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Effects of Burial by Sand on Seedling Growth and Survival in Six Tropical Sand Dune Species from the Gulf of Mexico

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ABSTRACT

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In this study, plants of six species (*Chamaecrista chamaecristoides, Palafoxia lindenii, Trachypogon gouini, Canavalia rosea, Ipomoea pes-caprae* and *Schizachyrium scoparium*) which grow in the sand dunes of the Gulf of Mexico were experimentally buried with sand at different depths. For all species, burial increased plant vigour in terms of biomass and leaf area. In general, buried plants allocated more biomass towards the aerial parts (except in *T. gouini*, in which the reverse was true). The tested species exhibited good tolerance to sand burial. Their germination occurred during the period when sand movement was at its lowest. Growth form of species affected their ability to withstand burial. For example, shrubby species were the most tolerant ones and herbaceous plants the least. Such tolerance to burial seems to be related to local distribution of species in the dune system.

ADDITIONAL INDEX WORDS: *Coastal dunes, burial, coastal plants, biomass, disturbance, seedling, growth, Mexico.*

INTRODUCTION

Plants growing on sandy shorelines along lakes and oceans are subject to a variety of environmental fluctuations that affect their growth and survival. Among the more important factors mentioned in the literature are moisture, sand deposition, sand erosion, changes in organic matter, pH and intensity of rabbit grazing (AYYAD, 1973; CRAWFORD and WISHART, 1966; ELDRED and MAUN, 1982; HARRIS and DAVY, 1986, 1987; HOBBS and GRACE, 1981; MORENO-CASASOLA, 1986; RANWELL, 1960, 1972). Of these, the burial of propagules and seeds has been detected as one of the most significant factors in survival and establishment (MAUN and RIACH, 1981; MORENO-CASASOLA, 1986; HARRIS and DAVY, 1987; SYKES and WILSON, 1990; CLARK, 1986; BARKER, HERLOCKER and YOUNG, 1989; MAUN and LAPIERRE, 1986; MARTINEZ and MORENO-CASASOLA, 1993). However, few species survive sand accretion and even fewer have been examined experimentally (EHRENFELD, 1990). The ability to survive burial is a problem to most sand dune species, and the germination and/or seedling responses have been studied mostly for temperate species (SYKES and WILSON, 1990; MAUN, 1989; HARRIS and DAVY, 1986; MAUN and LAPIERRE, 1986; MAUN and RIACH 1981; SELISKAR, 1990; RANWELL, 1958 and DISRAELI, 1984). Among these, grasses like *Ammophila arenaria, A. breviligulata* and *Calamovilfa longifolia* and forbs like *Solidago sempevirens* have been the most studied species (EHRENFELD, 1990). The responses of tropical sand dune species (from different families and with a wider variety of growth forms) to sand accretion have received less attention, except for the work done by MARTINEZ, VALVERDE and MORENO- CASASOLA, (1992), and in this case, only germination of buried seeds was studied.

Responses of sand dune plants to burial vary greatly. In some cases, plant growth is stimulated by sand burial (DISRAELI, 1984; SYKES and WILSON, 1990; MAUN and LAPIERRE, 1984; MAUN, 1985; BAYE, 1990; YUAN, MAUN and HOPKINS 1993; and ZHANG and MAUN, 1992). This enhancement in growth depends on the species and the depth and

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Table 1. *Species characteristics, local and geographic distribution and fruiting and germination periods observed at the study site.*

Species	Family	Growth Form	Habitat	Distribution	Fruiting period	Presence of Seedlings in the Dunes
Chamaecrista chamaecristoides (Collad) I. & B.	Leguminosae	Shrub, 60 cm high, with a maximum cover of 2 × 2 m	Arms and crests. Sometimes on the beach	Endemic of the coasts of Mexico	After the rainy season (Sept.–Oct.)	All year long, with a peak at the beginning of the rainy season, in June and July.
Palafoxia lindenii Gray	Compositae	Shrub, 70 cm high, with a maximum cover of 2 × 2 m	Beach, arms and crests	Endemic of the Gulf of Mexico	All year long	All year long, abundant during the rainy season.
Schizachyrium scoparium Michx.	Gramineae	Tufted culms, 80 cm high, with a maximum cover of 2 × 2 m	Arms and crests (mobile & stable dunes)	Wide distribution in North America	During the winter storms (Nov.–Jan.)	End of the winter storms (Jan.–Feb.)
Trachypogon gouini Fourn. ex Hemsl.	Gramineae	Tufted culms, 80 cm high with a maximum cover of less than 1 × 1 m	Arms and crests (semi-mobile dunes)	Endemic of the central part of the Gulf of Mexico	At the end of the rainy season (Sept.–Oct.)	End of the winter storms (Jan.–Feb.)
Canavalia rosea (Sw.) DC.	Leguminosae	Creeping runner branches can be 15 m long	Beach and first foredune	Pantropical	During the dry season (April–May)	During the rainy season
Ipomoea pes-caprae (L.) Sweet	Convulvulaceae	Creeping runner branches can be 50 m long	Beach and embryo dunes	Pantropical	After the rainy season (Oct.–Nov.)	During the rainy season

Figure 1. Location of the study site.

duration of burial. Other species can withstand sand accretion (SYKES and WILSON, 1990) and are able to recover when complete burial is followed by restoration of the original sand surface (HARRIS and DAVY, 1986; 1987). However, a high rate of sand mobility inhibits the growth of any but highly specialized plant species (SALISBURY, 1952).

In this study, plants of six species (both endemic and pantropical) that grow in the dunes of the Gulf of Mexico, were experimentally buried at different depths. The six species studied (*Chamaecrista chamaecristoides* (Collad) I & B var. *chamaecristoides*; *Palafoxia lindenii* (Gray); *Trachypogon gouini* Fourn. ex Hemsl.; *Canavalia rosea* (Sw.) D.C.; *Ipomoea pes-caprae* (L.) Sweet. and *Schizachyrium scoparium* Michx. var. *littoralis* (Nash) Hitch are almost always found growing in places with regular sand movement (MORENO-CASASOLA, 1986). They are among the pioneer colonizers of mobile dunes and beaches (Table 1). The objectives of these experiments were to investigate the responses of these species to sand burial.

METHODS

Study Site

The study site is located at the Coastal Biology Station CICOLMA along the Gulf of Mexico (19°36′ N; 32°22′40″ W) (Fig.1). This dune system includes all stages of stabilization, from mobile to stabilized dunes. MORENO-CASASOLA (1982) observed that, at the study site, topography and plant cover greatly affect some of the environmental conditions. For instance, plant cover decreases sand movement (20 cm a year *vs.* 60 cm a year in bare sand) and temperature (2–4°C cooler under vegetation), while humidity is increased (3–4% higher under different plant species). On the other hand, sand transportation is strongest on crests, leeward and windward slopes (60–100 cm a year) than on the arms of the dunes (10–30

cm a year). The vegetation from sand dunes is strongly influenced by these conditions. For further details on the micro-environments and the plant associations, refer to MORENO-CASASOLA (1982); MORENO-CASASOLA *et al.*, (1982); and MORENO-CASASOLA (1986).

Mean annual precipitation at this station fluctuates between 1200 and 1500 mm. The rainy season occurs during summer months from June to September, when 81% of the total annual rainfall is received. From November to February, winter storms ("Nortes") are common. Usually, 15 to 25 "Nortes" occur during these months. Such winter storms are responsible for the movement of large quantities of sand (POOGIE, 1962; MORENO-CASASOLA, 1982). The mean annual temperature is 25°C (GARCIA, 1988); the lowest monthly mean occurs in January (21.6°C) and the highest in May (28.1°C).

Since the greenhouse walls are made of white plastic screen and it is located at the Biology Station where the studied species normally grow, we can say that the experimental setup resembles natural conditions in terms of light and temperature. Also, the sand used came from nearby dunes, and the amount of sand added can certainly occur in natural conditions (MORENO-CASASOLA, 1982). Thus, the results obtained in the greenhouse corresponded closely to the plant responses on the dunes.

Greenhouse Experiments

Seeds were obtained from at least ten fruiting individual plants located in the microhabitats of each species. Considerable effort was made to collect only ripe seeds, samples of both large and small inflorescences and, as far as possible, to include the full range of seed sizes. Seedlings used in these experiments came from mixed seed samples from a single seed collection.

Seeds were placed in trays filled with a layer of sand from the study site. Preliminary experiments revealed that seeds of *C. chamaecristoides*, *C. rosea* and *I. pes-caprae* required mechanical scarification before germination. Prior to germination in the trays, seed coats of these species were scarified with a knife. The trays were left in the greenhouse (25°C) until the seedlings had emerged. A week after germination, seedlings with a homogeneous initial size were selected and the largest and smallest individuals were discarded. Seedlings were then transplanted individually into 5 kg plastic bags filled with sand from the study site. The bags had holes at the bottom for drainage. We added 1 g of solid fertilizer, (containing N, P, K in equal proportions 30% each) so that growing conditions for plants would not be limiting. The surface of the sand was watered with tap water as it dried out, normally, every second or third day. The sand below the surface remained moist but not waterlogged throughout. The bags were placed randomly on three benches in a greenhouse, at the Biology Station. Mean temperature inside the greenhouse was 25°C. The general substrate and nutrient conditions were similar for all species.

Two weeks after planting (three weeks after germination), seedlings were buried with sand. Due to different growth forms (Table 1), burial treatments consisted of partial or complete burial of growth meristems of all species except grasses and were not related to the size of the plant. Treatments consisted of the following burial depths: 0% (control—no sand was added), 50% (one half of the meristems was covered) and 100% (all the meristems, including the apical meristem, were buried). In the case of grasses, the leaves were considered as the reference points for burial. Thus, for the 50% treatment, the lower half of the leaves was covered and for the 100% all but the tip of the last leaf (1 cm long) were covered (Fig. 2). In all buried plants there was some green tissue (one half of the upper leaves) left above the sand surface. Two weeks later the plants were subjected to a second burial, following the procedure outlined above. In each case, dry sand was poured carefully around the stem of the plant in order to avoid bending the shoots. Also, the plants were held gently upwards as the sand was filled in around them. There were a total of 15 replicates per treatment.

Initial dry weight and leaf area were obtained after the second burial treatment (five weeks after germination) when five replicates per treatment were harvested. Thereafter, three more harvests were taken at 6 weeks intervals, with a total of four harvests for each species and each treatment. In each harvest, 5 replicates per species, per treatment, were used. Harvested individuals were chosen randomly. Plants were carefully removed from the pots, and sand washed from the roots. Leaf area was measured with a Delta-T leaf area meter and then plants were divided into roots, stem and leaves, dried at 70°C for 48 hrs and weighed.

Since *Ipomoea pes-caprae* seedlings grew very slowly at the beginning of the experiment, they

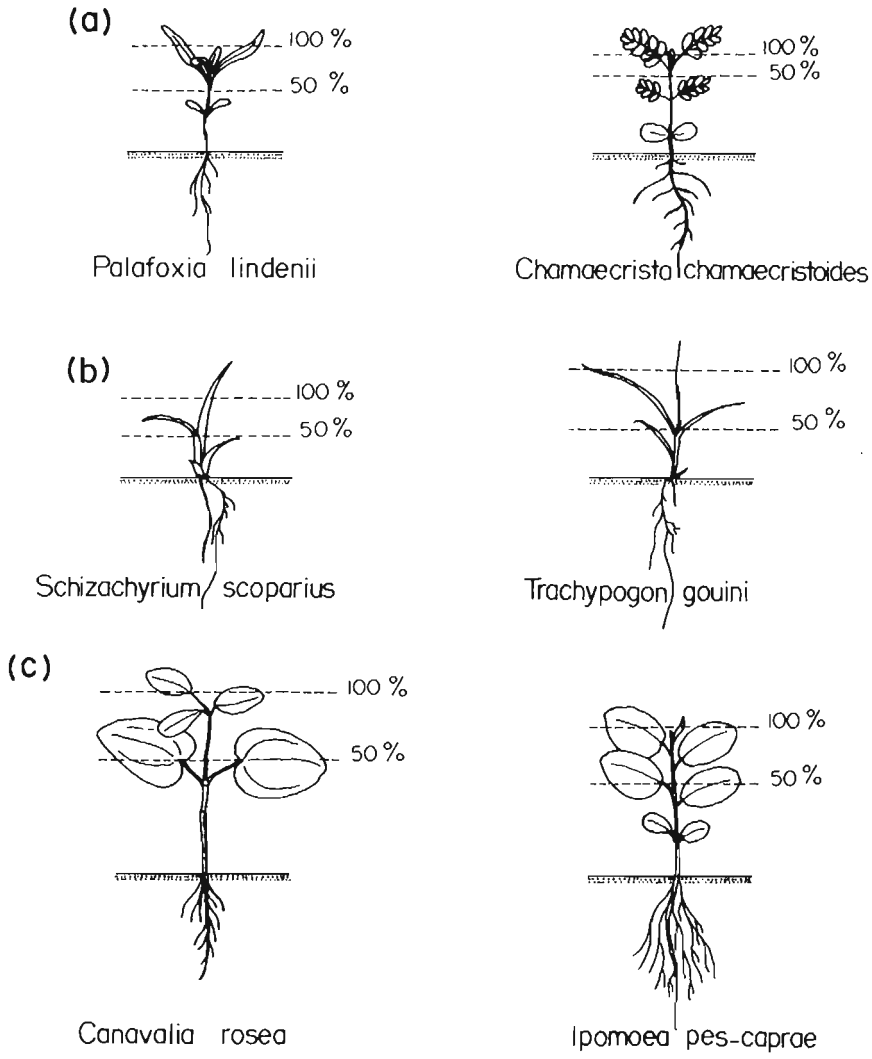

Figure 2. Diagram showing 50 and 100% burial treatments in seedlings of shrubs (a), grasses (b) and creepers (c).

were allowed to grow for 3 more weeks before the first burial. This explains the differences in time after germination presented in the results for this species.

Relative growth rate in plant biomass was determined according to the equation: RGR = (ln W_j − ln W_i)/(T_j − T_i) (j>i) (HUNT, 1982). Data were analyzed using an analysis of variance (ANOVA) followed by Tukey tests if ANOVA showed significant results (ZAR, 1984). Differences between treatments were analyzed for each harvest and each species.

RESULTS

Biomass

After burial with sand, biomass accumulation increased significantly in all species (Fig. 3). However, variability among individuals of *I. pes-caprae* was high and, thus, no significant differences were detected between control and the burial treatments. In *C. chamaecristoides* total dry weight increased significantly only when all the meristems were covered. In contrast, *T. gouini* accumulated a larger biomass at 50% than 100%

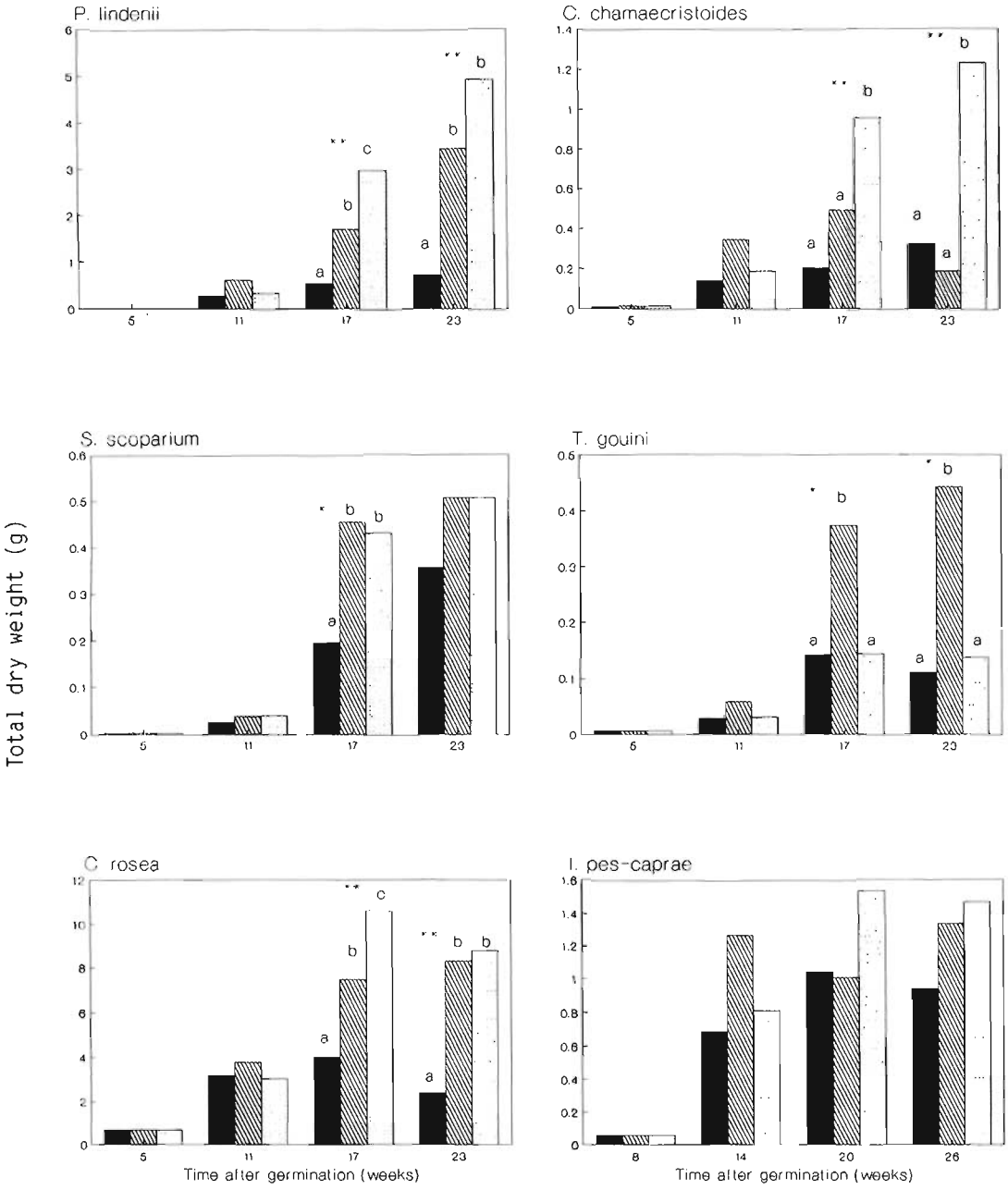

Figure 3. Total dry weight at four harvesting intervals in six tropical sand dune species exposed to different burial conditions. Different letters indicate significant differences (Tukey) (* $p < 0.05$, ** $p < 0.005$) between treatments within each harvest. ■ control; ▨ 50% of the growth meristems were covered; □ 100% of the growth meristems were covered with sand.

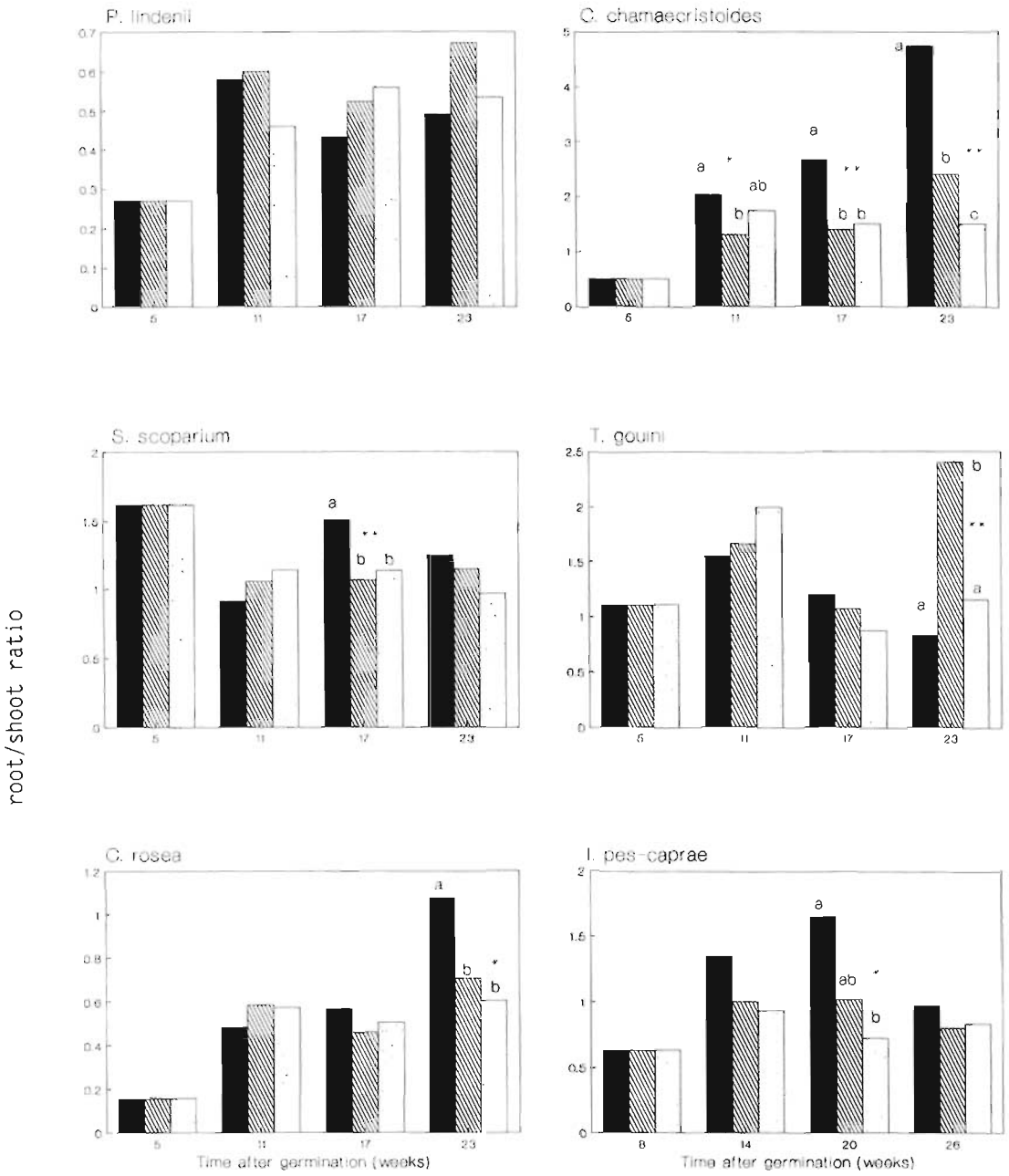

Figure 4. Root/Shoot ratio (R/S) of plants in the four harvests. Different letters indicate significant differences (Tukey) (* $p < 0.05$, ** $p < 0.005$) between treatments at each harvesting time. ■ control; ▨ 50% of the growth meristems were covered; □ 100% of the growth meristems were covered with sand.

burial of meristems. A greater amount of sand around the plants was inhibitory for this species. *P. lindenii, S. scoparium* and *C. rosea* increased their biomass in both burial treatments. However, the more the sand accumulation around them, the greater was the increase in biomass. The treated plants produced a larger biomass than the control, but at the end of the experiment, the differences between them gradually decreased.

Root-Shoot Ratio

Root-shoot ratio (R/S) decreased in *C. chamaecristoides, S. scoparium, C. rosea* and *I. pes-caprae,* increased in *T. gouini* and was not affected in *P. lindenii* (Figure 4). In the first four species as more sand accumulated around the plants, more biomass was allocated to the shoots, decreasing the root/shoot ratio. *C. chamaecristoides* showed this pattern in all the treatments and harvests; however, root/shoot ratio decreased significantly in only one of the harvests in *S. scoparium, C. rosea* and *I. pes-caprae.* These three species showed a pattern of decreasing the root/shoot ratio whith more sand accretion.

Following the same pattern as in biomass, root-shoot ratio of *T. gouini* was only affected when 50% of the leaves were buried. This was the only species in which root-shoot ratio increased with burial. Root-Shoot ratio did not change significantly in *P. lindenii.* This species was different from the rest in the sense that its root/shoot values were always less than 1, indicating that there was greater biomass allocated to shoots than to roots. In spite of the changes which occurred due to burial, all other species showed root/shoot ratios greater than one. This indicates that there was a larger biomass allocated to roots than to shoots. No adventitious roots were produced on the buried parts, except for two plants of *P. lindenii.*

Relative Growth Rate (RGR)

Relative Growth Rate increased significantly with burial in only three species (*P. lindenii, C. chamaecristoides* and *C. rosea*) (Table 2). Even in this case, only one harvest (the second one) gave significant differences. Growth rate in the rest of the species and harvests did not differ from the control lots.

Leaf Area and Specific Leaf Area

After burial, leaf area increased in all the species (Figure 5). The greater the sand accumulation around the plants, the greater was the leaf area per plant. *T. gouini* only showed a significant increase in leaf area when 50% of the leaves were buried. Buried leaves died and rotted before the first harvest, and hence, were not considered in the results.

Similar to leaf area, specific leaf area increased with sand burial (Figure 6). In *S. scoparium* no significant differences were detected between treatments, while *P. lindenii* and *C. rosea* significantly increased their specific leaf areas only in one harvest. The remaining three species (*C. chamaecristoides, T. gouini* and *I. pes-caprae*) showed differences in two harvests, always increasing their specific leaf area when more sand was added.

DISCUSSION

All the species studied were able to withstand sand burial. These results are similar to those obtained for temperate dune species (DISRAELI, 1984; MARSHALL, 1965; ELDRED and MAUN, 1982; MAUN and LAPIERRE, 1984; SYKES and WILSON, 1990) in which burial by sand also increased plant vigour. However, not all sand dune species can tolerate or are stimulated by sand accumulation. Usually, full burial may kill the plant (SYKES and WILSON, 1990; HARRIS and DAVY, 1987). In our case, we have no information concerning the responses of our species to full burial, and we do not know if they would be able to withstand larger amounts of sand covering them.

The ability to stay alive and emerge in mobile dunes is important. Our species responded positively to sand accretion, by increasing their leaf area and total biomass. Increased growth in dune plants following burial in sand has been documented for several species (MARSHALL, 1965; ELDRED and MAUN, 1982; ZHANG and MAUN, 1990, 1992; SYKES and WILSON, 1990; HARRIS and DAVY, 1987). However, it is not clear how accretion stimulates growth in plants from these environments. Many hypotheses have been suggested to explain this response of sand dunes plants, but there are few studies in which the explanations are based on experimental evidence. It has been said that changes in soil temperature; increased space for root development; higher nutrient and moisture availability (OLSON, 1958; MARSHALL, 1965; WILLIS *et al.,* 1959); a response to darkness (SYKES and WILSON, 1990) and interactions with endomycorrhizae (RALPH, 1978) are factors that play

Table 2. *Relative growth rate (g g^{-1} day^{-1}) in six species from tropical sand dunes, exposed to different burial conditions. One-way ANOVA tests showed that there are few significant differences among treatments in each harvest (done every 6 weeks). Different letters in each row indicate significant differences between treatments (Tukey * $p < 0.05$, ** $p < 0.005$).*

Species	Time (weeks)	Control	25%	75%	F
P. lindenii	5				
	11	0.090	0.107	0.093	1.92
		(0.01)	(0.01)	(0.01)	
	17	0.021 a	0.022 a	0.054 b	6.18*
		(0.01)	(0.01)	(0.008)	
	23	0.007	0.023	0.015	0.55
		(0.01)	(0.03)	(0.006)	
C. chamaecristoides	5				
	11	0.054	0.072	0.06	1.28
		(0.01)	(0.01)	(0.01)	
	17	0.009 a	0.012 a	0.033 b	7.19**
		(0.007)	(0.01)	(0.01)	
	23	0.006 a	−0.027 b	0.009 a	7.39**
		(0.02)	(0.006)	(0.02)	
S. scoparium	5				
	11	0.053	0.062	0.061	0.63
		(0.009)	(0.01)	(0.01)	
	17	0.045	0.053	0.058	0.65
		(0.01)	(0.01)	(0.01)	
	23	0.008	0.005	−0.003	0.26
		(0.03)	(0.01)	(0.01)	
T. gouini	5				
	11	0.035	0.043	0.033	0.59
		(0.005)	(0.01)	(0.01)	
	17	0.03	0.044	0.033	2.41
		(0.01)	(0.03)	(0.02)	
	23	−0.006	0.008	−0.022	0.84
		(0.04)	(0.03)	(0.02)	
C. rosea	5				
	11	0.035	0.039	0.033	0.86
		(0.01)	(0.006)	(0.004)	
	17	0.005 a	0.015 b	0.031 c	33.94**
		(0.004)	(0.008)	(0.005)	
	23	−0.014	0.003	−0.006	1.81
		(0.01)	(0.01)	(0.005)	
I. pes-caprae	8				
	14	0.053	0.067	0.059	1.40
		(0.01)	(0.01)	(0.007)	
	20	0.01	−0.004	0.01	1.74
		(0.01)	(0.02)	(0.005)	
	26	−0.009	0.01	−0.003	1.23
		(0.02)	(0.01)	(0.01)	

an important role in this response (ELDRED and MAUN, 1982). Endomycorrhizae enhance growth in *C. rosea, I. pes-caprae* (SALAS, 1994), *C. chamaecristoides* and *T. gouini* (Corkidi and Rincón, personal communication); whereas, long-term shaded conditions can negatively affect survival, biomass and leaf area (PEREZ-MAQUEO, 1992).

How does a plant deprived of light during the period of burial in sand put on more biomass than control? The 100% burial treatment had an increased leaf area, specific leaf area and decreased root/shoot ratio, relative to the controls. This means that the plants changed their morphology in relation to the new conditions and these changes probably enabled them to emerge after burial. Further, the extent of burial left some leaves above-ground which could produce photosynthates and provide energy to the growing point.

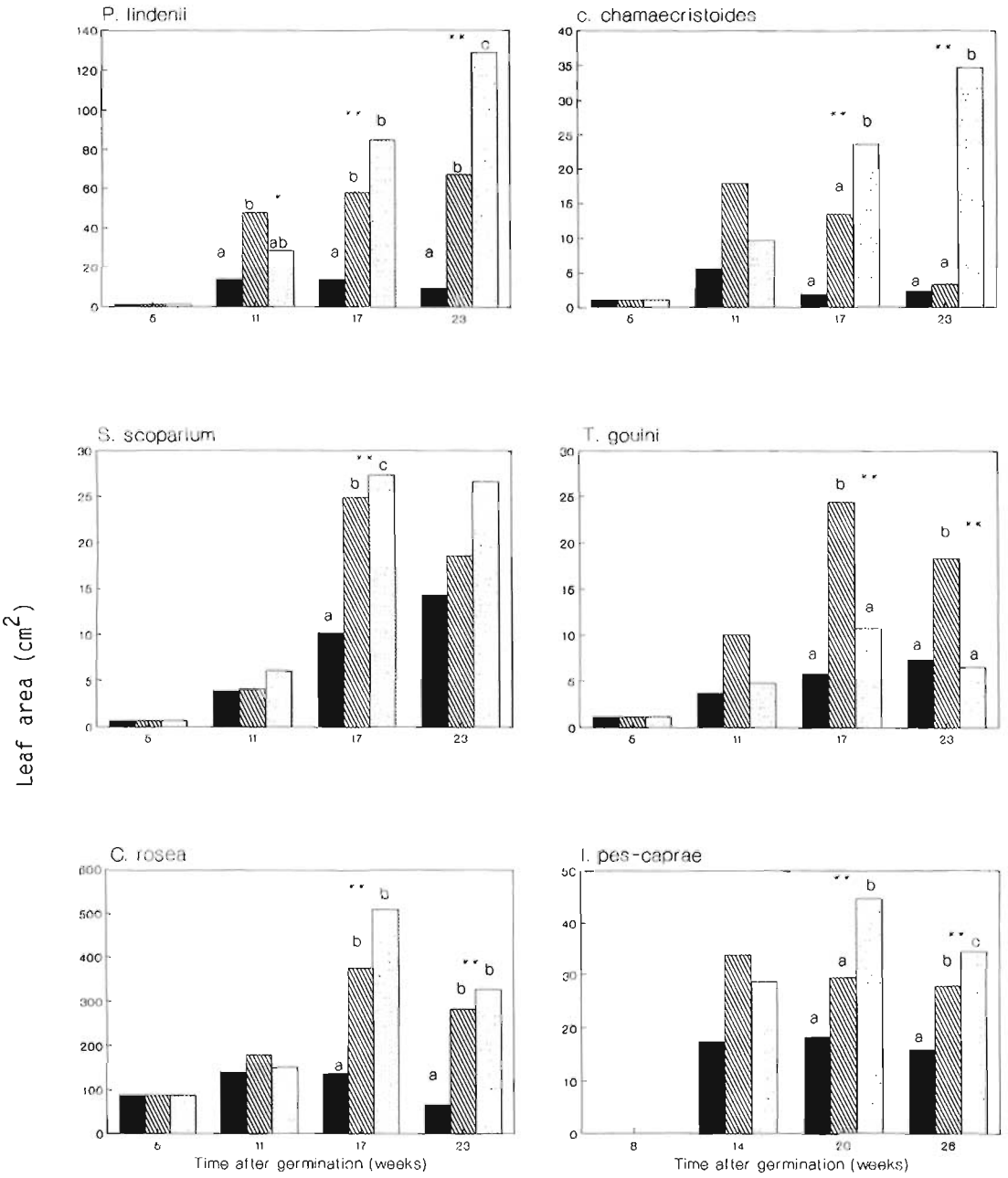

Figure 5. Leaf area in six tropical sand dunes species exposed to different burial conditions. Different letters indicate significant differences (Tukey) (* $p < 0.05$, ** $p < 0.005$) between treatments at each harvesting time. ■ control; ▨ 50% of the growth meristems were covered; □ 100% of the growth meristems were covered with sand.

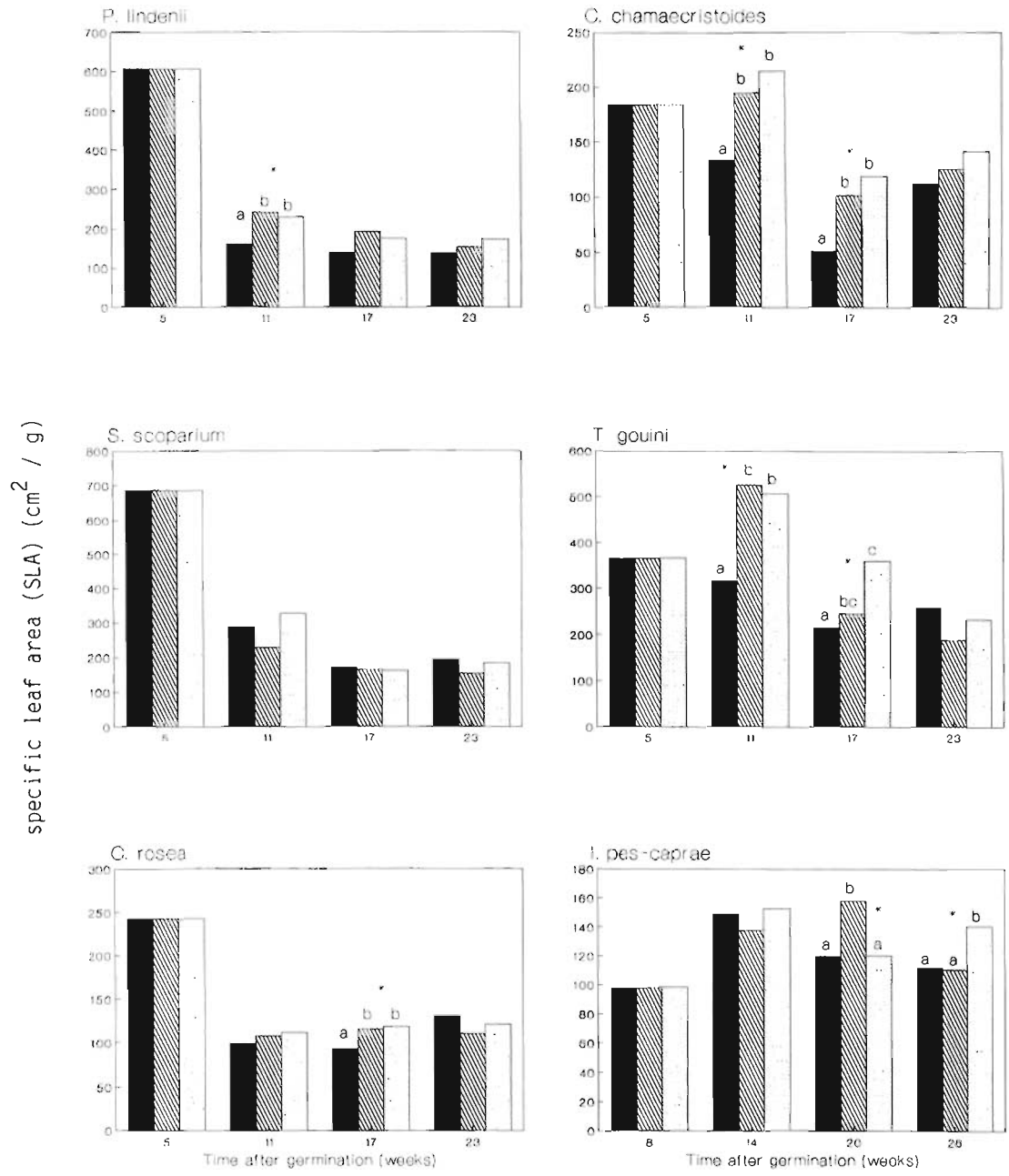

Figure 6. Specific Leaf Area in six tropical sand dunes species exposed to different burial conditions. Different letters indicate significant differences (Tukey) (* $p < 0.05$, ** $p < 0.005$) between treatments at each harvesting time. ■ control; ▨ 50% of the growth meristems were covered; □ 100% of the growth meristems were covered with sand.

YUAN, MAUN and HOPKINS (1993) have shown that buried plants from two grass species do exhibit higher photosynthetic rates. A similar response could happen in the studied species as well.

The decrease in root/shoot ratio observed in 5 species has been reported in many other dune species (SELISKAR, 1990; SYKES and WILSON, 1990; ELDRED and MAUN, 1982). Such a response enables the plants to sustain themselves above a rising sand surface. However, this response was not seen in all species. *T. gouini* was an exception and allocated a larger biomass towards the underground tissues. Probably, an increased space for root development stimulated its production.

Relative growth rate increased in only three species (*P. lindenii, C. chamaecristoides* and *C. rosea*) and only in the second harvest. In these species, the highest values were obtained in the 100% treatment. An increased RGR might be valuable when a seedling is emerging after burial.

Both root/shoot ratio and RGR values were quite inflexible in the six species studied. CHAPIN (1988) points out that plants from infertile soils (like those from sand dunes) show low maximum potential growth rate, and their root/shoot ratios are usually greater than 1. He suggests that there is lack of competition in low-fertility soils; that an individual plant with a low RGR is functioning closer to its physiological optimum, and these species have the possibility of luxury consumption. Hence, low and quite inflexible RGR values are common among these species.

Sand movement has been recognized by different authors as an important factor affecting the distribution and composition of coastal dune communities (VAN DER VALK, 1974; ELDRED and MAUN, 1982; ZHANG and MAUN, 1991; SYKES and WILSON, 1990; MORENO-CASASOLA, 1986; MAUN and LA-PIERRE, 1984), and the species studied seem to be adapted to this environmental factor. As shown in Table 1, seedlings of the six species germinate mainly during the rainy season. Thus, by the time the winter storms start, they have had time to grow and achieve a large enough size to tolerate sand movement (MARTINEZ and MORENO-CASASOLA, 1993). The distribution of these species in the dunes along the Gulf of Mexico (MORENO-CASASOLA, 1986) may be interpreted according to the differences in their tolerance limits to sand burial. Based on these results *C. chamaecristoides* should be more abundant on surfaces experiencing substantial sand deposition. According to the study by MORENO-CASASOLA (1986) it was, in fact, the case. Similarly, *P. lindenii* (which was also stimulated by sand accumulation) also inhabits mobile sites, with less sand movement. *T. gouini* grows predominantly in more stabilized sites such as arms and dune hollows, where there is less sand deposition and some increase in plant cover. The response of this grass to partial burial has also been observed in another grass from temperate sand dunes: *Ammophila breviligulata* (ELDRED and MAUN, 1982). *I. pes-caprae* and *C. rosea* grow on the beach, where there is less sand movement (due to wave action) than in the mobile parts of the dunes (PEREZ-MAQUEO unpublished). Their larger seeds (155.2 and 609.9 g per seed respectively) (PEREZ-MAQUEO, 1992) may also be important in the plants' ability to emerge after burial. HARRIS and DAVY (1987) suggest that for a positive growth response plants require large reserves that would provide energy for the growth of new shoots. Indeed, young seedlings of *C. rosea* and *I. pes-caprae* have such reserves which enable them to withstand sand burial. Finally, *S. scoparium* has a wide distribution in the dunes and also inhabits different types of habitats inland. This species is tolerant to a wide variety of conditions.

In conclusion, this study shows that the species studied are tolerant to sand burial, and their vigour is enhanced after plants are covered by sand. It is possible that the tolerance limits are higher than the burial treatments used in this experiment. Growth form affects species' ability to tolerate burial and thus, sand movement. Shrubs were the most tolerant ones, even though the species tolerant to sand burial reported in the literature are usually herbs or creepers.

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□ RESUMEN □

La mayoría de las plantas de dunas costeras se enfrentan al problema de tener que sobrevivir en condiciones de enterramiento. Existen numerosos estudios al respecto, sin embargo, las especies de zonas tropicales han recibido mucha menos atención que las templadas. En el presente trabajo, plántulas de seis especies de dunas costeras (*Chamaecrista chamaecristoides, Palafoxia lindenii, Trachypogon gouini, Canavalia rosea, Ipomoea pes-caprae* y *Schizachyrium scoparium*) que crecen en el Golfo de México, fueron cubiertas experimentalmente con arena, alcanzando diferentes profundidades. En todas las especies se detectó un incremento en el vigor de las plantas en términos de biomasa y área foliar. En general, las plantas enterradas asignan más biomasa hacia las partes aéreas, con la excepción de *T. gouini,* en la que ocurrió lo contrario. La forma de crecimiento afecta la capacidad de tolerar el enterramiento: las especies arbustivas fueron las más tolerantes, mientras que las herbáceas fueron las menos tolerantes. Parece ser que dicha tolerancia juega un papel importante en la distribución local de las especies dentro del sistema de dunas costeras.