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# COMPARISON OF VERTICAL DISTRIBUTION OF LIVE AND DEAD FINE ROOT BIOMASS IN SIX TYPES OF CUBAN FORESTS

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Root biomass (diameter of roots less than 1 mm) in six Cuban forests of various types, which display significant variation in root dry mass, was studied. Root biomass can be specific for individual types of studied forests. Information on the vertical distribution of fine roots is essential in order to obtain unbiased estimates of fine root biomass. The upper 0–10 cm soil layer of both submontaneous evergreen narrow-leaved and semi-deciduous narrow-leaved forests contained the bulk of dry mass of live roots equal to 855 and 657 g $m^{-2}$, respectively, representing 76 and 61% of fine live roots recorded in the whole investigated soil profile. Different root distribution was observed in the mangrove forests where a larger amount of live fine roots (393 and 590 g $m^{-2}$) in deeper soil layers (10–25 cm), representing 57 and 65% of fine live roots recorded in the whole soil profile was found. The results showed significant differences in the vertical distribution of fine roots between mangrove and other types of tropical forest. Insights into below-ground carbon dynamics of tropical lowland and montane forests had significant implications on tropical forest carbon cycle.

Keywords: Evergreen forests, mangroves, root dry mass, semi-deciduous forests, soil depth

## INTRODUCTION

A significant proportion of the forest net production is allocated for the formation of fine roots which are large and dynamic components of these ecosystems (Vogt et al. 1996). Gill and Jackson (2000) observed the average turnover rates of 56%, annually, for forest fine roots. Therefore fine root mortality transfers considerable amounts of organic matter and nutrients into the forest soil. Fine root data can also be indicative of how root dynamics (the production and turnover of roots) in forests might alter in response to elevated temperatures, altered precipitation and nitrogen deposition (Gill & Jackson 2000). Dry matter of both live and dead fine roots can vary strongly during a seven-year period, where reduced soil fertility and volumetric soil water content lead to fine root biomass decline (Espeteta & Clark 2007). Furthermore, Powers et al. (2013) found that live fine root biomass vary more than dead root biomass. Root productivity is limited by water supply during the dry season in semi-deciduous lowland forests in Panama (Cavelier 1992). According to findings of Graefe et al. (2008), the average root loss rate decreases with elevation, indicating an increase in mean root longevity with increasing elevation. However, it was suggested that adverse soil conditions in the uppermost stand at 3060 m may reduce root longevity in South Ecuador, therefore additional factors, besides temperature, can control root dynamics in tropical mountain forests (Graefe et al. 2008). In addition, field study also showed that along the flooded forest gradient, fine root mass declines during the flood events (Chacon et al. 2008). However, such decline was more pronounced in the zone with shorter floods.

Root damage is often described as i) a decline in the amount of living fine roots, ii) an increase in the amount of dead versus live fine roots, and iii) an increasing amount of dead medium and coarse roots (Persson et al. 1995). That is why root biomass is considered as the most important stabilising element in various ecosystems (Fiala 1997). Damage of the fine root system may thus be expressed as the higher mortality rate compared to regeneration rate. Understanding, how disturbances caused by both anthropogenic activities and naturally occurring extreme climatic events influence the fine root biomass, is needed for the prediction of forest ecosystem functioning. A high root mortality following disturbances, such as droughts and fire may result in significant decline in nutrient availability (Silver & Vogt 1993, Asbjornsen et al. 2005, Beard et al. 2005). Fine root biomass decreased with intensity of disturbance, but forest disturbance intensity had no influence on the vertical distribution of the fine root biomass in the profiles (Leuschner et al. 2006).

As the world´s forests play a major role in regulating nutrient and carbon cycles, there is much interest in estimating their biomass. Knowledge about the amount of roots, particularly the active and live roots, and their distribution in the soil profile of different forest stands provide us with information essential for comparison between different forests. Variation in fine root biomass was quantified in the following forests: submontaneous evergreen broad-leaved forest (SEBF), submontaneus evergreen narrow-leaved forest (SENF), semi-deciduous broad-leaved forest (SDBF) and semi-deciduous narrow-leaved forest (SDNF) (Table 1). They belong to the major forest types distributed in north western part of Cuba. In addition, two species of mangroves were examined, i.e. *Rhizophora mangle* (mangrove forest—MRF) and *Avicennia germinans* (mangrove forest—MAF), which are important and productive forest resources in many tropical and subtropical countries which sustain a high ratio of root to shoot biomass (Fiala & Hernández 1993).

Moreover, a relatively broad set of data have been collected on the total fine root biomass of various types of Cuban forests (Fiala & Hernández 1993). However, the purpose of the present study was to present data focused on vertical distribution of both living and dead fine roots of chosen Cuban forests. Thus, the main objective of the study was to characterise vertical fine root distribution in several typical Cuban forests. It was hypothesised that:

(1) There is a lower accumulation of both living and dead fine roots in soil of submontaneous forests than that in dry habitat of semi-deciduous forests of lowland.

(2) Due to slower decomposition rate, a larger accumulation of dead dry mass of fine roots occurs in dry habitat of semi-deciduous forests reflected also in a larger total fine root dry

**Table 1** Study sites of various types of Cuban forests (Alain 1964, 1969, Acuna & Acuna 1967, Samek 1973), mean annual temperature (MAT), mean annual precipitation (MAP), altitude (m asl), soil characteristics (Orttega, 1982) and nomenclature (Alain 1964, 1969)

| Type of forest | Locality, MAT, MAP | Prevailing plant species | Soil type |
|---|---|---|---|
| Evergreen broad-leaved forest (SEBF) | Sierra del Rosario - Vallesito (22° 52' N, 82° 57' W, 425 m asl) 24.8 °C, 1800–2000 mm | *Pseudolmedia spuris, Matayba apelata, Prunus occidentalis* | Brown ferruginous soil |
| Evergreen narrow-leaved forest (SENF) | Sierra del Rosario - Salon (22° 52' N, 82° 57' W, 400 m asl) 24.8 °C, 1800–2000 mm | *Hibiscus elatus, Lasiacis divaricata, Lithachne pauciflora, Olyra latifolia, Psychotria horizontalis, Policourea domingensis, Dendropanax arboreus* | Brown ferruginous soil |
| Semi-deciduous narrow-leaved forest (SDNF) | Yaguaramas – Cienfuegos (22° 15' N, 80° 41' W, 25 m asl) 25 °C, 1400–1600 mm | *Lysiloba bahamense, Bursera simaruba* | Soils belonging to the Mocarrero series |
| Semi-deciduous broad-leaved forest (SDBF) | Carapachibey - Isla de la Juventud (21° 28' N, 82° 55' W, 2 m asl) 25 °C, 1200–1400 mm | *Bursera simaruba, Pithecellobium lentiscifolium* | Organic soil in the holes of rock above coral limestone |
| Mangrove forest (MRF) | Majana (22° 41' N, 82° 47' W, temporally or permanently flooded ) 24.5 °C, 1200–1400 mm | *Rhizophora mangle* | Very salinised marl with peat organic sedimentary deposit |
| Mangrove forest (MAF) | Majana (22° 41' N, 82° 47' W, temporally or permanently flooded ) 24.5 °C, 1200–1400 mm | *Avicennia germinans* | Fibrous peat, half salinised, on marl with bio-alluvial deposit |

mass in comparison with submountaneous evergreen forests.

(3) A reduction of the amount of both live and dead fine roots occurs with increasing soil depth.

## MATERIALS AND METHODS

### Study sites

Six various forest stands, situated in the western part of Cuba and in Isla de la Juventud were studied in 1987 and 1989. They were located in the regions of Cienfuegos, Sierra del Rosario, Isla de la Juventud province (Table 1).

### Root collection

Fine root samples were randomly collected in each study forests in ten soil blocks (10 × 10 cm and 15 cm deep). In mangroves, fine roots were assessed in twenty soil cores (5 cm in diameter, to the depth of 15 cm). In order to describe vertical distribution and proportion of fine live and dead roots in different soil layers, three soil cores or blocks were excavated deeper and divided successively from the depth 0–5, 5–10, 10–15, 15–20 and 20–25 cm. Samples were washed in the laboratory on sieves (mesh size 0.1 mm) and dried to constant weight at 70–80 °C. Roots were separated into < 1 mm fine root diameter and separated into live and dead categories, according to their colour and mechanical consistency. The additional vital staining technique with Congo red was also used for this purpose (Ward et al. 1987).

### Statistical analysis

The data were evaluated by analysis of variance (ANOVA) using the statistical package, STATISTICA 12. One-sample T-tests was used to determine if the mean of a single variable differed significantly from the constant. Significance levels were reported in the figures and tables ($p < 0.05$). All data tested was of normal distribution.

## RESULTS AND DISCUSSION

### Total biomass of fine roots

The data indicated lower amount of live root biomass in submontaneous forest than lowland semi-deciduous forests (Table 2). Specifically, the lowest dry mass of total fine roots was assessed in both submontaneous evergreen broad-leaved (212 g $m^{-2}$) and narrow-leaved forests (160 g $m^{-2}$). Fine live roots were only 64 and 90 g $m^{-2}$ in these stands, respectively (Table 2). Amount of live root biomass is affected by root longevity, since greater average fine root longevity is found under moist conditions compared to dry conditions (Pregitzer et al. 1993). In the present study, higher amount of total fine roots were recorded in both semi-deciduous forests in the range of 371–410 g $m^{-2}$. Vogt et al. (1996) evaluated large data-sets and concluded that climatic variable and nutrient storage pools successfully predict fine root net primary production, whereas fine root biomass is better predicted by nutrients in litterfall. The estimated values lie within the range for fine roots (< 2 mm diameter, 25 cm depth) was reported for various tropical forests. For example, mean fine root dry mass ranges from 134 to 234 g $m^{-2}$ of two dry tropical evergreen forests and the live biomass fraction of fine roots fluctuate from 45 to 203 g $m^{-2}$ during dry periods, reaching values from 141 to 359 g $m^{-2}$ during wet periods (Visalakshi 1994). On the contrary, Cavelier (1992) found that fine root biomass is larger in the mountains (200 g $m^{-2}$), while only 144 g $m^{-2}$ is assessed in lowlands. Biomass of fine roots (< 2 mm) range from 300 to 1300 g $m^{-2}$ depending on slope position in moist tropical montane forest (Vance & Nadkarni 1992). Root mat is presented on the forest floor which contained 50–70% of the below-ground fine root biomass. However, a root mat was not present on the forest floor of studied forests. In comparison with evergreen and semi-deciduous forests, the Cuban mangrove stands were characterised by very high values of both total and live fine root biomass, 1358 and 554 g $m^{-2}$ respectively in *Avicennia,* and 1594 and 758 g $m^{-2}$ respectively in *Rhizophora* (Table 2). Thus, data obtained in mangroves were significantly higher in comparison with other studied forests.

Root dry mass also showed a seasonal course, which is in agreement with Girardin et al. (2013) and Kho et al. (2013) who pointed at a strong seasonality of fine root net primary production in tropical forests. Similarly, root mass showed a pronounced seasonal pattern with unimodal peaks obtained during October–December period in tropical dry evergreen forests in India (Visalakshi 1994). Therefore, the root sample collections took place in rainy period, i.e. in

**Table 2** Dry mass of live and dead fine roots (g DW $m^{-2}$) of several Cuban forests (soil layer 0–15 cm)

| Forest | SEBF | SENF | SDNF | SDBF | MRF* | MAF* |
|---|---|---|---|---|---|---|
| Live fine roots | $64^{a}$ | $90^{ab}$ | $87^{ab}$ | $200^{b}$ | $758^{d}$ | $554^{c}$ |
| Dead fine roots | $148^{ab}$ | $70^{a}$ | $284^{b}$ | $210^{ab}$ | $851^{c}$ | $804^{c}$ |
| Total fine roots | $212^{a}$ | $160^{a}$ | $371^{a}$ | $410^{a}$ | $1594^{c}$ | $1358^{b}$ |

Different letters indicate significant differences within each parameter ($p < 0.05$) according to LSD-test, n =10 or 20

the peak of fine root production. Nevertheless, the highest values of dry mass of fine roots are found in the microphylleous forests, where soil moisture was lower (Hernández & Sánchez 2012). The results do not fully support our hypothesis that a large fine root biomass occurs in submontaneous forests. Greater values of fine root mass, mainly dead mass, is rather related to lower soil moisture in semi-deciduous forest (Hernández & Sánchez 2012). In addition, values of standing fine root biomass are higher in sandy loam soil than in clay soil in oligotrophic Bornean rain forest (Kochsiek et al. 2013). In Cuba, soil moisture varies according to the site (Hernández & Sánchez 2012). The results showed the importance of the upper soil layers in the dynamics of soil moisture and fine root biomass production. In the forests, the average root turnover rate is represented annually about 49% of dry mass (Partel & Wilson 2002, Lin et al. 2011). According to Fujimaki et al. (2008) the fine root decomposition is generally faster in dry evergreen forest than dry deciduous forests. The results are in agreement with the second hypothesis. These results also corresponded with a greater accumulation of dead undecomposed fine root mass recorded only in semi-deciduous narrow-leaved forest, which indicated both their faster root mortality and slower rate of root decomposition.

Amount of root biomass of different mangrove forest varied considerably. Lugo & Snedaker (1974) deduced that the variability in the mangrove biomass data is attributed to age, stand history and structural difference. The largest root biomass is found in the mangrove (*Rhizophora*) of southern Thailand (220–236 ton $ha^{-1}$), due to high precipitation, nutrient rich mud flat and little human influence. Mostly, lower values (around 9 ton $ha^{-1}$) are reported in tropical America (including Cuba), Florida and Japan (Fiala & Hernández 1993). However, the root biomass also differs from species to species. In the present study, root biomass assessed in the both mangrove sites showed some differences between both species.

## Vertical distribution of fine roots

The absolute values of fine root biomass obtained from the vertical analysis were not comparable with the presented data in Table 2 (n =10 or 20), because of lower replication of samples in the vertical analysis (n = 3). However, the evaluation of vertical distribution in the frame of individual forest types is valuable. A reduction of the amount of fine roots was found with increasing soil depth in most of the investigated forests (Table 3, Figure 1). Thus, the third hypothesis was confirmed. In the upper 0–5 cm soil layer of submontaneous evergreen forests (345 and 650 g $m^{-2}$) and of semi-deciduous forests (505 and 136 g $m^{-2}$), a substantially greater amount of dry mass of fine live roots was concentrated. These amounts represented 53 and 57%, respectively, and 45 and 72% of root dry mass recorded in the entire soil profile studied (Table 4). Similarly Noguchi et al. (2014) estimated that more than 74 and 93% of the fine root biomass is distributed within the upper 20 and 40 cm soil layer, respectively. Fine roots share 80–90% of roots in the upper 20 cm layer at all sample plots located in the Amazonian rain forests (Pavlis & Jeník 2000), and nearly two thirds of roots occur in the same soil layer in deciduous tropical forest in Mexico (Castellanos et al. 1991). On the other hand, Soethe et al. (2006) found that vertical distribution of root lengths is very similar in both dry and rainy seasons. The current data showed an exception in root distribution in mangrove forests, where a larger amount of fine roots both live (on average 491 g $m^{-2}$) and dead (on average 698 g $m^{-2}$) were found in deeper soil layers, 10–25 cm (Table 3, Figures 1e, f). For example,

**Table 3** Dry mass ± SD of live and dead fine roots (g DW m$^{-2}$) of several Cuban forests in soil layer 0–25 cm

| Soil depth | | SEBF | SENF | SDNF | SDBF | MRF | MAF |
|---|---|---|---|---|---|---|---|
| 0–5 cm | Live roots | 345 ± 183$^{ab}$ | 650 ± 222$^{b}$ | 505 ± 349$^{b}$ | 136 ± 18$^{a}$ | 170 ± 11$^{a}$ | 122 ± 28$^{a}$ |
| | Dead roots | 966 ± 389$^{a}$ | 449 ± 154$^{a}$ | 2154 ± 1489$^{b}$ | 125 ± 18$^{a}$ | 102 ± 6$^{a}$ | 226 ± 14$^{a}$ |
| | Total roots | 1311 ± 572$^{ab}$ | 1100 ± 376$^{a}$ | 2659 ± 1838$^{b}$ | 260 ± 31$^{a}$ | 272 ± 17$^{a}$ | 349 ± 41$^{a}$ |
| 5–10 cm | Live roots | 91 ± 55$^{ab}$ | 205 ± 58$^{c}$ | 152 ± 68$^{bc}$ | 26 ± 1$^{a}$ | 151 ± 59$^{bc}$ | 170 ± 50$^{bc}$ |
| | Dead roots | 161 ± 97$^{a}$ | 192 ± 54$^{a}$ | 473 ± 248$^{b}$ | 35 ± 1$^{a}$ | 123 ± 50$^{a}$ | 238 ± 70$^{a}$ |
| | Total roots | 252 ± 152$^{ab}$ | 397 ± 112$^{bc}$ | 625 ± 316$^{c}$ | 61 ± 1$^{a}$ | 275 ± 109$^{ab}$ | 408 ± 120$^{bc}$ |
| 10–15 cm | Live roots | 89 ± 38$^{ab}$ | 191 ± 84$^{bc}$ | 262 ± 146$^{c}$ | 27 ± 1$^{a}$ | 169 ± 68$^{bc}$ | 140 ± 23$^{abc}$ |
| | Dead roots | 111 ± 46$^{a}$ | 153 ± 68$^{a}$ | 117 ± 65$^{a}$ | 34 ± 3$^{a}$ | 332 ± 142$^{b}$ | 142 ± 24$^{a}$ |
| | Total roots | 200 ± 84$^{ab}$ | 344 ± 152$^{bc}$ | 379 ± 211$^{bc}$ | 61 ± 4$^{a}$ | 501 ± 210$^{c}$ | 282 ± 46$^{abc}$ |
| 15–20 cm | Live roots | 57 ± 25$^{a}$ | 81 ± 15$^{ab}$ | 137 ± 76$^{bc}$ | - | 194 ± 57$^{c}$ | 141 ± 19$^{bc}$ |
| | Dead roots | 71 ± 31$^{a}$ | 119 ± 22$^{ab}$ | 74 ± 41$^{a}$ | - | 384 ± 110$^{c}$ | 178 ± 24$^{b}$ |
| | Total roots | 128 ± 56$^{a}$ | 200 ± 37$^{ab}$ | 211 ± 116$^{ab}$ | - | 578 ± 168$^{c}$ | 318 ± 43$^{b}$ |
| 20–25 cm | Live roots | 65 ± 36$^{bc}$ | 5 ± 2$^{a}$ | 22 ± 6$^{ab}$ | - | 227 ± 45$^{d}$ | 112 ± 27$^{c}$ |
| | Dead roots | 81 ± 45$^{b}$ | 4 ± 1$^{a}$ | 31 ± 8$^{ab}$ | - | 200 ± 41$^{c}$ | 160 ± 35$^{c}$ |
| | Total roots | 146 ± 81$^{b}$ | 9 ± 3$^{a}$ | 53 ± 15$^{ab}$ | - | 427 ± 86$^{d}$ | 272 ± 61$^{c}$ |

Different letters indicate significant differences at $p < 0.05$ according to Tukey-test, n = 3

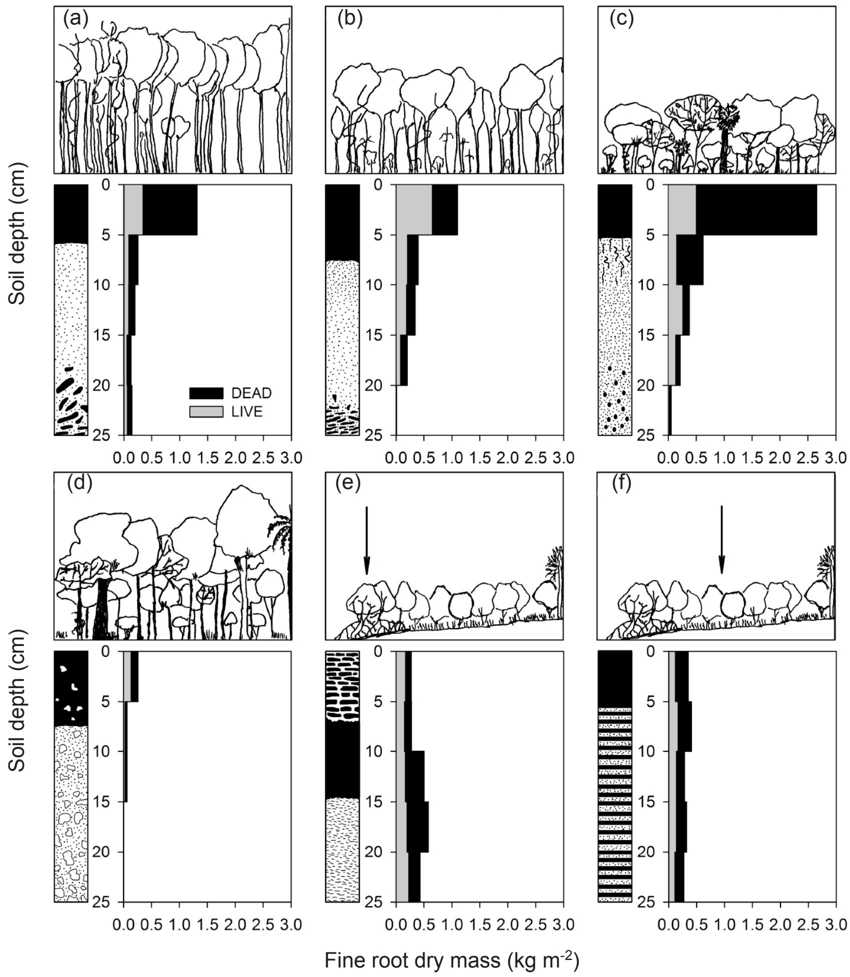


**Figure 1** Scheme of above-ground parts of studied forest stands: a = submontaneous evergreen broad-leaved forest (SEBF), b = submontaneus evergreen narrow-leaved forest (SENF), c = semi-deciduous narrow-leaved forest (SDNF), d = semi-deciduous broad-leaved forest (SDBF), e = two species of mangroves *Rhizophora mangle* (MRF) and f = *Avicennia germinans* (MAF); vertical distribution of live and dead roots (g DW m$^{-2}$) and description of soil profile

**Table 4** Percentage distribution of live, dead and total dry mass of fine roots in several Cuban forests in soil layer 0–25 cm

| Soil depth | | SEBF | SENF | SDNF | SDBF | MRF | MAF |
|---|---|---|---|---|---|---|---|
| 0–5 cm | Live roots | 53b | 57b | 47b | 72c | 19a | 18a |
| | Dead roots | 69d | 49c | 76d | 64d | 9a | 24b |
| | Total roots | 64bc | 54b | 68c | 68c | 13a | 21a |
| 5–10 cm | Live roots | 14a | 18ab | 14a | 14a | 17a | 25b |
| | Dead roots | 12a | 21b | 17ab | 18a | 11a | 25b |
| | Total roots | 12a | 19ab | 16ab | 16ab | 13a | 25b |
| 10–15 cm | Live roots | 14a | 17a | 24b | 14a | 19ab | 20ab |
| | Dead roots | 8a | 17b | 4a | 18b | 29c | 15b |
| | Total roots | 10a | 17b | 10a | 16b | 24c | 17b |
| 15–20 cm | Live roots | 9a | 7a | 13ab | - | 21b | 21b |
| | Dead roots | 5a | 13b | 3a | - | 34d | 19c |
| | Total roots | 6a | 10a | 5a | - | 28c | 20b |
| 20–25 cm | Live roots | 10b | 0.4a | 2a | - | 25d | 16c |
| | Dead roots | 6b | 0.5a | 1ab | - | 17c | 17c |
| | Total roots | 7b | 0.4a | 1a | - | 21c | 17c |

Different letters indicate significant differences at $p < 0.05$ according to Tukey's-test, n = 3

in *Rhizophora* site, situated close to the sea, both total and live root biomass was conspicuously accumulated in deeper 10–25 cm soil layer (73 and 65% respectively, of total and live fine roots recorded in the entire soil profile investigated). Larger amount of detritus was accumulated in the soil of Cuban mangrove stands, especially in *Avicennia* site (Fiala & Hernández 1993). Different types of mangrove forests show different patterns of litter accumulation, decomposition and its export (Lugo & Snedaker 1974, Cintron et al. 1985, Twilley et al. 1986). The current observation of the relatively high accumulation of organic detritus in *Avicennia* site corresponded with the conclusions of Hesse (1961) that *Avicennia* mud (undecomposed plant remnants) decomposes at a slower rate than *Rhisophpra* mud. The results pointed to various intensity of accumulation of live and dead fine root dry mass in Cuban forests. It confirmed the assumption of the effect of soil depth on the reduction of root dry mass, above all, in semi-deciduous forest.

## CONCLUSIONS

The present study concluded that a lower accumulation of live fine roots was found in the soil of submontaneous forests than in dry semi-deciduous forests of lowland. Thus, the first hypothesis was confirmed. Secondly, the results were in agreement with the second hypothesis, since a greater accumulation of dead undecomposed fine root mass was recorded in dry habitat of semi-deciduous narrow-leaved forest in comparison with submountaneous evergreen forests. Finally, a reduction of the amount of fine roots with increasing soil depth was found in most of the investigated forests, thereby the third hypothesis was confirmed partly.

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