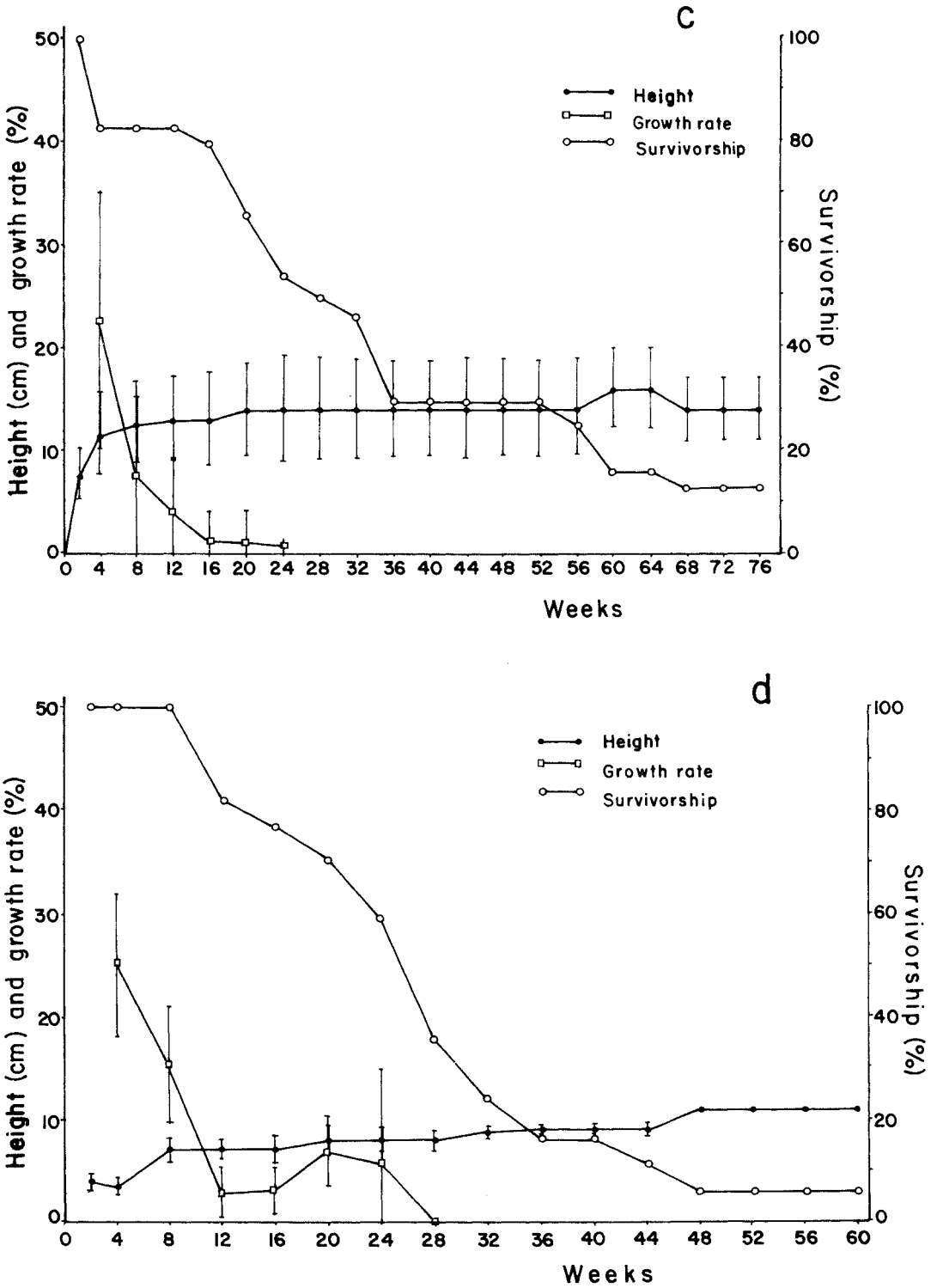


Fig. 2. Height, growth rate and mortality of seedlings of *Avicennia germinans* planted under different environmental conditions c: seedlings from 12 m trees planted under their parents, d: seedlings from 12 m trees planted near dwarf trees.

TABLE No. 3

Height growth rate and mortality of seedlings of *Avicennia germinans* (L.) L. planted under different environmental conditions. Salinas, Puntarenas, Costa Rica. (N = Number of seedlings; AX: Average height (cm); S: Standard deviation; GR: Growth rate; S.V.: survivorship).

Weeks	Fruits from trees less Than 1 m in height planted near their parents. (controls)						Fruits from trees of a 12 m height planted near trees less than 1 m in height (treatments)						Fruits from trees less than 1 m in height planted under trees of 12 m in height (treatments)						Fruits from trees of a 12 m height planted under their parents. (controls)					
	N	AX	S	G.R.	S	S.V.	N	AX	S	G.R.	S	S.V.	N	AX	S	G.R.	S	S.V.	N	AX	S	G.R.	S	S.V.
2	18	4.7	1.1	-	-	100.0	17	4.4	0.7	-	-	100	43	10.8	2.6	-	-	100	24	7.7	2.6	-	-	100
4	17	7.2	2.0	33.1	15.8	43.5	17.0	6.0	1.4	25.1	12.6	100	40	13.3	2.1	18.1	10.2	93.2	19	11.6	3.8	24.7	12.7	79.2
8	15	8.1	2.2	12.2	10.3	83.3	17.0	7.1	2.0	15.1	11.0	100	39	14.2	2.2	2.5	10.2	90.2	19	12.6	4.0	7.8	7.6	79.2
12	11	8.7	2.2	3.5	6.3	61.1	14.0	7.1	1.9	2.1	5.8	82.3	39	14.4	2.2	1.7	3.2	90.2	19	13.2	4.5	4.0	5.2	79.2
16	11	9.1	2.2	2.8	5.1	61.1	13.0	7.5	2.4	3.8	6.0	76.4	36	14.4	2.4	0.5	1.7	83.2	19	13.3	4.4	1.0	3.1	79.2
20	9	9.8	2.0	2.9	4.6	50.0	12.0	8.2	2.3	7.0	7.8	70.6	34	14.7	2.2	0.8	2.7	79.7	16	13.9	4.5	1.0	2.9	66.7
24	9	9.9	2.0	0.0	0.0	50.0	10.0	8.1	1.9	6.2	9.0	58.8	28	15.1	2.5	0.2	1.0	65.2	13	14.1	5.2	0.3	1.0	54.2
28	6	9.8	1.5	0.0	0.0	33.2	6.0	8.2	1.3	0.0	0.0	35.3	25	15.1	2.6	0.0	0.0	58.0	12	14.3	5.4	0.0	0.0	50.0
32	4	10.5	0.6	0.0	0.0	16.7	4.0	8.8	1.0	0.0	0.0	23.5	24	15.1	2.5	0.0	0.0	55.8	11	14.2	5.5	0.0	0.0	45.8
36	4	10.5	0.6	0.0	0.0	16.7	3.0	9.0	1.0	0.0	0.0	17.6	24	15.2	2.5	0.0	0.0	55.2	7	13.7	4.7	0.0	0.0	29.2
40	2	11.0	5.7	0.0	0.0	16.7	3.0	9.0	1.4	0.0	0.0	17.6	24	15.2	2.5	0.0	0.0	55.2	7	13.7	4.7	0.0	0.0	29.2
44	2	11.0	0.0	0.0	0.0	1.1	2.0	9.0	1.4	0.0	0.0	11.8	23	15.3	2.3	0.0	0.0	53.2	7	13.7	4.7	0.0	0.0	29.2
48	2	11.0	0.0	0.0	0.0	11.1	1.0	11.0	0.0	0.0	0.0	5.9	22	15.6	2.4	0.0	0.0	51.2	7	13.7	4.7	0.0	0.0	29.2
52	0	-	-	-	-	-	1.0	11.0	0.0	0.0	0.0	5.9	22	15.6	2.4	0.0	0.0	51.2	7	13.7	4.7	0.0	0.0	29.2
56							1.0	11.0	0.0	0.0	0.0	5.9	21	15.4	2.3	0.0	0.0	48.7	6	14.3	4.8	0.0	0.0	25.0
60							1.0	11.0	0.0	0.0	0.0	5.9	21	15.4	2.3	0.0	0.0	48.7	4	16.3	4.8	0.0	0.0	16.7
64							0.0	-	-	-	-	21	15.4	2.3	0.0	0.0	0.0	48.7	4	16.3	4.8	0.0	0.0	16.7
68												21	15.4	2.3	0.0	0.0	0.0	48.7	3	19.2	3.9	0.0	0.0	12.5
72												19	15.2	2.1	0.0	0.0	0.0	44.5	3	14.2	3.5	0.0	0.0	12.5
76												17	15.4	2.1	0.0	0.0	0.0	44.5	3	14.2	3.5	0.0	0.0	12.5
77												17	15.4	2.1	0.0	0.0	0.0	44.5	3	14.2	3.5	0.0	0.0	12.5

tion to the height of the plants, but in all plants the general tendency is that smaller trees allocate a larger proportion of the total biomass to roots and leaves, and taller plants allocate a larger proportion to branches (Fig. 3).

Spearman's Rho rank correlations values were greater for roots vs branches (r: 0.91 ; p < .001); roots vs leaves (r: 0.83; p < .001); roots vs plant width (r: 0.78 ; p < .001). For roots vs height, Rho was smaller (r: 0.52 ; p > .001 < .005). According to this, branches, leaves and plant width are the most important factors that control biomass allocation to roots.

**Leaf life-span:** There were no significant differences in growth rate of leaves for the three size classes of trees (Table, 4; Fig. 4). Leaves from the taller trees were larger (p < .001) than leaves from dwarf and medium size trees (Table, 4). Leafs from dwarf and medium size trees show very similar survivorship curves,

that fit fairly well Pearl's type I survivorship curve and had a longer life-span. On the contrary, leaves from taller trees had shorter life-span than leaves from dwarf and medium size trees (p < .01) and fit better type II curve (Table, 4; Fig. 5).

DISCUSSION

Plant form is primarily oriented towards the optimal acquisition of those resources that guarantee their survival and success; such as light, water, nutrients, or pollinators and dispersors, (Waller 1986).

The dwarf habit of *A. germinans*, is characterized by wide crowns, wide angles of branching, a larger proportion of biomass in roots and leaves, earlier and more profuse branching and longer leaf life-span; in plants growing in open and high salinity areas could be interpreted as being adaptive or a stress response (Polja-

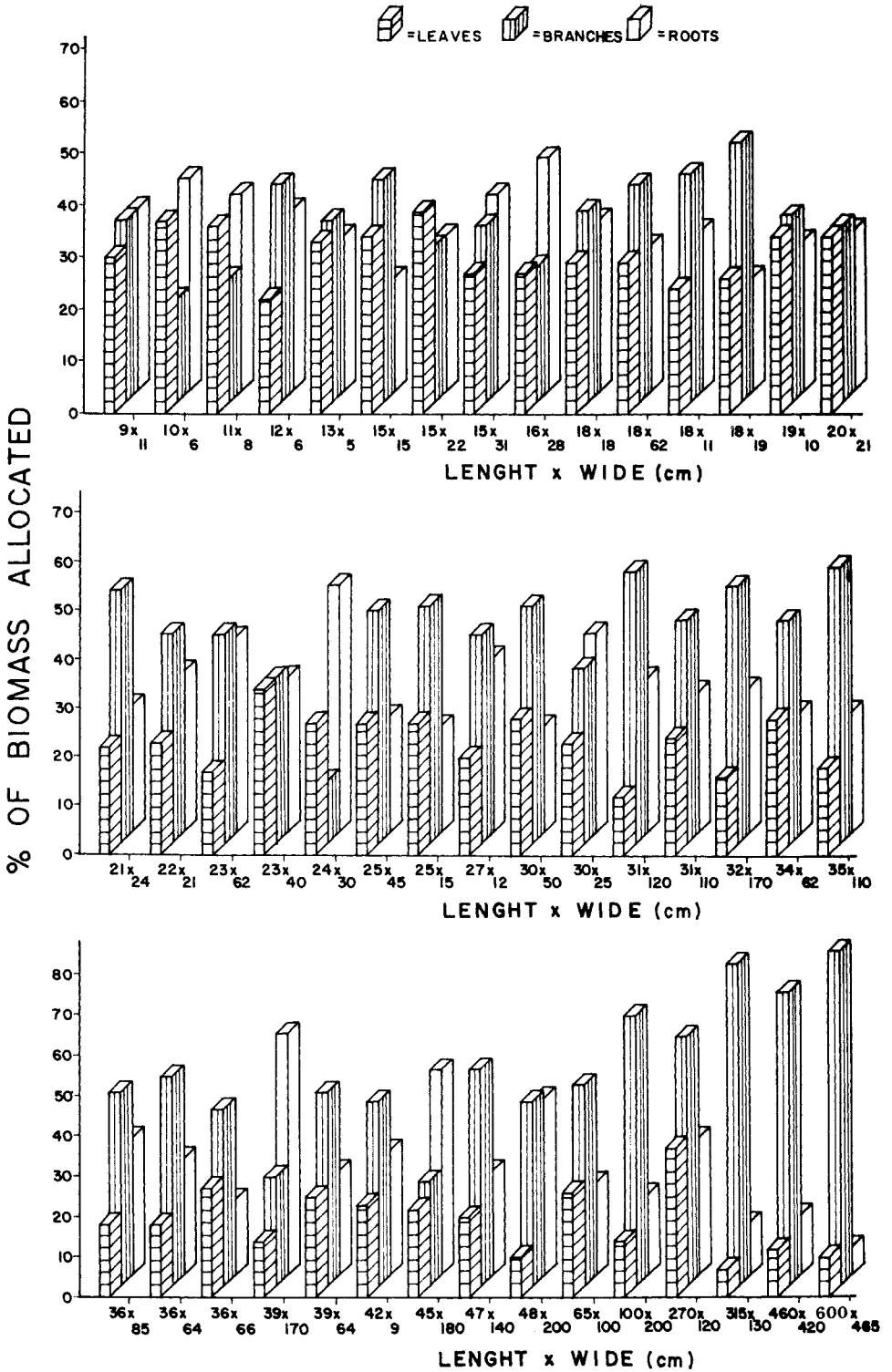


Fig. 3. Biomass allocation to leaves, branchers and roots in trees of *Avicennia germinans* of different heights growing along a salinity gradient.



TABLE 4

Size, growth rate and survivorship of leaves of *Avicennia germinans* (L.) L.  
The trees grow along a salinity gradient. Salinas, Puntarenas, Costa Rica.

(N: number of samples; S.V.: survivorship; A.S.: average size (mm); S: standard deviation; G.R.: growth rate)

Weeks	Tree height 1 m					Tree height 1-2.5 m					Tree height 5-7 m								
	N	S.V.	A.S.	S	G.R.	N	S.V.	A.S.	S	G.R.	N	S.V.	A.S.	S	G.R.	S			
0	30	100	6.4	3.0	-	30	100	7.1	2.2		30	100	6.9	3.4					
2	30	100	12.5	3.5	49.3	15.4	30	100	13.9	5.4	48.3	15.8	26	86.7	17.4	9.0	63.9	20.7	
4	29	100	27.7	9.5	54.8	15.0	26	86.7	32.5	7.8	52.4	13.9	23	80.0	52.2	19.5	59.2	18.1	
8	29	95.8	52.0	9.9	42.4	11.5	26	86.7	49.5	13.9	34.3	11.5	7	56.7	81.8	29.0	38.2	16.8	
12	29	95.8	55.6	10.0	-6.0	5.7	26	86.7	51.5	14.0	5.2	7.2	10	33.3	83.1	26.1	0.9	16.1	
16	28	95.8	57.0	10.0	-2.6	2.9	25	83.3	51.9	13.4	0.9	3.2	7	23.3	98.9	15.6	1.4	3.3	
20	22	91.7	57.0	10.2	0.0	0.0	25	83.3	51.8	13.0	-0.2	2.5	7	23.3	102.4	15.9	3.2	7.4	
24	22	87.5	54.4	10.0	0.0	0.0	25	83.3	51.6	13.0	-0.6	2.9	7	23.3	104.4	15.9	0.5	1.4	
28	22	87.5	54.4	10.0	0.0	0.0	25	83.3	51.3	13.2	-0.4	1.8	6	23.3	98.3	13.8	-2.5	3.6	
32	22	87.5	54.4	10.0	0.0	0.0	25	83.3	51.3	13.2	0.0	0.0	5	16.6	102.4	13.4	0.0	0.0	
36	19	63.3	53.7	10.5	0.0	0.0	20	66.6	49.0	13.4	0.0	0.0	5	16.6	102.4	13.4	0.0	0.0	
40	18	60.0	53.5	10.7	0.0	0.0	13	43.3	42.3	13.8	0.0	0.0	2	6.6	113.5	12.0	0.0	0.0	
44	6	20.0	54.3	9.6	0.0	0.0	6	20.0	48.6	11.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	
48	2	3.3	57.0	0.0	0.0	0.0	2	0.0	0.0	0.0	0.0	0.0							
52	0	0.0	0.0	0.0	0.0	0.0													

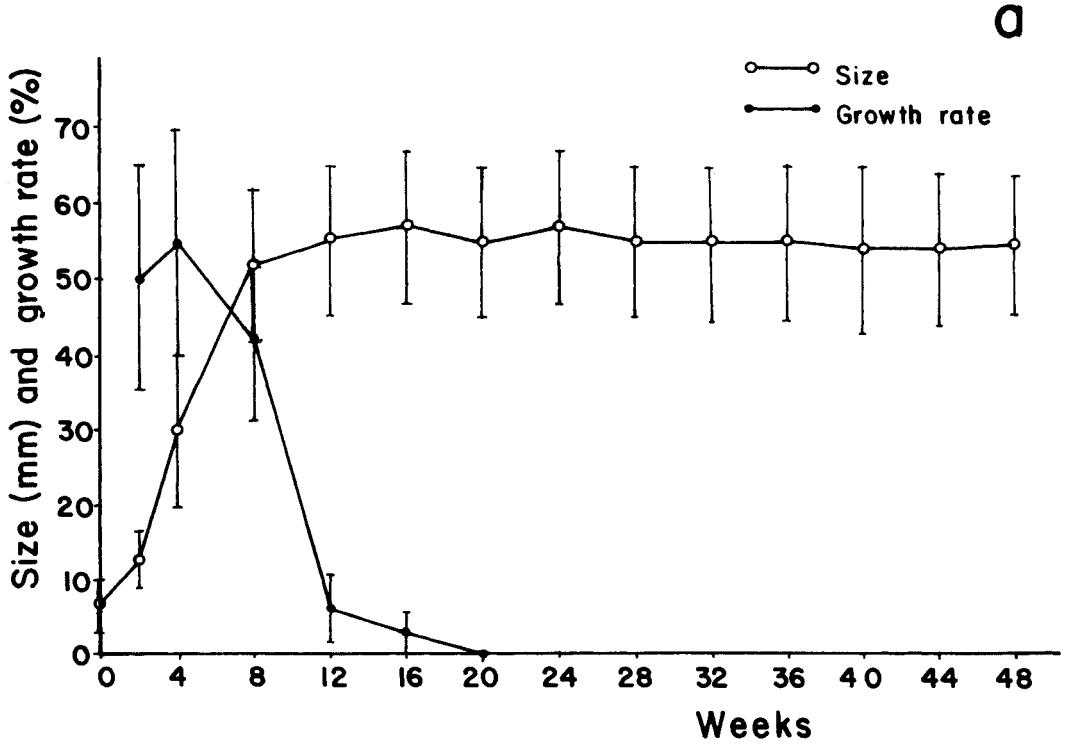


Fig. 4. Size and growth rate of leaves of *Avicennia germinans* for trees growing along a salinity gradient. a: Trees below 1 m in height.

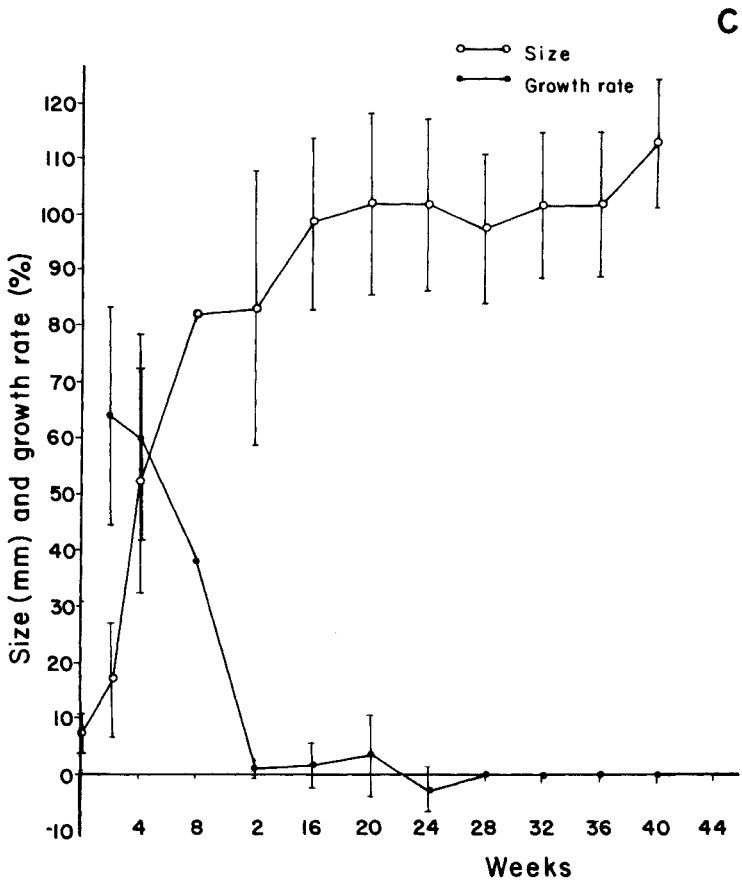
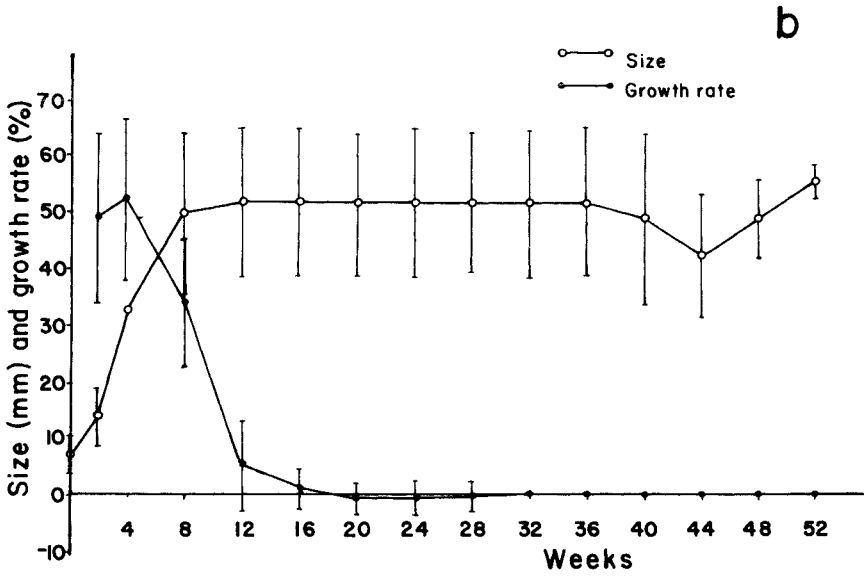


Fig. 4. Size and growth rate of leaves of *Avicennia germinans* for trees growing along a salinity gradient, b: Trees between 1 and 2.5m., c: Trees between 5 and 7m.

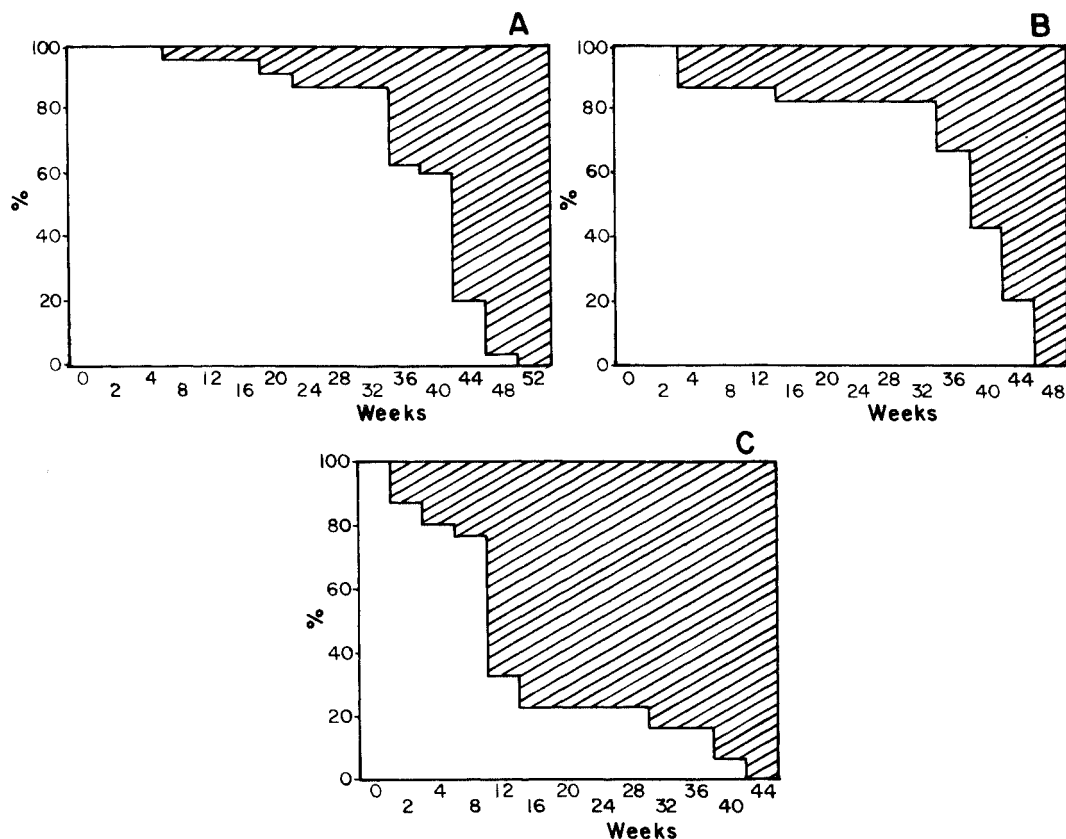


Fig. 5. Survivorship of leaves of *Avicennia germinans* from trees growing along a salinity gradient. A: trees below 1 m in height, B: trees between 1 and 2.5 m; C: trees between 5 and 7 m.

koff-Mayber 1975) to high salinity, low water potentials and high light intensity.

To obtain water (and nutrients), from high osmotic soil solutions; halophytes have to adjust the osmotic pressure in their tissues (Bernstein 1961; Stewart and Lee 1974, Starey Wyn-Jones 1975), by relocating high soluble organic compounds such as proline, glycine betaine, quaternary ammonium compound, sorbitol and reducing sugars (Cavaliere and Huang 1981, Jefferies 1977). This reduces the amount of nitrogen available for growth and reproduction.

The effect of salinity as a factor that reduces growth rate and size in salt marsh species has been documented widely in the field, and in the laboratory (Hyder & Greenway 1965, Linthurst and Seneca 1981, Parrondo, Gosselink and Hopkinsom 1978, Smart and Barko 1978). This effect has also been documented for mangrove communities (Cintron *et al.* 1978, Jiménez and

Soto 1985, Soto and Jiménez 1982, Soto and Corrales 1986).

The location of divergent branches from the central axis in a low and horizontal position reduces the effort of the plant to rise the water from the soil. That these low osmotic potentials impose a limit on the height a plant can reach in a high salinity environment, is supported by the observation that many dwarf individuals produce higher and more vertically oriented branches during the rainy season (the active growth period), that die during the dry months, one or two years later. If the branches persist, they carry a lower cover of leaves. Contrastingly, trees in dense and shaded stands grow taller, start branching when approaching the canopy, have narrower crowns in relation to the height and angles of branching are narrower; an strategy oriented specially to "compete" for light (Givnish 1982). Table. 2.

There are differences in the height of branching along the trunk and the angles of branching, among tropical humid and dry forest trees (specially savannas). This has been associated with light intensity (Halle, Oldeman and Tomilson 1978, Richards 1976).

These differences in branching pattern seem to have an environmental and genetic component. Seedlings from dwarf parents growing in the open area with high soil salinity, produced an earlier and more profuse branching pattern than seedlings from dwarf parents in shaded areas (an environmental difference). Seedlings from tall trees growing in both areas either show very low percentage of branching or none (a genetic difference). (Table 2). The fact that seedlings from dwarf parents in shaded conditions present a low rate of branching suggests that, even when there is a genetical difference in the dwarf plants, this has to be triggered by the environment, possibly by a combination of both high salinity and high light intensity.

*Spartina alterniflora* presents latitudinal genetic differences (Anderson & Treshow 1980). Sharrock (1976) has shown that the differences in leaf morphology in two varieties of *Alimione portulacoides*, a salt marsh plant, has a genetical basis. Stalter and Batson (1969) concluded that dwarf and tall forms of *S. alterniflora* were ecotypes, but later researchers (Mooring, Cooper and Seneca 1971, Shea Warren and Niering 1975) concluded that they were genetically similar.

To precisely determine genetical differences between the dwarf and tall plants of *A. germinans*, more research at the physiological and biochemical level will be necessary.

Despite the uniformity of their appearance and design, the subunits of which the plant is constructed are not always on an equal footing with one another. There is a clear need for the plant to organize growth in such a way that plant partes do not interfere with one another later in life, and to ensure a balance between leaves, supporting shoots and roots (Waller 1986). This close relationship between compartments is evident in trees of *A. germinans* of different sizes growing under different conditions (Fig. 3) Dwarf trees allocate a larger proportion of biomass to roots and leaves. Taller trees allocate more biomass to branches (Fig. 3).

In low light intensity plants can respond to shading with two strategies: 1: allocate more

biomass to grow taller and avoid shading or, 2: allocate more biomass to leaves to intercept more light (Abrahamson and Gadgil 1973). Tall plants of *A. germinans* in dense stands fit these predictions. They allocate a larger proportion of the total biomass to branches as a response to high growth. Leaves are also larger in taller trees (Table 4; Fig. 4). Herbs respond to dense cover increasing their height and the biomass allocated to branches to compete for light (Givnish 1982).

The accumulation of a larger proportion of dead biomass in relation to live tissue in larger trees could also contribute to explain the low percentage of the total biomass in leaves and roots in larger plants (Halle-Oldeman and Tomilson 1978, Schlesinger and Gill 1980) Fig. 3.

Leaves roots and branches are integrated in the sense that they depend on one another via the phloem and xylem (Waller 1986) thus the plant has to keep the proportion of the biomass allocated to the different compartments in equilibrium to cope with the environment. Deviations from this equilibrium must be more harmful for plants growing in harsh conditions.

The postfire response of individual shoots of the shrub *Rhus glabra* included significant reductions in height, and production of woody, leaf and reproductive tissue, when compared to unburned shoots (Knaps 1986)

The allocation of a higher proportion of biomass to roots in dwarf and wide crown plants (Fig. 3) "makes sense", specially in soils with low nutrient concentration and low omotic potentials. A larger leaf area demands more water and nutrients for evapotranspiration and photosynthesis. Results in other plants support this point of view.  $C_3$  plants (*Hordeum vulgare* and *Avena sativa*) and  $C_4$  plants (*Panicum miliaceum* and *P. crus-galli*) growing in low nitrogen fertilization levels, had shoot: root ratios shifted in favour of an increasing root proportion (Gebauer *et al.* 1987). *Typha latifolia* also allocates a larger proportion of biomass to roots in low nutrient conditions (Grace and Wetzal 1981). In *Lolium perenne* and *Trifolium repens* Davidson (1969) found that the growth of roots relative to foliage growth is increased by deficiencies in available moisture, nitrogen and phosphorus in the soil.

The dwarf habit could also be adaptive in thermoregulation. Plants in open and high light intensity areas, can control their temperature via evapotranspiration, a process that demands

water, or via modifications of the general morphology of the individual and their parts (Parthurst and Loucks 1972, Vogel 1968).

The rate of heat transfer to the environment from citrus trees, was greater for smaller than for taller trees (Turrell and Austin 1975). Round leaves lose heat via connection more efficient than elongated leaves (Vogel 1968). Leaves of *A. germinans* from dry and high salinity areas were smaller and roundish than leaves from tall trees and humid areas (Soto and Corrales 1986).

Leaf life-span is another component of the general strategy of dwarf plants to cope with the harsh environment where they live. Leaves from dwarf plants are smaller and live longer (Table 4; Fig. 4 and 5). Since photosynthesis is limited by high salinity (Hall and Flowers 1973; Longstreth and Novel 1979, Smart 1982) and low nutrient concentration (Al-Mufti *et al* 1977, Chabot and Hicks 1982, Chapin, Johnson and McKendrick 1980), extended leaf longevity is required to pay back the investment in leaves in less productive conditions (Chabot and Hicks 1982, Kibuzawa 1984).

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