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Influence of the subterranean rodent *Ctenomys australis* (Tuco-tuco) in a sand-dune grassland

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Abstract

Plant communities on sand dunes with and without burrows of the subterranean rodent *Ctenomys australis* (tuco-tuco) were studied to quantify this species participation on the landscape formation. Below- and above-ground plant biomass was estimated. Vegetation biomass, richness and diversity of patches with and without burrows (macrospatial scale) and vegetation associated to mound and intermound areas (microspatial scale) were compared. Total plant biomass was not different in areas with and without *C. australis*. Areas without tuco-tucos presented twofold numbers of different species and significantly higher species diversity than areas where animals were present. On the other hand, although plant biomass was higher in intermound areas neither species richness nor diversity values showed statistically significant differences. Results indicate that *C. australis* alters plant community composition and keeps succession on pioneer stages without altering total biomass. As an overall effect dune development is arrested and its stabilization is restrained.

Introduction

Effects of mound-building and feeding activities on plant community dynamics and soil nutrient status were evaluated for many species of subterranean rodents (SPENCER et al. 1985; GRANT and MCBRAYER 1981; INOUYE et al. 1987; SWIHART 1991). Disturbance related to burrowing can alter patterns of species richness and spatial and temporal aspects of plant succession (TILMAN 1983). Moreover, REICHMAN et al. (1993) presented evidence that fossorial herbivores generate distinct edge patterns in overlying plant communities, and suggested that these patterns may initiate competition-induced waves of plant biomass. Despite the worldwide ecological importance of tuco-tucos and their widespread occurrence in South America (REIG et al. 1990), only CONTRERAS (1973) emphasized the participation of *Ctenomys* sp. as an active agent modifying soil ecosystems. More recently, CONTRERAS and GUTIERREZ (1991) analysed the impact of *Spalacopus cyanus* within Neotropical ecosystems.

Ctenomys australis inhabits sand dune grasslands. As these coastal sandy environments are very vulnerable to eolic and hydric erosion, vegetation plays an important role in the process of building the dunes and stabilizing the sand. In the present study, plant community on sand dunes with and without burrows of *C. australis* is characterized with the aim of quantifying tuco-tucos participation on the landscape formation.

Table 1. Comparisons of dry biomass of vegetation in absolute values (g/m^2), species richness and diversity (H) in areas with and without burrows of *C. australis.* Data are shown as X ± SE with percentage of total biomass in parenthesis (%). Percentage values lower than 1% are not given. *P < 0.05

SPECIES	Areas with *C.a*	Areas without *C.a*	
Grasses			
Catapodium rigidum		0.02 ± 0.02	*
Cenchrus pauciflorus		1.86 ± 0.89 (1.9)	*
Lophochloa phleiodes		0.43 ± 0.27	*
Panicum racemosum	58.97 ± 7.71 (53.79)	42.00 ± 3.00 (42.96)	*
Poa sp.	4.27 ± 1.29 (3.89)	7.36 ± 1.94 (7.53)	*
Stipa sp.		1.96 ± 1.22 (1.82)	*
Forbs			
Achyrocline satureioides	1.22 ± 1.22 (1.11)	8.70 ± 3.75 (8.9)	*
Calystelgia soldanella		0.35 ± 0.24	*
Compuesta 1		1.89 ± 1.83 (1.93)	*
Gamochaeta spicata		0.08 ± 0.06	*
Gnaphalium leucopeplum	4.41 ± 3.14 (4.02)	0.41 ± 0.41	*
Grindelia aegialitis	0.70 ± 0.45		*
Hydrocotyle bonariensis	35.91 ± 12.63 (32.75)	30.86 ± 6.69 (31.56)	*
Medicago minima		0.69 ± 0.48	*
Oenothera mollisima	4.15 ± 2.99 (3.78)	1.35 ± 0.55	ns
BIOMASS			
Total	109.63 ± 11.01	97.76 ± 9.12	ns
Above	82.74 ± 7.27	71.51 ± 6.68	ns
Below	26.90 ± 9.95	26.25 ± 5.95	ns
Grasses	63.24 ± 7.82	53.44 ± 5.62	*
Forbs	46.39 ± 12.72	44.32 ± 7.00	ns
Litter	0.92 ± 0.66	9.17 ± 1.20	*
DIVERSITY			
Richness	7 species	14 species	
H′	0.5044	0.6644	*
H′ max	0.845	1.176	
J′	0.597	0.565	

ANOVA F 0.05, 1, 38 = 4.104
t 0.05 (2) 1.95 = 1.97

Material and methods

The study area is located 10 km south of Necochea, Buenos Aires, Argentina. It consists of a 4–10 km wide coastal dune fringe which slopes into the inland natural grassland. Sand dunes reach altitudes ranging from 30 to 50 m above sea level, and extend 200 to 2000 m (Frenguelli 1928). The grassland where *C. australis* density averages 16 individuals/ha exhibits a vegetation cover of about 20%, with dominant plants including *Poa* sp., *Panicum racemosum* and *Calistelgia soldanella* (Malizia et al. 1991). The site was exposed to slight grazing by cattle.

Bioenergetics constraints restrict *Ctenomys australis* to occupy sandy and deep soils with poor cover vegetation (Busch 1989; Malizia et al. 1991). Excavation activities in deep soils can be verified only by soil material that tuco-tucos bring to the surface at the openings of their tunnel system. Moreover, in

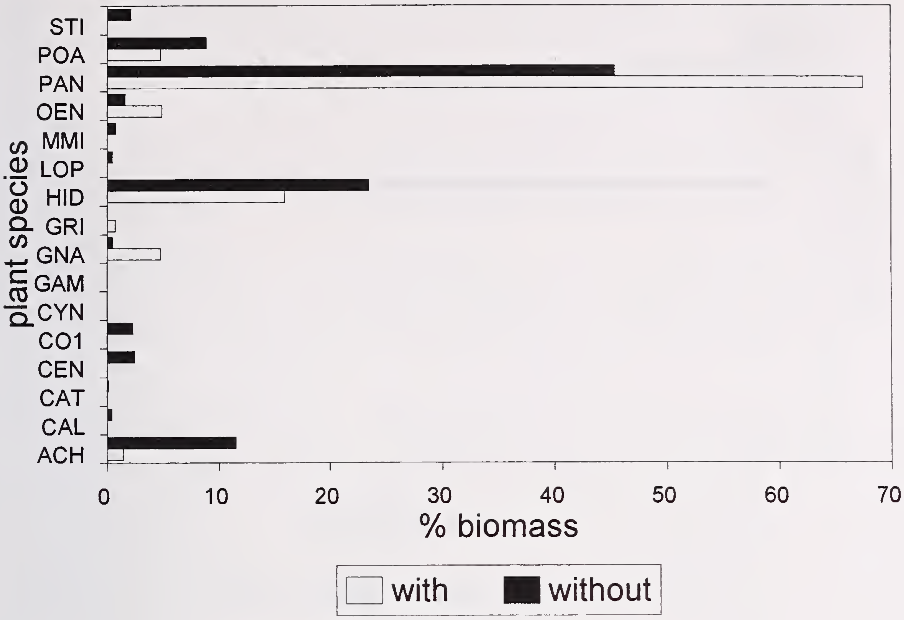

Fig. 1. Percentage of above ground biomass in areas with and without burrows of *Ctenomys australis* for each species. STI *Stipa* sp., POA *Poa* sp., PAN *Panicum racemosum*, OEN *Oenothera mollisima*, MMI *Medicago minima*, LOP *Lophocloa phleiodes*, HID *Hydrocotyle bonariensis*, GRI *Grindelia aegialitis*, GNA *Gnaphalium leucopeplum*, GAM *Gamochaeta spicata*, CYN *Cynodon dactylon*, CO1 Compuesta 1, CEN *Cenchrus pauciflorus*, CAT *Catapodium rigidum*, CAL *Calistelgia soldanella*, ACH *Achyrocline satureioides.*

shallower soils (at the edge of *C. australis* distribution), the resultant burrow is rather superficial, so that it is possible to identify removed earth (mounds) along much of this stretch of land.

Two scales of analysis were defined: macrospatial, in which vegetation of patches with and without burrows is compared; and microspatial, where vegetation associated to mound and intermound areas is compared.

A) Macrospatial: Two 10 × 10 m experimental plots were established in sand dunes where presence of *C. australis* was verified. All above- and below-ground plant material (to a depth of 20 cm) was collected in ten 1 m^2 squares located randomly in the plots. Similar procedure was applied in areas exhibiting no signs of *C. australis* activity to be used as control. No obvious differences were apparent among these areas other than the presence or absence of burrows of tuco-tucos.

B) Microspatial: Two 10 × 10 m experimental plots were established in sand dunes fixed by vegetation. Within each plot, ten 1 m^2 squares were located randomly, choosing the mound nearest to that point. All plant material was collected as indicated above. Similar procedure was applied in control plots where squares were located by randomly selecting the nearest point not occupied by a mound.

The study was conducted during early summer of 1992 when grassland condition improved the chance of detecting tuco-tuco effects. All vegetation samples (80 × 1 m^2 squares) were separated by species in above- and below-ground plant fractions, oven dried at 70 °C for 72 h and weighed to estimate plant biomass. Species richness (S) and diversity (H′) were calculated from this biomass data.

Statistical differences were evaluated by one way ANOVA, and Hutcheson t-test (Zar 1984) was performed to contrast species richness. Log transformations (log x + 1) were performed on all biomass data to normalize the variance structure.

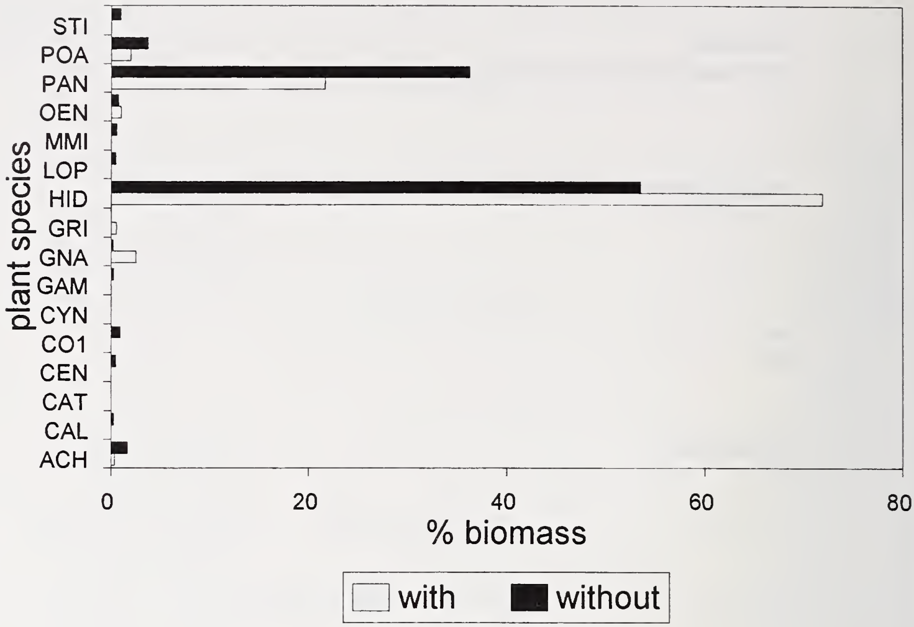

Fig. 2. Percentage of below ground biomass in areas with and without burrows of *Ctenomys australis* for each species. STI *Stipa* sp., POA *Poa* sp., PAN *Panicum racemosum*, OEN *Oenothera mollisima*, MMI *Medicago minima*, LOP *Lophocloa phleiodes*, HID *Hydrocotyle bonariensis*, GRI *Grindelia aegialitis*, GNA *Gnaphalium leucopeplum*, GAM *Gamochaeta spicata*, CYN *Cynodon dactylon*, CO1 Compuesta 1, CEN *Cenchrus pauciflorus*, CAT *Catapodium rigidum*, CAL *Calistelgia soldanella*, ACH *Achyrocline satureioides*.

Results

A) Macrospatial scale

There were no differences in total, above and below-ground plant biomass in areas with and without *C. australis*. However, in this latter areas, litter biomass was higher (Tab. 1). With respect to grassland composition, areas with *C. australis* had significantly higher grass biomass than areas without tuco-tucos (Tab. 1). Although *Panicum racemosum* was the most abundant plant species and the one that contributes most heavily to grass biomass, its biomass was significantly different in areas with and without tuco-tucos. Furthermore, this plant species was more abundant and practically the only grass in areas with *C. australis*. Areas without tuco-tucos were, on the other hand, inhabited by five other species, three of which (*Cenchrus pauciflorus*, *Poa* sp., *Stipa* sp.) represented each more than 1% of the total biomass. All these latter species showed statistically significant differences in biomass between areas (Tab. 1).

There were no differences for total forb biomass (Tab. 1) between areas. Although *Hydrocotyle bonariensis* was the most representative species in both areas, it was significantly more abundant in areas with tuco-tucos. In these latter areas it was present with other four species, three of which (*Achyrocline satureioides*, *Gnaphalium leucopeplum*, *Oenothera mollisima*) contributed each with more than 1% of the total biomass. In areas without *C. australis*, *H. bonariensis* was present together with seven other species, but only

Table 2. Comparisons of dry biomass of vegetation in absolute values (g/m^2), species richness and diversity (H) in mound and intermound areas. Data are shown as X ± SE with percentage of total biomass in parenthesis (%). Percentage values lower than 1% are not given.
*P < 0.05

SPECIES	Mound Areas	Intermound Areas	
Grasses			
Cynodon dactylon	0.002 ± 0.002		*
Lagurus ovatus		0.02 ± 0.02	*
Lophochloa phleiodes	0.21 ± 0.07	0.28 ± 0.21	ns
Panicum racemosum	78.02 ± 12.06 (60.33)	145.24 ± 18.79 (64.05)	*
Poa sp.	6.36 ± 1.15 (4.92)	9.58 ± 1.59 (4.22)	*
Stipa sp.	0.05 ± 0.02	0.073 ± 0.05	*
Forbs			
Achyrocline satureioides	1.53 ± 1.27 (1.18)	20.00 ± 10.72 (8.82)	*
Adesmia incana	0.36 ± 0.26	0.28 ± 0.22	ns
Ambrosia tenuifolia	2.43 ± 1.22 (1.88)	8.14 ± 2.83 (3.58)	*
Calystelgia soldanella		0.01 ± 0.01	*
Compuesta 1	1.65 ± 1.33 (1.27)	1.38 ± 1.40	ns
Gamochaeta spicata		0.016 ± 0.01	*
Gnaphalium leucopeplum		1.52 ± 1.52	*
Hydrocotyle bonariensis	1.34 ± 0.83	2.19 ± 0.67	*
Medicago lupulina	0.17 ± 0.17	1.04 ± 1.00	*
Medicago minima	1.94 ± 0.72 (1.50)	1.77 ± 0.98	ns
Oenothera mollisima	1.63 ± 3.42 (8.99)	8.58 ± 3.60 (3.78)	ns
Solidago chilensis	23.61 ± 8.28 (18.26)	26.60 ± 7.67 (11.73)	ns
BIOMASS			
Total	129.32 ± 14.02	226.74 ± 20.75	*
Above	90.38 ± 8.92	166.25 ± 15.94	*
Below	38.94 ± 5.61	60.53 ± 5.89	*
Grasses	84.64 ± 14.57	155.19 ± 5.89	*
Forbs	44.64 ± 6.92	71.54 ± 11.98	*
Litter	14.94 ± 20.2	26.08 ± 3.30	ns
DIVERSITY			
Richness	14 species	17 species	
H′	0.569	0.573	ns
H′ max	1.146	1.230	
J′	0.496	0.465	

ANOVA F 0.05, 1, 38 = 4.104
t 0.05 (2) 1.95 = 1.97

two comprising each one more than 1% of total biomass. With the exception of *O. mollisima*, all forbs presented significant differences in biomass for the analysed areas. *G. leucopeplum* and *Grindelia aegialitis* were more abundant in areas with tuco-tucos and the other ones in areas without tuco-tucos (Tab. 1).

P. racemosum and *H. bonariensis* together represented 87 and 75% of plant biomass in areas with and without tuco-tucos, respectively (Tab. 1). The former contributed principally with above-ground biomass ($F = 812.23$, $P < 0.05$ and $F = 413.29$, $P < 0.05$ in areas with and without *C. australis*, respectively). Whereas below-ground biomass appears to be more representative than above-ground biomass for *H. bonariensis*, there were no statistically significant differences in each type of area (F = 0.12, P > 0.05 and F = 0.42, P > 0.05). Furthermore, as shown in figures 1 and 2, presence of *C. australis* favours above ground biomass development in detriment to below ground biomass for *P. racemosum*, whereas the contrary situation was found for *H. bonariensis*.

The plant community, characterized by species richness and diversity indices, showed interesting differences. Areas without *C. australis* showed twofold number of species compared with areas with tuco-tucos and also a significantly higher species diversity (Tab. 1).

B) Microspatial scale

All categories of plant biomass analysed, except litter, were higher in intermound areas (Tab. 2). Within grasses, only *P. racemosum* and *Poa* sp. showed significant differences between areas, contributing each one with more than 1% of total plant biomass (Tab. 2). The same results were found for the forbs *Achiroclyne saturoides* and *Solidago chilensis* (Tab. 2). *P. racemosum* and *S. chilensis* were the most conspicuous species, representing 78 and 76% of total biomass for mounds and intermounds, respectively. Here also *P. racemosum* contributes differentially with above-ground biomass in mound and intermound sites (F = 151.45, P < 0.05; F = 134.59, P < 0.05). The latter species presented similar abundance of both plant fractions (F = 0.34, P > 0.05, F = 0.73, P > 0.05). Furthermore,

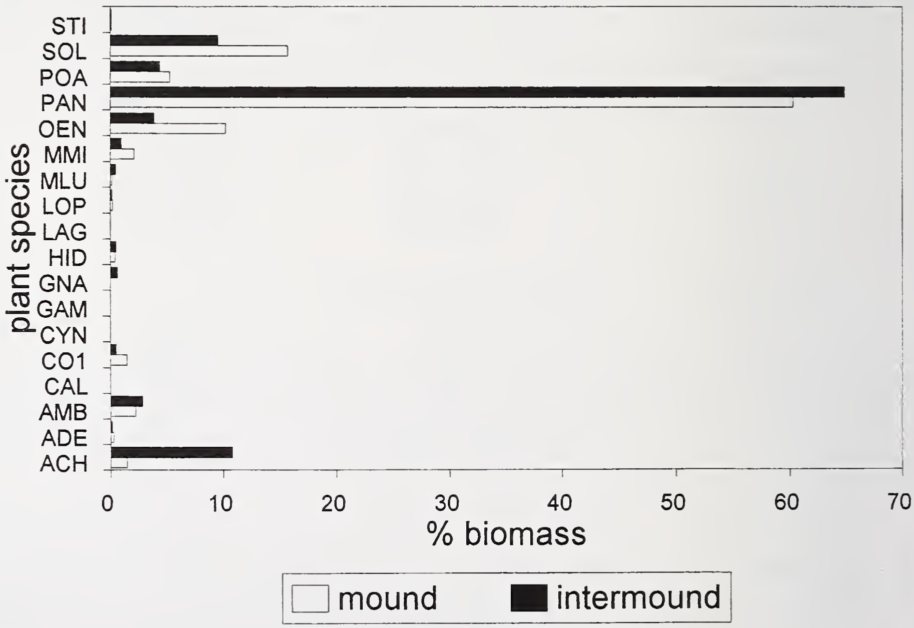

Fig. 3. Percentage of above ground biomass in mound and intermound areas for each species. STI *Stipa* sp., SOL *Solidago chilensis*, POA *Poa* sp., PAN *Panicum racemosum*, OEN *Oenothera mollisima*, MMI *Medicago minima*, MLU *Medicago lupulina*, LOP *Lophocloa phleiodes*, LAG *Lagurus ovatus*, HID *Hydrocotyle bonariensis*, GNA *Gnaphalium leucopeplum*, GAM *Gamochaeta spicata*, CYN *Cynodon dactylon*, CO1 Compuesta 1, CEN *Cenchrus pauciflorus*, CAL *Calistelgia soldanella*, AMB *Ambrosia tenuifolia*, ADE *Adesmia incana*, ACH *Achyrocline satureioides*.

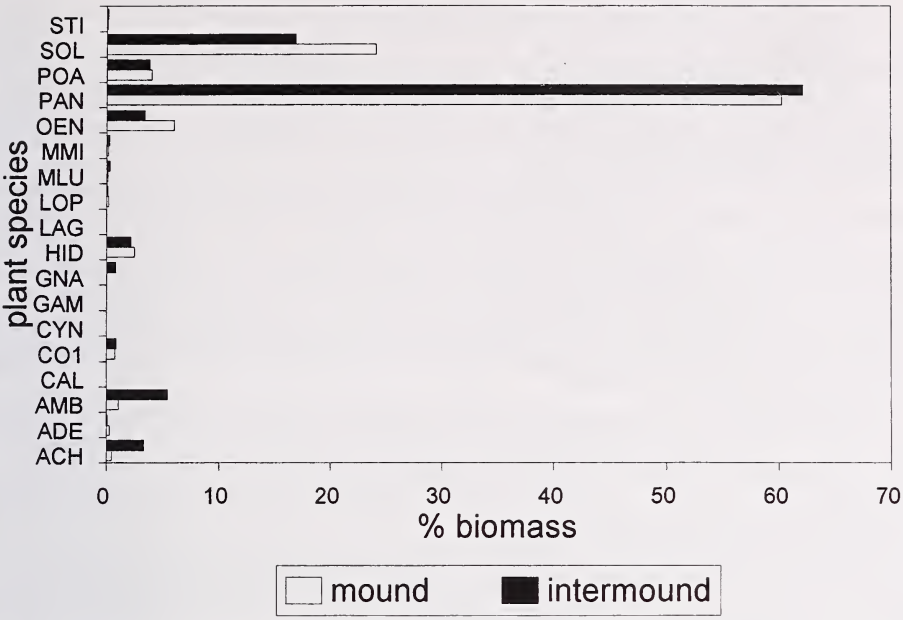

Fig. 4. Percentage of below ground biomass in mound and intermound areas for each species. STI *Stipa* sp., SOL *Solidago chilensis*, POA *Poa* sp., PAN *Panicum racemosum*, OEN *Oenothera mollisima*, MMI *Medicago minima*, MLU *Medicago lupulina*, LOP *Lophocloa phleiodes*, LAG *Lagurus ovatus*, HID Hydrocotyle bonariensis, GNA *Gnaphalium leucopeplum*, GAM *Gamochaeta spicata*, CYN *Cynodon dactylon*, CO1 Compuesta 1, CEN *Cenchrus pauciflorus*, CAL *Calistelgia soldanella*, AMB *Ambrosia tenuifolia*, ADE *Adesmia incana*, ACH *Achyrocline satureioides*.

below and above ground plant biomass per species showed the same pattern in mound and intermound areas (Figs. 3, 4).

Neither species richness nor diversity values between site types showed statistically significant differences.

Discussion

Vegetation is critical in the stabilization of dunes and also promotes their growth, by providing a trap for wind-blown sand. In the coastal dunes of Buenos Aires province, the perennial grass, *Panicum racemosum*, is the first colonizer. This grass only grows well when it is being continually covered by fresh wind-blown sand. Other important early colonizers are *Poa lanuginosa*, *Hydrocotyle bonariensis*, *Calistelgia soldanella* and *Adesmia incana*, but if for any reason, sand is exposed to the wind and loose grains blown away, the *Poa* and *Adesmia* community is replaced by the dune grass *Panicum racemosum*. With increasing stability, soil development and protection from salt spray, the dunes are invaded by species of European origin, such as *Erodium cicutarium*, *Poa annua*, *Cynodon dactylon* and specially *Medicago minima* (Cabrera 1941).

Tuco-tucos mound-building activity results in barren areas open to wind erosion that impinge on plant community and arrests the succession on the earlier pioneer stages. Thus, areas with tuco-tucos have lower plant diversity and half the number of species than those without tuco-tucos. Furthermore, the pioneer perennial grass, *Panicum racemosum*, is the dominant plant in dunes inhabited by tuco-tucos.

SPENCER et al. (1985) noted changes in abundance and composition of certain plants near pocket gopher burrows because of differential consumption resulting from dietary preferences. *C. australis* proved to be a herbivore generalist as it consumed almost all plant species available in the grassland (COMPARATORE et al. 1995). As a consequence, differences in dune community composition cannot be attributed to competitive release mediated by selective feeding.

Feeding and burrowing activities by mole rats and pocket gophers not only reduced locally overlying vegetation, but also enhanced plant biomass directly adjacent to the disturbance, producing a sharp edge effect (REICHMAN and SMITH 1985; REICHMAN and JARVIS 1989). Moreover, REICHMAN et al. (1993) revealed a pattern of biomass extending from disturbances, suggestive of a competition-induced wave. At Necochea dunes, total average biomass was not different for areas with and without tuco-tucos, but was higher in intermound than in mound patches suggesting that mound-building activity by tuco-tucos enhanced plant growth near mounds.

Other studies have demonstrated that as a consequence of burrowing activities, high soil turnover promotes the development of favorable conditions for the recruitment of bulbs of geophytes. This mechanism may account for the maintenance of the coexistence of geophytes and mole rats (LOVEGROVE and JARVIS 1986) and this plant species and coruros (CONTRERAS and GUTIÉRREZ 1991).

Panicum racemosum and *Hydrocotyle bonariensis*, the dominant plant species in this study, are geophytes without bulbs. Their dominance in unstable areas with tuco-tucos may be associated to the fact of being continually covered by fresh wind-blown sand that favors its development.

In conclusion, *Ctenomys australis* alters plant community composition and keeps succession on pioneer stages without altering total biomass. As an overall effect, dune development is arrested and its stabilization is restrained. In consequence, mound-building activities maintain suitable habitats for *C. australis* according to its energetic and thermoregulatory restrictions.

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Zusammenfassung

Einfluß des unterirdisch lebenden Nagetieres Ctenomys australis (Tuco-tuco) in einer Sanddünen-Landschaft

Um den Einfluß des Nagers *Ctenomys australis* (Tuco-tuco) an der Landschaftsgestaltung zu bestimmen, wurden die Pflanzengesellschaften von Sanddünen mit und ohne unterirdischen Gangsystemen dieser Säuger untersucht. Die Biomasse von Pflanzen wurde ober- und unterirdisch bestimmt. Verglichen wurden Biomasse, Artenreichtum und Diversität der Pflanzengesellschaften in Gebieten mit und ohne Bauten (macrospatial scale), sowie auf Bauhügeln und dazwischen (microspatial scale).

Die totale Pflanzenbiomasse unterschied sich in Gebieten mit und ohne *C. australis* nicht. In Gebieten ohne Tuco-tucos fanden sich doppelt so viele Arten und eine signifkant höhere Artendiversität. Keine signifikanten Unterschiede waren bei Flächen zwischen den Hügeln und direkt auf den Hügeln zu erkennen, obwohl die Pflanzenbiomasse zwischen den Erdhügeln größer war.

Die Ergebnisse zeigen, daß *C. australis* die Zusammensetzung der Pflanzengemeinschaft verändert und die Sukkzession in Pionierstadien hält, ohne dabei die totale Biomasse zu verändern. Als Gesamteffekt läßt sich also sowohl eine Hemmung der Dünenentwicklung als auch ihre Stabilisation beobachten.

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