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Biomass partitioning in *Paspalum notatum* stands on slope relief in the anthropic savanna of Cuba

Distribuce biomasy v porostech *Paspalum notatum* na svahovém reliéfu v antropické savaně Kuby

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The average total aboveground biomass and total underground biomass ranged respectively, from 626 to 1358 and from 1182 to 1735 g.m^{-2} in three *Paspalum notatum* stands growing in different parts of a slope relief representing a soil catena in the anthropic savanna of northwestern Cuba. The more favourable the water and nutrition regime of habitat (towards the lowest part of the relief) the greater was the living aboveground biomass (649 g.m^{-2}) and living rhizome biomass (1023 g.m^{-2}) and smaller was the amount of living roots (99 g.m^{-2}). The proportion of the total biomass occuring aboveground increased (from 34.1 to 43.9 %) while that in underground decreased (from 65.9 to 56.1 %) from the upper to the lowest part of the relief, while the proportion of living rhizomes increased (from 38.5 to 57.7 %), but that of the living root biomass decreased (from 17.8 to 5.6 %).

Introduction

Climatic conditions in the tropical zone permit an exploitation of grasslands during the whole year. In Cuba, cattle grazing has been based traditionally on grasslands, used as extensivelly managed systems. The dominant plant species of these ecosystems, known as natural or non cultivated pastures, are endemical or naturalized gramineae of low productivity (Funes et al. 1979). *Paspalum notatum* Flügge stands (datum of plant species introduction is unknown) have been utilized by farmers of whole island as pastures for a long time. The nutritive value of this grass has been already highly appreciated by the old ranchers of the country, above all in the west and central Provinces of Cuba. *Paspalum notatum* is one of the most common grasses in the Cuban anthropic savannas, above all in two types of high grass savannas, i.e., in both savanna with *Roystonea regia* (H. B. K.) O. F. Cook and *Ceiba pentandra* (L.) Gaertn. and savanna with *Roystonea regia* (H. B. K.) O. F. Cook (Borhidi et Herrera 1977). Nowadays, Cuba is covered by natural and anthropic savannas approximately to an extent of 50 % (Fiala et Herrera 1988) and both types of the mentioned anthropic high grass savannas represent about 45 % of this area (see Borhidi et Herrera 1977).

Although several authors have summarized data on the ecology of savannas in the last years (e.g. Bourliere et Hadley 1970, Huntley et Walker 1982, Cole 1986, Stanton 1988) data on underground biomass and biomass distribution in grass stands of tropical countries are often lacking, which is evident above all in comparison with studies of grasslands of the temperate zone. Nevertheless, different authors have focussed attention on this aspect in herbaceous savanna ecosystems: e.g., Lamotte (1975) studied the structure and functioning of the savanna ecosystem, including the underground biomass, in the South Africa; Menaut et Cesar (1979, 1982) worked on the same aspects in the Ivory Coast; Medina (1982) published data on physiology and ecology of grasses in the neotropical region, reporting underground biomass as well. In Cuba, the first data on underground biomass of different grass stands (man made and seminatural pastures) were published by Yepes et Alfonso (1972) and Sagué et Hernández (1978). Fiala et Herrera (1988) studied the aboveground and underground biomass of savanna ecosystems in three regions of Cuba (Isla de la Juventud, Yaguaramas and Sierra del Rosario). Garcia and Hernández (1990) made references to the root biomass of a woodland savanna in Peladas hill and Hernández and Armas (1990) studied seasonal dynamics of underground biomass in anthropic grassland situated in the northeastern part of the Sierra del Rosario.

Our studies, included in the MAB Project number 3, were conducted in the anthropic savanna in the Biosphere Reserve of the Sierra del Rosario. In this area, multidisciplinary studies have been realized, resulting in important contributions to the knowledge of ecosystems of this region and to the improvement of their production and management (Herrera et al. 1988). Our studies presented in this paper are focussed on the assessment of differences above all in the amount of living and dead underground biomass and of changes in the underground to aboveground biomass ratios along the slope of the relief and representing the soil catena.

Material and methods

Our study site was in the western part of the Cuba (in the Pinar del Rio Province) near the village of Cayajabos, situated about 20 km northwest of Artemisa (altitude approximately 150 m, see Fig. 1). Biomass partitioning was studied in *Paspalum notatum* stands growing along the slope (cca 30o, facing the west) in the typical waved relief of the lower part of the Sierra del Rosario, mostly covered by antropic savanna stands (above all the high grass savanna with *Roystonea regia*).

The above- and underground plant biomass of *Paspalum* stands was sampled on September 22, 1989. Each sampling site was situated in a different part of the slope relief: (i) upper part of the slope (referred to as U-site), (ii) the lowest part of the slope (L-site) situated on the small flat area at bottom of a small valley of undulating relief, (iii) central part of the slope situated approximately in the middle, between U- and L-sites (M-site) (see Fig. 1).

The plant community of *Paspaletum notati* Ricardo, Garsia Cruz et Lauzón 1990, described by Ricardo (1990), is characterized by the dominant *Paspalum notatum*. On both U- and M-sites other very common plant species were *Paspalum plicatum* Micht., *Sporobolus indicus* (L.) R. Br., *Desmodium triflorum* (L.) DC. and *Desmodium canum* (J. F. Gmel.) Schinz et Thell. The plant cover degree and stand height were respectively 90 % and 0.4 m, and 70-80 % and 0.3-0.4 m on U- and M-sites. On the L-site, *Paspalum notatum* covered almost the whole surface (practically without any other plant species) and the stand height reached 0.6-0.7 m. The experimental sites were neither fertilized nor pastured. The area of the studied sites had

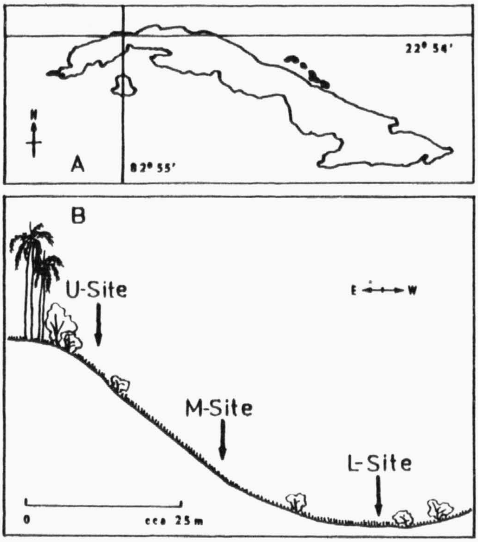

Fig. 1. Schematic map indicating the position of the studied anthropic savanna in Cuba (A) and diagram of the slope relief (cross section) with marked positions of the sampling sites (B).

been burned in April 1989 (irregular, accidental fire established by man). The stand had received no fire treatment for several years before.

The substrate consisted of the clay loam soil (brown soil), belonging to the Pinar del Rio Series. Chemical features of the soil from three study sites of the soil catena are given in Table 1. The climate is tropical, moderately dry with an annual mean air temperature of 24.4 °C, annual mean precipitation of 1450 mm (Cayajabos pluviometric station, years 1964 to 1989), and with 3 to 4 months of a dry period (according to the Institute of Hydroeconomy of the Habana Province).

The aboveground plant material (including litter) was collected from five 0.25 × 0.25 m plots on each site. Underground plant organs were taken in ten soil cores (50 mm in diameter) to a depth of 0.2 m, placed within the same quadrats used for aboveground sampling. Three of the soil cores were cut into four layers: 0-0.05, 0.05-0.1, 0.1-0.15, and 0.15-0.2 m to study the vertical distribution of underground plant biomass. All samples were transported to the laboratory and soil cores were washed in nylon bags and sieves of 0.5 mm mesh size. The aboveground plant material was separated into living biomass, standing dead and litter. Underground samples were separated mannualy and identified visually into total roots and living and dead other underground plant organs, mostly rhizomes of *Paspalum notatum*. Three additional soil cores of the same size were taken from each site, cut into 50 mm sections, according to the soil layers. After washing of samples in nylon bags (mesh size 0.5 mm), living and dead roots were distinguished by vital staining with Congo red solution (Ward et al. 1978, Tesařová et al. 1982) and separated under a 1.5 x magnifying glass. All samples were dried at 70 - 80 °C and weighed. Data of living and dead root and rhizome dry mass were then used to determine the percentage of living root and rhizome biomass.

Parts of the rhizome systems of *Paspalum notatum* with attached roots were excavated on studied sites on October 25, 1989 to find differences in their formation (morphology).

The chemical analyses of the soil samples (Tab. 1), all taken on October 25, 1989, were accomplished by the following methods: pH in H_2O and 1 mol KCl extracts electrometrically, soil moisture content gravimetrically, total P by Egner's colorimetric method in Ca-lactate extract (Hraško et al. 1962). Exchangeable cations Ca^{2+} and Mg^{2+} were determined using complexometric titration (Kubíková 1971), total C and N by elemental analyzer CHN 1106 (Carlo Erba).

Statistical evaluation of data involved standard procedures. Stands were compared by SNK-test.

Table 1. Characteristics of the studied sites: pH, soil moisture and nutrients contents in the 0-0.05 m (a) and 0.05-0.15 m (b) soil layers. Soil samples were collected at the end of the 1989 rainy season. All contents related to dry mass.

		pH (H_2O)	pH (KCl)	Soil moisture (%)	Ca^{2+} ($mg.kg^{-1}$)	Mg^{2+} ($mg.kg^{-1}$)	PO_4-P ($mg.kg^{-1}$)	C (%)	N (%)
U - site	a)	6.11	5.30		7130	693	226	2.42	0.23
				30.3					
	b)	5.95	4.88		7220	693	203	1.74	0.20
M - site	a)	5.53	4.70		5870	1253	198	2.52	0.23
				32.9					
	b)	5.15	4.44		5680	1113	127	1.62	0.19
L - site	a)	6.26	5.01		6860	1131	276	3.15	0.30
				38.7					
	b)	6.01	5.11		6780	1058	233	2.41	0.24

Table 2. Live, dead and total above- and underground biomass (in $g.m^{-2}$) in Paspalum notatum stands in the anthropic savanna of Cuba. Recorded at the end of the 1989 rainy season.

	U - site x	U - site s_x	M - site x	M - site s_x	L - site x	L - site s_x	Significant differences (significance level = 0.05)
Aboveground biomass							
Live biomass							
Paspalum notatum	361	29.9	223	28.3	649	79.3	L > U, M
Other species	37	13.1	15	5.1	0	-	
Total	398	60.0	238	23.8	649	79.3	L > U, M
Dead biomass							
Standing dead	213	58.3	147	17.8	476	52.9	L > U, M
Litter	66	10.6	241	34.7	233	20.1	U < M, L
Total	279	65.8	388	45.5	709	42.1	L > U, M
Total aboveground biomass	677	124.1	626	67.3	1358	117.5	L > U, M
Underground biomass							
Live roots	162	12.9	105	7.6	99	15.7	U > M, L
Dead roots	492	41.7	298	15.6	335	50.8	U > M, L
Total roots	654	54.5	403	22.7	434	66.4	U > M, L
Live rhizomes	350	69.1	436	52.6	1023	166.8	L > U, M
Dead rhizomes	303	49.3	343	104.1	278	88.9	
Total rhizomes	653	90.6	779	129.9	1301	188.0	L > U, M
Live underground biomass	512	77.6	541	54.3	1122	176.4	L > U, M
Dead underground biomass	795	77.9	641	106.9	613	127.6	
Total underground biomass	1307	133.9	1182	134.5	1735	247.1	
Root and rhizome detritus	205	36.1	266	24.9	352	57.2	L > U

Note: x - arithmetic mean

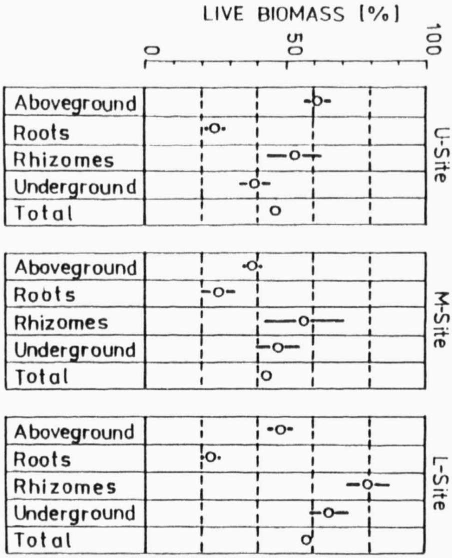

Fig. 2. The percentage of living above- and underground biomass in *Paspalum notatum* stands in the anthropic savanna of Cuba. Vertical bars indicate + two standard errors.

Results

Aboveground biomass

The aboveground biomass of the three *Paspalum notatum* stands studied is given in Table 2. The total aboveground biomass (including standing dead and litter) ranged in a narow amplitude in stands situated on the higher parts of the slope (677 g.m^{-2} U-site, 626 g.m^{-2} - M-site) while down on the L-site it amounted to 1358 g.m^{-2}; this represents an increase of 100 and 117 % in comparison with other stands (statistically significant, see Tab.2). The share of the aboveground living biomass in percent of the total aboveground biomass was highest on the U-site (61 %), intermediate (47.3 %) on the L-site and the lowest (38.2 %, Fig.2) on the M-site. The living aboveground biomass was also highest down on the L-site (649 g.m^{-2}); it varied at about 398 g.m^{-2} on the U-site, and only at about 238 g.m^{-2} on the M-site. On both M- and L-sites the amount of dead dry matter (standing dead + litter) was higher (62 and 52 %, respectively) in comparison with the U-site (41 % of total aboveground biomass). The highest amount of standing dead was found on the L-site (476 g.m^{-2}, 35 % of total aboveground biomass). A nearly similar percentage of standing dead (32 %, 213 g.m^{-2}) was also recorded in the *Paspalum* stand on the U-site. On the contrary, a great amount of litter was accumulated on the soil surface (241 g.m^{-2}, 38 % of total aboveground dry mass) on the M-site, i.e., approximately 175 g.m^{-2} more than on the U-site. In the stand on the L-site, the amount of litter was nearly the same as on the M-site (233 g.m^{-2}), but it represented only 17 % of the total aboveground biomass.

Underground biomass

Paspalum notatum stand on L-site had the highest average total underground biomass of 1735 g.m^{-2}, both other stands having less by over 400 g.m^{-2}. Even greater differences (about 600 g.m^{-2}, statistically significant, Tab. 2) were also found between living underground biomass of both ***Paspalum*** stands growing on the slope and down on the L-site. On the contrary, unsignificant differences were in dead underground dry matter; it ranged between 613 g.m^{-2} (L-site) and 795 g.m^{-2} (U-site). On the other hand, relatively great differences were found in the percentage share of living underground biomass (roots and rhizomes) in the total underground biomass (see Fig. 2). This share was highest in the ***Paspalum*** stand on the L-site. In this stand growing on the lowest part of the slope, a conspicuous amount of thick long and heavy rhizomes were formed and most of them were alive (nearly 80 %, see Fig. 3). On the contrary, in the stand on the U-site only 53.6 % of the rhizome biomass was alive. There were no significant differences in the dry mass of dead rhizomes - varying at about 300 g.m^{-2} in all stands. Consequently, there were very high (over 500 g.m^{-2}) differences in the living rhizome biomass between stands on U- and M-sites and the stand growing on the lowest part of the slope (see Fig. 4). An opposite relationship was found in the root biomass: the highest amount of both living and total root biomass (statistically significant, Tab. 2) was found on the upper part of the slope (U-site). The ***Paspalum notatum*** stand had here the highest total root biomass of 654 g.m^{-2}, the stands on both other sites having around 400 g.m^{-2}; less than 27 % of living biomass was present in each of the three stands studied. On the L-site, the percentage of living roots in the total root biomass attained 22.8 %, corresponding to 99 g.m^{-2} of the living root biomass only. The living root biomass amounted to 162 g.m^{-2} on the U-site and the dry matter of dead roots (492 g.m^{-2}) was the highest here as well.

In all ***Paspalum*** stands under study, about or more than 90 % of the total root biomass was found in the upper 0-0.15 m soil layer. The same percentage of the total underground biomass (including root and rhizome biomass) was accumulated more closely to the soil surface, i.e., in the 0-0.10 m soil layer. Figure 5 shows the vertical distribution of the living, dead and total root and rhizome biomass in three ***Paspalum notatum*** stands under study. The values for total root biomass ranged from 245 g.m^{-2} (L-site) to 356 g.m^{-2} (U-site) in the 0-0.05 m soil layer. The amount of the total underground biomass (in the same upper soil layer) reached much higher values; it was about 1000 g.m^{-2} in both stands situated on the slope (U- and M-sites) and even 1546 g.m^{-2} in the stand in the lowest part (L-site); it represents 88 % of the total underground biomass found in the whole soil profile 0-0.2 m (Tab. 3). The soil layer of 0-0.05 m is the principal zone of rhizome development of ***Paspalum notatum***. In this soil layer, rhizomes comprised about 65 % (U-site) to 84 % (L-site) of the total underground biomass. No rhizomes occurred below this zone.

Changes in the percentage of living roots found in each 0.05 m soil layer are shown in Figure 6. In all ***Paspalum*** stands the percentage of living roots in the total root biomass was relatively low, varying mostly between 21.2 and 33.3 %. An exception was the stand on the L-site, where only 16.3 % of living root biomass was found in the top soil layer. Thus the ***Paspalum*** stand on the L-site had only 40 g.m^{-2} of living root biomass in the

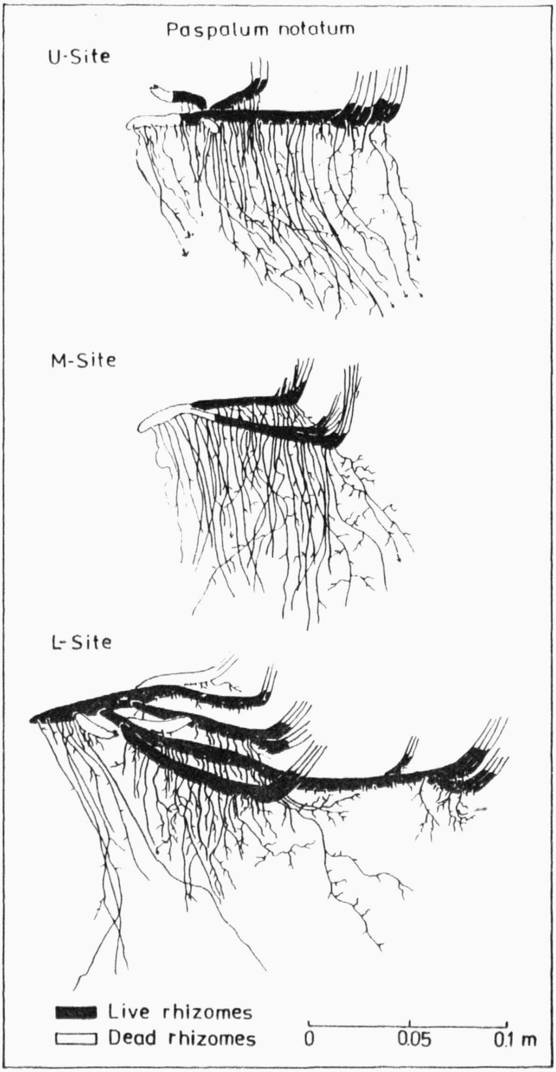

Fig. 3. Rhizome and roots of *Paspalum notatum* showing their length and diameter in stands growing in the anthropic savanna of Cuba.

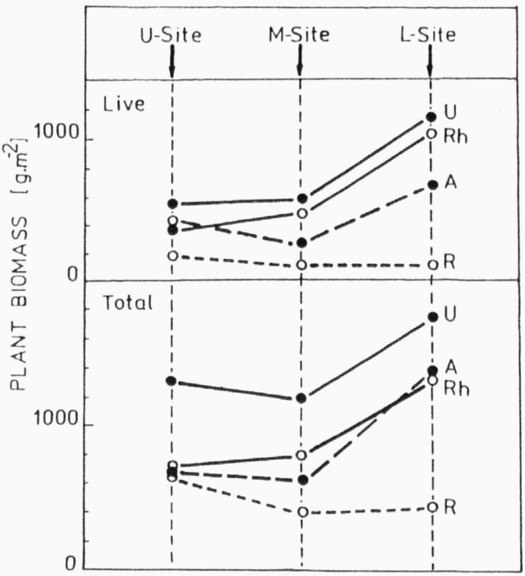

Fig. 4. Live and total biomass of aboveground and underground plant parts in *Paspalum notatum* stands in the anthropic savanna of Cuba. A - aboveground biomass, U - underground biomass, R - root biomass, Rh - rhizome biomass.

upper 0-0.05 m soil layer, representing 8.3 % of the total root biomass found in the whole soil profile studied. In comparison, the amount of living root biomass in the two other stands was about twice as high or more (74 g.m^{-2} - M-site, 93 g.m^{-2} - U-site). The *Paspalum* stand on the U-site was probably characterized by a greater accumulation of both living and dead root biomass in the deeper soil layer (0.05-0.2 m, 80 g.m^{-2}, 11.5 %). On the contrary, the greatest concentration of root biomass in the 0-0.05 m top layer was found in the stand situated in the middle of the slope; 17.0 % of the living and 60.3 % of total root biomass of the soil profile (0-0.2 m). In the upper soil layer of 0-0.05 m, the total living underground biomass was greatest on the L-site (1063 g.m^{-2}), i.e., by 553 g.m^{-2} more than on the M-site and 620 g.m^{-2} more than on the U-site. The amount of dead underground dry mass in the same soil layer ranged from 483 (L-site) to 566 g.m^{-2} (U-site); it represented (in both stands) about 40 % of the underground biomass of the whole examined soil profile (see Tab. 3).

Biomass partitioning

The total biomass (living and dead above- and underground plant parts) varied only little (from 1808 to 1984 g.m^{-2}) and the same applies to the total living biomass (from 779 to 910 g.m^{-2}) of the two *Paspalum* stands growing on the U- and M-sites. The stand on the lowest part of the slope differed from the others by a conspicuously greater amount of total (3093 g.m^{-2}) and living (1771 g.m^{-2}) plant biomass. Changes in this total plant

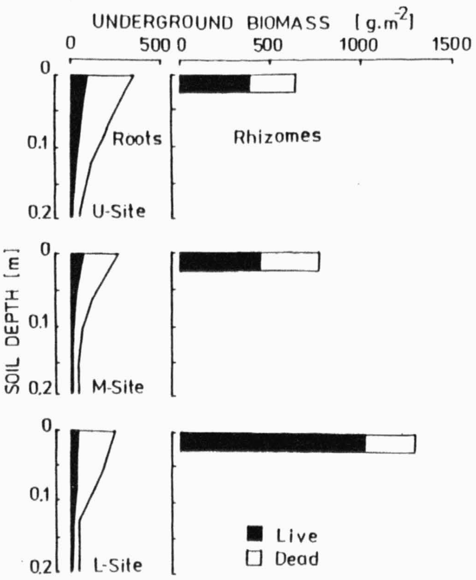

Fig. 5. Vertical distribution of the living and dead root and rhizome biomass in *Paspalum notatum* stands in anthropic savanna of Cuba.

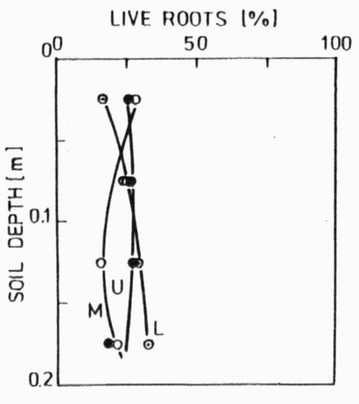

Fig. 6. The share of living roots in percent of the total root biomass in different layers of the soil profile in *Paspalum notatum* stands in the anthropic savanna of Cuba. U - U-site, M - M-site, L - L-site.

Table 3. Vertical distribution of the total root and underground biomass (% T) in Paspalum notatum stands in the anthropic savanna of Cuba. Recorded at the end of the 1989 rainy season. The percentage of live (% L) and dead (% D) root and underground biomass found in each 0.05 m soil layer are shown as percentages of the total root and underground biomass found in the whole profile (0-0.2 m).

Soil depth (m)	U - site			M - site			L - site		
	% L	% D	% T	% L	% D	% T	% L	% D	% T
Root biomass									
0.0 - 0.05	13.3	37.8	51.1	17.0	43.3	60.3	8.3	42.2	50.5
0.05 - 0.10	7.2	20.2	27.4	5.2	16.6	21.8	6.8	20.2	27.0
0.10 - 0.15	4.3	11.0	15.3	1.5	8.8	10.3	3.5	8.5	12.0
0.15 - 0.20	1.1	5.1	6.2	1.7	5.9	7.6	3.4	7.1	10.5
0.0 - 0.20	25.9	74.1	100.0	25.4	74.6	100.0	22.0	78.0	100.0
Underground biomass									
0.0 - 0.05	34.2	38.9	73.1	41.7	44.0	85.7	49.2	38.8	88.0
0.05 - 0.10	3.9	11.2	15.1	1.8	6.0	7.8	1.8	4.9	6.7
0.10 - 0.15	2.3	6.2	8.5	0.6	3.2	3.8	0.8	2.0	2.8
0.15 - 0.20	0.6	2.7	3.3	0.6	2.1	2.7	0.8	1.7	2.5
0.0 - 0.20	41.0	59.0	100.0	44.7	55.3	100.0	52.6	47.4	100.0

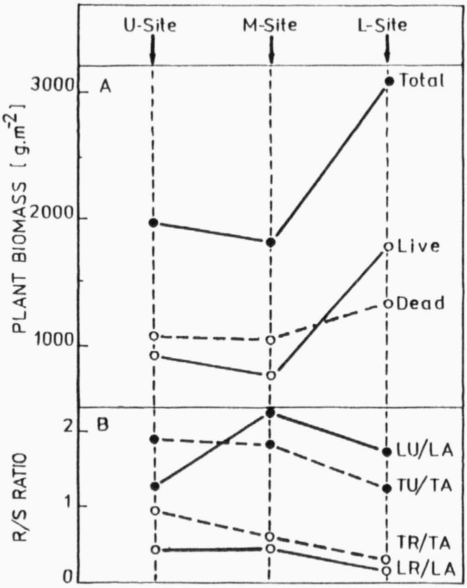

Fig. 7. Live, dead and total plant biomass and changes in underground to aboveground biomass ratios (R/S ratios) in ***Paspalum notatum*** stands in the anthropic savanna of Cuba. LU/LA - living underground/living aboveground biomass, TU/TA - total underground/total aboveground biomass, LR/LA - living root/living aboveground biomass, TR/TA - total root/total aboveground biomass.

biomass and in underground to aboveground biomass ratios are demonstrated in Figure 7. The total underground to aboveground biomass and the total root to aboveground biomass ratios probably decreased with inclination of the slope: they attained the values 1.93 and 0.97 on the U-site and 1.28 and 0.32 on the L-site, respectively. The highest living underground/aboveground biomass ratios were found on the M- and L-sites. However, the lowest living root/aboveground biomass ratio (0.15) was recorded in the stand growing on the L-site.

Figure 8 shows changes in the percentage distribution of total and living biomass into different plant parts, i.e., aboveground shoots, roots, rhizomes and all underground parts. In spite of great differences between the plant biomass of *Paspalum* stands growing on the U- and M-sites and the stand on the lowest part of the slope (see Fig. 4), the proportion of the total underground biomass slightly decreased, while the aboveground biomass increased towards the lowest part of the relief (from 34.1 % - U-site to 43.9 % - L-site). The proportion of the living rhizome biomass represented an increase of 18.9 % on the L-site in comparison with the stand on the U-site. This increase was also reflected

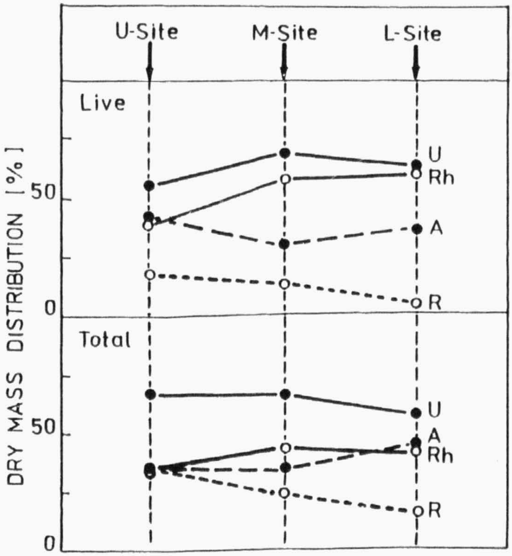

Fig. 8. Dry mass distribution into living and total aboveground and into individual underground organs, i.e., rhizomes and roots, in *Paspalum notatum* stands in the anthropic savanna of Cuba. The percentages of biomass of individual plant parts are shown as percentages of total living (Live) and total living + dead (Total) plant biomass. Description as in Fig. 4.

in a greater proportion of living underground biomass (63.3 %) on the L-site than on the U-site (56.3 %).

Discussion

Aboveground biomass

Studies of the savanna communities of Cuba indicate that their total aboveground plant biomass mostly ranges between 600 and 1300 $g.m^{-2}$ of dry mass (Pérez et Šmíd 1984, Menendéz 1986, Fiala et Herrera 1988). Our aboveground samples were collected towards the end of the rainy season, when the maximum of living biomass occurs (see Pérez et Cárdenas 1990). However, in this part of the year, when the rainy period terminates, the share of dead biomass in the total aboveground biomass can vary considerably, i.e., approximately between 50 - 80 % (Pérez et Šmíd 1984, Fiala et Herrera 1988). Our results indicated lower values (41 - 62 %). Hernández L. (unpublished) estimated the plant biomass of the *Paspalum notatum* stands on the same sites and by a similar method at the end of the dry period (see Tab. 4). The values of the total aboveground biomass were close to our data recorded at the end of rainy season. However, the living aboveground biomass from the end of the dry season of the next year represented only about 50 % (M-site) and even about 30 % (U- and L-sites) of the living aboveground biomass recorded at the end of rainy season. The share of dead biomass in the total aboveground biomass was between 77 and 86 % at the end of dry season 1990.

Underground biomass

The total amounts of underground biomass recorded on U- and M-sites were very similar to data found by Fiala and Herrera (1988) in other savanna communities of Cuba. They ranged around or slightly over 1000 g.m^{-2}. There were no great differences between the total underground biomass of the same *Paspalum* stands recorded at the end of the rainy and of the next dry period (Tab. 2, 4). However, Hernández and Fiala (1992) recorded the higher total root biomass in the same *Paspalum notatum* stand during dry period of the current year 1989 (in January - 729 g.m^{-2}). A large decrease in total root biomass was recorded in this stand during the rainy period 1989 (Hernández et Fiala 1992). Other published data on the total underground biomass of various savanna stands vary considerably. The lowest values (230 and 345 g.m^{-2}) were recorded in the *Trachypogon* savannas of Central Venezuela and South Africa savanna ecosystem (Medina 1982, Huntley et Morris 1982). On the other hand values as high as 1050 or even 1900 g.m^{-2} were also recorded (Menaut et Cesar 1979, 1982). Such great differences also occures in the Cuban pasture stands: in *Panicum purpureum* 1653 g.m^{-2} but in *Trichopogon* sp. and *Hyparrhenia* sp. stand 260 g.m^{-2} only (Yepes et Alfonso 1972, Sagué et Hernández 1978). Similar relationship (the lowest and the greatest amount of underground biomass in the central part and at the basis of the slope) was also described by Lastres and Francéz (1987) for a semideciduous tropical forest in the Sierra de La Guira in Pinar del Río Province (Cuba). Different rates of the decomposition of dead underground plant material are reflected in different rates of accumulation of not yet fully decomposed underground plant parts and they considerably affect the amount of dead and total underground plant biomass (see, e.g., Bernard et Fiala 1986, Seischab et al. 1985, Fiala 1990a, b). Studies of the underground plant biomass of temperate meadows showed that the total underground biomass increased with increasing soil moisture content of the site (Fiala 1990b). However, the highest living underground plant biomass was recorded in stands situated around the center of the soil moisture gradient and the lower values occurred on both the wettest and the driest site. The highest amount of dead underground plant matter was accumulated on both extreme sites.

The share of the living underground biomass (39 - 65 %) and especially living root biomass (23 - 26 %) was relatively lower in *Paspalum* stands than in other anthropic savannas (68 - 74 % living roots) or natural savanna communities (33.8 - 50.4 % living roots) of Cuba (Fiala et Herrera 1988). Hernández et Fiala (1992) reported that the proportion of fine roots in total root biomass was lower in the same *Paspalum notatum* stand during rainy period (with increasing soil moisture content), i.e., the greatest part of total root biomass was formed by coarse roots (about 65 %). Thick and hard roots of *Paspalum notatum* are probably slowly decomposed, due to their morphological character and mechanical consistence (see Boot 1989). Thus a relatively greater part of root biomass was formed by dead roots at the end of the rainy period 1989. The plant forms an extensive flat rhizome system (Fig. 9). Rhizomes (about 5 - 10 mm thick, mainly 50 - 200 mm long) spread within the uppermost soil layer (0-0.03 m). Roots arise mainly at horizontal

Table 4. Above- and underground biomass (in $g.m^{-2}$) in Paspalum notatum stands in the anthropic savanna of Cuba. Recorded at the end of the 1990 dry season (according to Hernandez L. unpublished).

	U - site		M - site		L - site		Significant differences (significance level = 0.05)
	x	s_x	x	s_x	x	s_x	
Aboveground biomass							
Live biomass	106	13	127	35	204	28	L > U
Dead biomass	632	179	437	162	977	18	L > M
Total biomass	738	191	564	165	1181	44	L > M
Underground biomass							
Total roots	359	91	335	11	299	21	
Live rhizomes	659	368	497	335	1134	345	
Dead rhizomes	292	93	246	182	396	198	
Total rhizomes	951	354	743	516	1530	536	
Total underground biomass	1310		1078		1829		
Root and rhizome detritus	211	43	239	18	271	9	

Note: x - arithmetic mean
s_x - standard error
The aboveground biomass and rhizome biomass were collected from three 0.25 x 0.25 m plots. Root biomass was assessed in three soil cores (50 m in diameter) to a depth of 0.15 m. For further detailed description of method see the chapter Material and methods.

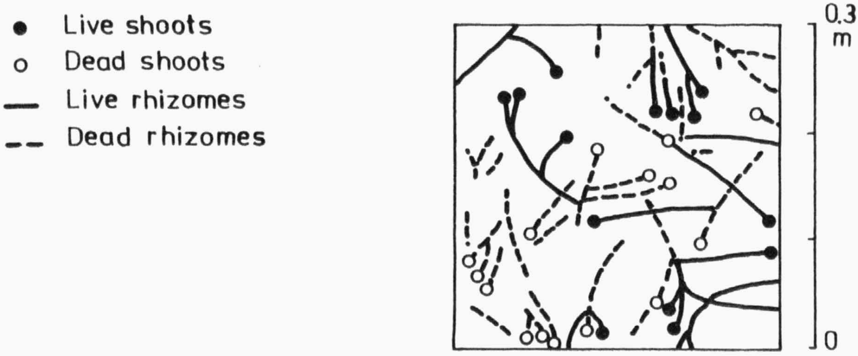

Fig. 9. Horizontal projection of a part of the rhizome system of *Paspalum notatum* growing on the M-site of the slope relief in the anthropic savanna of Cuba. The rhizome system was uncovered to a depth of 10 to 15 mm on October 1989.

rhizomes and stretch downwards not only vertically but above all aslantly to both sides forming in this way a dense net of roots in the upper soil layer. In the stands on M- and U-sites 38 and 47 % of the rhizome biomass was dead, respectively. However, thick hard dead roots were still connected with many dead rhizomes (Figs. 3, 9). In this way, the dead roots form a very important part of the whole net of the root system. *Paspalum notatum* may probably in this way relatively well enhance the resistence of the top soil layer against water erosion on sloped areas of the anthropic savannas.

The lowest amount of living roots (22.8 %, 99 g.m^{-2}) was in the *Paspalum* stand on the L-site, i.e., in the relatively wettest and nutrient-rich habitat (Tab. 1). However, a careful examination indicated that many roots which had been formed on rhizomes died (on rhizomes remained only several milimeters long root rests, Fig. 3). This was probably an effect of the increased soil moisture content or of the periodically flooding of the habitat during the rainy period. Nevertheless, at the end of dry period, the total root biomass on the L-site presented again the lowest values (about 10 % of total plant biomass, Tab. 4).

Although the roots of *Paspalum notatum* penetrate even to depth of 0.65 m (Hernández et Fiala 1992), the main part of total underground biomass was concentrated in the upper 0-0.05 m or 0-0.1 m soil layer. It was particularly due to the great biomass of rhizomes, which grow mainly near the soil surface. Nevertheless, the principal part of roots (more than 90 %) was also in the upper part of the soil profile (0-0.15 m). In the relatively driest habitat (M-site), the greatest amount of both living and total root biomass was in the 0-0.05 m soil layer, whereas on the U-site roots were also distributed in the deeper soil layer of 0.05-0.1 m (more than 40 % of total root biomass). A similar distribution (nearly 30 % of total root biomass in the 0.05-0.15 m soil layer) was noted in the relatively wettest and nutrient-rich habitat of the L-site, which may also reflect differences in the morphology of the plant, i.e., especially in a greater size of plant organs.

In the West and South African savannas 80 % of the root biomass was found deeper in the 0 to 0.3 or 0.5 m soil layers (Creswell et al. 1982, Huntley et Moris 1982, Menaut et Cesar 1979, 1982). However, shallow root systems were also described from other Cuban natural and anthropic savanna stands (more than 80 % of both living and total underground biomass in the 0-0.2 m soil layer) and from pasture stands (83 % and 90 % of the total root biomass in the 0-0.25 m layer, respectively) (Yepes et Alfonso 1972, Sagué et Hernández 1978, Fiala et Herrera 1988, Hernández et Fiala 1992).

Our sampling plots had been burned at the end of the dry period (April) of the current year 1989. Many authors reported an increased aboveground and underground production after fire. This increase often ranged from 30 to 60 % but reach even 90 % in some cases (Menaut et Cesar 1982). There was no difference in effects between minwinter fires and fires occuring immediately after the first spring rains (Trollope 1984). However, burns applied during the summer, when the grass was actively growing, had a disastrous effect on the productivity and basal cover of the grass sward. The research of Menaut et Cesar (1979) has shown that after burning of savannas (in the Lambo Reserve - the West Africa) the root biomass decreased to increase again after an early development of the aboveground plant parts. Kucera et Dahlman (1968) reported that annually burned plots (tall grass prairie) had more roots and rhizomes. The total underground biomass in the 0-0.05 m layer was 39 % less on unburned than on burned plots in six years. Rhizomes were more severely affected than roots. Hernández et Fiala (1992) reported that there were no great changes in total root biomass in the soil layer of 0-0.15 m of the same *Paspalum notatum* stand during the first months after fire. Nevertheless, the highest increase in root biomass in the upper soil layer (0-0.05 m) was recorded in the next months after fire.

Results of other studies (see, e.g., Menaut et Cesar 1982, Shrimall et Vyas 1975, Hernández et Fiala 1992) suggest that the lower values of underground biomass observed during the wet months may be due to a high rate of death and decay of the roots. Nevertheless, an increased soil moisture (L-site) and probably also a lower soil temperature in the high and dense stand on the L-site can result in a decrease of the living root/total root ratio (LR/TR ratio) (to 0.2 approximately) in response to the accumulation of dead underground roots. The greatest amount of underground plant detritus on the L-site (352 $g.m^{-2}$) supportes probably this conclusions (Tab. 2, 4). The living to total underground biomasss ratio can roughly indicate tha rate of root decomposition or the intensity of accumulation of undecomposed underground plant material. Data obtained by Hernández and Fiala (1992) indicate a very rapid turnover of the total root biomass in the *Paspalum notatum* stand in 1989 (annual root disappearance was 1070 $g.m^{-2}.yr$-1). Stanton (1988) reported that relative to temperate grasslands, the root turnover in tropical systems is quite rapid (to 93 and 97 % per year) and that fast decomposition may result in lower values of root biomass.

Biomass partitioning

Paspalum notatum stands on the three sites under study allocated the total biomass quite differently. The variation of R/S ratios and in the distribution of biomass to different plant organs reflects the strategy of plants in the allocation of biomass in different habitats. No great differences between various plant parts were recorded on the U-site. The differences in biomass allocation (above all living biomass) increased with the increased inclination of the slope. Greatest diferences in the biomass distribution showed rhizomes and roots.

The biomass was allocated to shoots and rhizomes nearly in the same extent (about 40 % of living and 30 % total biomass) in the stand on the U-site, which is partly shadowed by trees and shrubs during the first hours of the day. Increased temperature of the soil (M-site - dry and sunny part of the slope) and increased moisture content and fertility of the habitat (L-site) coincided apparently with decreased ratios of the total underground, living root, and total root biomass to the aboveground biomass. While the smallest proportion of the biomass was allocated to roots on the L-site, the largest proportion represented here the *Paspalum* rhizomes. The same relationship was also recorded in *Paspalum notatum* stands at the end of the dry period (Tab. 4). Of various environmental factors exerting a complex influence on the growth and production of *Paspalum*, the favourable temperature, water and nutrition regime of the L-site was probably related to the larger proportion of the rhizome biomass, which was two times greater than the shoot biomass. The biomass of underground plant organs and the R/S ratio increase with decreasing temperature (see, e.g., Brouwer 1966, McNaughton 1966, Davidson 1969, Turner 1972, Sims et al. 1978, Fiala 1976, Marshall 1977).

Fiala et Herrera (1988) reported relatively higher values of underground biomass ratios for some savanna stands in Cuba. They ranged from 1.71 to 2.21, when all biomass is considered, and from 2.5 to 3.8, when only the living biomass is taken into account. Nevertheless, the lowest values of these ratios were recorded in an anthropic savanna community.

In conclusion we should like to summarize that our data on both living and total aboveground biomass on U- and M-sites fall towards the lower values, whereas the living aboveground on the L-site (approximately two times as high) belongs to the highest values recorded in various savanna stands (see, e.g., Hopkins 1968, Bourliere et Hadley 1970, San José et Medina 1975, Lamotte 1975, Menaut et Cesar 1979, 1982, Medina 1982, Peréz et Šmíd 1984, Menendéz 1986, Fiala et Herrera 1988). Values of the total underground biomass fall approximately into the center of the range of data presented in the literature (see Discussion - Underground biomass). Nevertheless, the amount of the total underground biomass on the L-site is one of the highest values indicated by the above mentioned studies. Underground to aboveground biomass ratios found in *Paspalum notatum* stands belong to the lower R/S ratios recorded in tropical grasslands (see Werger 1983, Stanton 1988).

The biomass amount and distribution in three *Paspalum notatum* stands indicated that there existed considerable differences in biomass allocation patterns. In general, the more favourable the site (wetter and nutrient-richer habitat) the greater was the shoot and rhizome growth of *Paspalum* and the smaller was the root production. Our study has shown that the growth of *Paspalum notatum* in different environmental conditions of the soil catena is manifested by differences in the growth patterns, but at a relatively high and stable biomass allocation into the aboveground plant parts.

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Souhrn

Ve třech porostech *Paspalum notatum* v antropické savaně severozápadní Kuby, které se nalézaly v různých částech svahu představující půdní katénu, byla studována distribuce rostlinné biomasy do nadzemních a podzemních orgánů. Veškerá nadzemní biomasa porostu se v průměru pohybovala od 626 do 1358 g.m^{-2} a veškerá podzemní biomasa od 1182 do 1735 g.m^{-2} sušiny. Živá nadzemní biomasa představovala 38,2 až 61 %, biomasa živých oddenků 53,6 až 78,6 % a kořenů jen 22,8 až 26,1 % jejich veškeré biomasy. Čím bylo stanoviště vlhčí a živinami bohatší (dolní část svahového reliéfu), tím větší byla živá nadzemní biomasa (649 g.m^{-2}) a biomasa živých oddenků (1023 g.m^{-2}) a menší množství živých kořenů (99 g.m^{-2}). Zatímco procentuální distribuce biomasy do nadzemních částí se měnila od horní k dolní části svahu jen málo (z 34,1 na 43.9 %), zastoupení živých oddenků ve veškeré biomase výrazně vzrostlo (z 38,5 na 57,7 %) a naopak množství živých kořenů se zmenšilo (ze 17,8 na 5,6 %).

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