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Root behavior of savanna species in Brazil's Pantanal wetland

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HIGHLIGHTS

- Field data were collected to calculate the root biomass of savanna woody species as a function of tree diameter.
- Tree diameter at ground level is useful for estimating the root biomass of savanna woody species.
- Shorter root systems and lower root biomass can be an indication of savannas in wetland areas due to the effects of elevated water table.

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ABSTRACT

The objective of this study was to determine the maximum depth, structure, diameter and biomass of the roots of common woody species in two savanna physiognomies (savanna woodland and open woody savanna) in Brazil's Pantanal wetland. The root systems of 37 trees and 34 shrubs of 15 savanna species were excavated to measure their length and depth and estimate the total root biomass through allometric relationships with stem diameter at ground level. In general, statistical regression models between root weight and stem diameter at ground level showed a significance of $P < 0.05$ and R^2 values close to or above 0.8. The average depths of the root system in wetland savanna woodland and open woody savanna are 0.8 ± 0.3 m and 0.7 ± 0.2 m, respectively, and differ from the root systems of savanna woody species in non-flooding areas, whose depth usually ranges from 3 to 19 m. We attribute this difference to the adaptation of woody plant to the shallow water table, particularly during the wet season. This singularity of woody species in wetland savannas is important when considering biomass and carbon stocks for national and global carbon inventories.

1. Introduction

Woody plants in savanna ecosystems maintain their physiological activities during the dry season, despite very low rainfall (Quesada et al., 2004). They come into leaf, flower, and fructify in the dry season (Oliveira and Gibbs, 2000), indicating the access of root to groundwater and the water table. For instance, Canadell et al. (1996) noted roots of woody plants reaching great depths, in the order of 40 m in arid biomes such as deserts, sclerophyllous forest, and tropical savannas.

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The plants in Brazil's central-western savannas exhibit root behavior similar to that of savannas around the world (Rawitscher et al., 1943). Rossato et al. (2012) identified woody species in Brazil's central-western savannas with conspicuous access to groundwater at several depths, including the water table. These plants can develop root systems reaching depths of 3 to 19 m (Rawitscher et al., 1943).

In the savannas of Venezuela, Africa, and Brazil's central-west, the ratio between below-ground and above-ground plant biomass (BG:AG) is usually >1 (Castro and Kauffman, 1998; Rutherford, 1983; Sarmiento and Vera, 1979). However, Ribeiro et al. (2011) found a BG:AG ratio of <1 in Brazil's central-western savanna. Jackson et al. (1996), who reviewed the BG:AG ratios in several vegetation biomes, found <1 only in cultivated areas and forest. The literature contains few reports about root biomass in savannas, although such information is important for estimating biomass and carbon stocks in wetland savannas.

The Pantanal region is an important wetland in central-South America in Brazil, Bolivia and Paraguay, covering an area approximately of 140,000 km^2 in Brazil (Silva and Abdon, 1998). The main type of vegetation in this wetland is savanna (locally known as 'cerrado'). Most plant species in the Pantanal wetland are the same species that occur in Brazil's non-flooding central-western savanna (Ratter et al., 2003). Both regions have unfertile soils, with a predominance of sandy spodosols in the Pantanal (Fernandes et al., 2007) and oxisols and spodosols in the non-flooding savannas of Brazil's central-west (Reatto et al., 1998). The regional climate is markedly seasonal, with rainfall prevailing between October and April, with an annual average of 1500 mm in the non-flooding central-western region (Gan et al., 2004) and 1180 mm in the Pantanal wetland (Soriano and Alves, 2005).

The present study aims to determine the variation in depth, structure and biomass of the roots of common trees and shrubs species in two savanna physiognomies in Brazil's Pantanal wetland. Given that root studies are usually time consuming, difficult and expensive, an additional goal of this work is to develop statistical regression models of stem diameter at ground level and root biomass, enabling possible future estimations of root biomass based solely on stem diameter data and thus, preventing destructive tree sampling.

2. Materials and methods

2.1. Study site

Flooding in the Pantanal varies greatly in annual and interannual intensity due to changes in rainfall distribution and quantity in both plains and highlands. The plains landscape is almost flat, with a declivity of less than 25 cm km^{-1}, where water flows slowly through the terrain (Carvalho, 1986). In savanna woodland (broken tree canopy, with underlying shrubs and ground-level vegetation) and open woody savanna (broken woody layer of shrubs with sparser trees and grasses), flooding occurred only during the exceptionally wet years of 1905, 1913, 1920, 1982, 1988 and 1995 (Bergier and Resende, 2010). Annual flooding, however, has never reached the savanna forest (dense canopy with sparser ground-level vegetation and semideciduous forest, located on somewhat higher terrain (Fig. 1)). The vegetation types in relatively higher topography are in fact the product of a non-flooding area. However, despite the absence of flooding, the level of the water table rises in the rainy season to about 1.5 m below the soil surface (Gradella et al., 2009).

2.2. Root surveys

Woody native species were sampled in two savanna physiognomies: savanna woodland (19°00′42.7′′S; 56°38′29.5′′W) in April 2008, and open woody savanna (18°59′45′′S; 56°39′44′′W) in November 2009 in the Nhumirim Experimental Farm, located in the sub-region of Nhecolândia, Pantanal wetland, Brazil.

The usual botanical definitions presented by Font Quer (1985) were considered for shrubs as woody plants, with a height of less than 5 m, and multiple ramifications from the base, without a dominant stem; subshrubs as plants with a woody base, ramified, with heights ranging from 0.5 to 2 m; and trees as woody plants at least 5 m in height with a dominant stem that ramifies after reaching a certain height, forming the tree canopy.

Ten or more individuals of the most common species with different stem diameters were sampled in both savanna physiognomies (Castro and Salis, 2012; Salis et al., 2008). The subshrub species *Annona dioica* A.St.-Hil. (25), shrub species *Byrsonima cydoniifolia* Mart. (10), and tree species, *Curatella americana* L. (10) and *Mouriri elliptica* Mart. (10) were sampled by the wandering-quarter method (Brower and Zar, 1984), and were excavated and weighed to develop statistical regression models to estimate root biomass. Fourteen trees of 10 species in the savanna woodland were also sampled: *Bowdichia virgilioides* Kunth, *Caryocar brasiliense* Cambess., *Casearia sylvestris* Sw., *Cecropia pachystachya* Trécul, *Dipteryx alata* Vogel, *Sapium haematospermum* Müll.Arg., *Simarouba versicolor* A.St.-Hil., *Stryphnodendron adstringens* (Mart.) Coville, *Tabebuia aurea* Benth. & Hook.f. (2) and *Zanthoxylum rigidum* Humb. & Bonpl. (4) by the wandering-quarter method (Brower and Zar, 1984). These trees were excavated and analyzed as a single category to model the root biomass for less common species, following the methodology described by Anderson and Ingram (1993). Some individuals of *Annona dioica, Mouriri elliptica* and *Tabebuia aurea* were sampled in both savanna physiognomies.

The trees were uprooted using a tractor. The soils of the Pantanal of Nhecolândia are sandy, with 94% to 99% of sand content (Cunha, 1980), which makes fieldwork easy. After the roots were loosened, the broken roots, including lateral

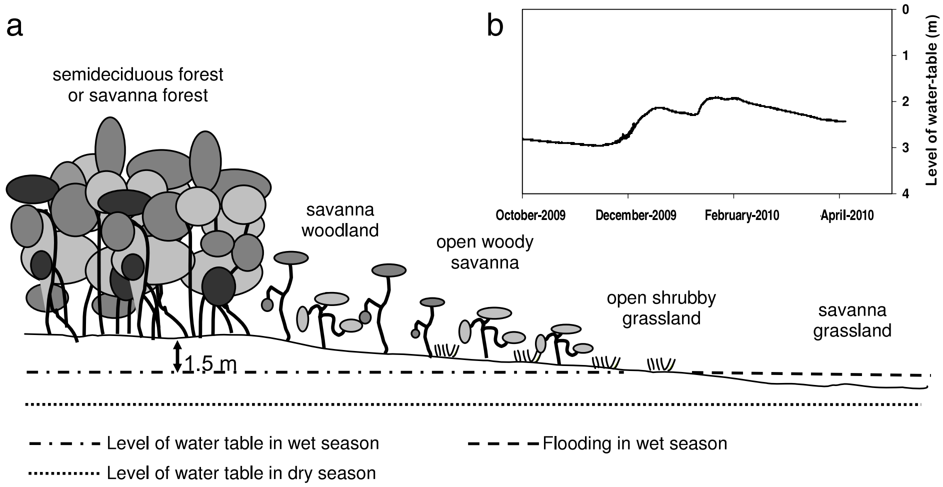

Fig. 1. (a) Gradient of physiognomies in the Nhecolândia Pantanal wetland associated with maximum flooding patterns and water table level. Root depth is limited by the water table shown in the plot in (b). The plot was obtained at the Nhumirim Experimental Farm using data provided by the project "Multi-scale analysis of biodiversity patterns to define sustainable management criteria for cattle ranches in the Pantanal", supported by Embrapa.

roots, were dug out entirely by hand. Schematic diagrams of the roots of the most common species and of different root architectures were drawn. The stem diameter at ground level (DGL), total height above ground level, root depth, root biomass, diameter and number, and length of lateral branching roots were all recorded.

The measured stem diameters and root weights were employed in statistical regression models to determine a and b constants from the different allometric equations ($Y = a + bX$, $Y = ae^{Xb}$, $Y = aX^b$), where Y is the dry weight of root biomass (B) and X is the stem diameter at ground level (D). Stem diameter is easily determined, even from savanna trees and shrubs that often have several ramifications. The stem diameters of plants with more than one stem at ground level were determined individually and added up to determine the "total basal area". An equivalent diameter was then calculated to this total basal area, and was used in the regressions models.

3. Results

The landscape of this study is composed of savanna woodland trees with heights ranging from 1.6 to 11.1 m and open woody savanna with smaller trees of 1.6 to 3.5 m in height and shrubs of 0.4–2.6 m (Table 1). The subshrub *Annona dioica* and shrub *Byrsonima cydoniifolia* (=*B. orbignyana* A. Juss.) had trunks ramified at ground level. Other tree species such as *Curatella americana* and *Mouriri elliptica* were also sometimes ramified.

The root depths in both savanna physiognomies presented non-normal distribution statistics by the Shapiro–Wilk test. Averages root depths were not significantly different (Mann–Whitney non-parametric test, $P < 0.05$) in the two physiognomies (0.8 ± 0.2 m in savanna woodland and 0.7 ± 0.2 m in open woody savanna). The deepest recorded root depths were 1.4 m (*Zanthoxylum rigidum*) for savanna woodland and 1.1 m (*Tabebuia aurea*) for open woody savanna (Table 1). Most of the tree species have roots well above the water table level (Fig. 1). The average length of lateral roots was 2.7 ± 1.7 m in savanna woodland and 1.8 ± 1.4 m in open woody savanna. The longest length of lateral roots was 8 m (*Cecropia pachystachya*) in savanna woodland and 4.5 m (*Diospyros hispida*) in open woody savanna (Table 1). Lateral roots with diameters ranging from 2 to 16 cm were found between 10 and 20 cm below the soil surface in both savanna physiognomies (Fig. 2).

The root biomass of individual trees in the savanna woodland varied from 0.7 to 147.4 kg, representing in average 23±9% of the total plant biomass, and varied from 0.5 to 10.4 kg (average 31 ± 11%) in open woody savanna. Only one individual of *Curatella americana* and one of *Caryocar brasiliense* showed greater root biomass, i.e., 50% and 54% of the total plant biomass, respectively (Table 1). These data demonstrate that the tree biomass in both savanna physiognomies is higher in the above-ground fraction of plant tissues.

The root biomass of *Byrsonima cydoniifolia* shrubs in open woody savanna varied from 0.2–3.4 kg, which is equivalent to an average of 23 ± 6% of the total biomass and similar to our findings for the tree species. However, the subshrub *Annona dioica* showed greater root biomass in both physiognomies, with an average of 54±12% in open woody savanna and 69±9% in savanna woodland.

The species under study showed a good relationship between dry weight of root biomass and stem diameter at ground level. These relationships are usually better explained by an exponential equation. All the regression models showed a level of significance of $P < 0.05$ and R^2 values close to or higher than 0.8 (Fig. 3).

Table 1
Root morphology of 71 woody individuals analyzed in two savanna physiognomies in Nhecolandia Pantanal wetland, Brazil.

Species[a]	Stem diameter at ground level (cm)	Height (m)	Average root depth (m)	Maximum length of lateral root branch (m)	Root biomass (kg) and (% of root biomass)
Savanna woodland					
Annona dioica A.St.-Hil. (10), DS	2–9	0.6–1.7	0.7 ± 0.2	-	0.1–2.0 (53–82)
Casearia sylvestris Sw. (1), ET	10	5.3	1.0	1.0	3.0 (20)
Cecropia pachystachya Trécul (1), ET	19	11.1	1.2	8.0	23.9 (17)
Curatella americana L. (10), ET	8–28	2.7–9.6	0.8 ± 0.3	1.1–4.0	0.7–56.2 (16–54)
Dipteryx alata Vogel (1), ST	30	9.3	1.0	5.0	147.4 (23)
Mouriri elliptica Mart. (10), ET	7–25	2.8–5	0.7 ± 0.2	1.0–2.5	1.8–28.8 (12–34)
Sapium haematospermum Müll.Arg. (1), ET	14	4.8	1.0	–	1.8 (17)
Simarouba versicolor A.St.-Hil. (1), ST	10	8.3	1.0	–	1.3 (15)
Tabebuia aurea Benth. & Hook.f. (1), DT	29	8	1.2	3.7	115.2 (34)
Zanthoxylum rigidum Humb. & Bonpl. (4), DT	10–21	4.3–7	1.1 ± 0.3	1.1–6.5	1.9–17.4 (14–23)
Average	12.7 ± 7.2	4.1 ± 2.6	0.8 ± 0.2	2.7 ± 1.7	13.7 ± 30.1 (34.9 ± 22.1)
Open woody savanna					
Annona dioica (15), DS	1.8–10	0.4–1.8	0.8 ± 0.1	0.2–3.0	0.03–3.2 (38–74)
Bowdichia virgilioides Kunth (1), DT	9	3.6	1.0	0.7	2.7 (27)
Byrsonima cydoniifolia Mart. (10), ES	4.5–12	1.3–2.6	0.6 ± 0.1	0.3–4.0	0.2–3.4 (17–34)
Caryocar brasiliense Cambess. (1), DT	6	1.6	0.7	1.0	1.1 (50)
Diospyros hispida A.DC. (1), DT	7	2.8	0.5	4.5	–
Mouriri elliptica (1), ET	19	3.2	0.6	2	10.4 (20)
Stryphnodendron adstringens (Mart.) Coville (1), DT	5	1.9	0.7	2.4	0.5 (28)
Tabebuia aurea (1), DT	9.5	3.5	1.1	1.5	1.3 (32)
Average	7 ± 3.4	1.7 ± 0.7	0.7 ± 0.2	1.8 ± 1.4	1.3 ± 1.9 (39.9 ± 17.8)

[a] Values in parentheses indicate the number of sampled individuals of each species. DS = Deciduous subshrub, DT= Deciduous tree, ES = Evergreen shrub, ET = Evergreen tree, ST = Semideciduous tree.

4. Discussion

Canadell et al. (1996) reviewed the maximum depth of roots in various biomes and found deeper roots in more arid areas such as deserts, sclerophyllous forests and savannas. Rawitscher et al. (1943), Rawitscher (1948) and Oliveira et al. (2005), who studied woody species of upland savanna in South America, and Rutherford (1983), who studied African savannas, also observed deep roots ranging from 3 to 19 m reaching the water table. Most species in the Pantanal are typical of savanna vegetation occurring in Brazil's central-western plateau, such as *Annona dioica, Byrsonima* spp., *Caryocar brasiliense, Stryphnodendron adstringens* (=*S. barbatimam* Mart.), and *Tabebuia aurea* (=*Tecoma caraiba* Mart.), which were described by Rawitscher (1948) as having deep roots (varying from 3 to 8 m). In these same species, we observed shorter roots (<1.4 m) in two savanna physiognomies in the Pantanal wetland. This characteristic had already been observed by Dubs (1992) in savanna forest of the Pantanal in eight savanna tree species displaying root depths no greater than 1.2 m. This "shortness" of roots found in savanna physiognomies of the Pantanal can be explained by the fact that the water table is closer to ground level. According to Gradella et al. (2009), the water table can reach 1.5 m below the soil surface in areas of semideciduous forest in the Pantanal, which probably limits the growth of plant roots.

The physiognomies of savanna woodland and open woody savanna occur slightly below the topographic level of the forested areas; hence, these landscapes can be more influenced by the water table. We believe that the water table in the Pantanal plays an important role in determining plant root depth.

Savanna species cannot tolerate hypoxia in roots (Joly and Crawford, 1982); hence, woody plants in the Pantanal have a relatively narrower soil layer where roots can grow freely. The maximum depth of the root system is thus limited by the maximum level the water table reaches in the rainy season, when the groundwater is recharged. In the Llanos (Venezuelan savannas), Foldats and Rutkis (1975) observed restricted root growth and occasionally full decay of younger absorbing roots in *Curatella americana* because of anoxic conditions induced by the rising water table.

Some savanna species such as *Stryphnodendron adstringens* can occur across a wide gradient of savanna physiognomies, adapting to different water table depths (Rossato et al., 2012). This species also occurs in open woody savanna in the Pantanal. From the data shown in this article, the same wide plasticity may also be occurring in *Curatella americana, Tabebuia aurea* and *Mouriri elliptica*.

The first lateral root branches develop between 10 and 20 cm below the soil surface. Sternberg et al. (2004) and Scholz et al. (2008) reported an analogous root architecture in savanna tree species in Brazil's central-western region. These authors suggest that the function of greater root development in tropical savannas may be to absorb nutrients from the top layers of the soil profile, where the availability of nutrients is greater. In *Curatella americana*, Foldats and Rutkis (1975) observed

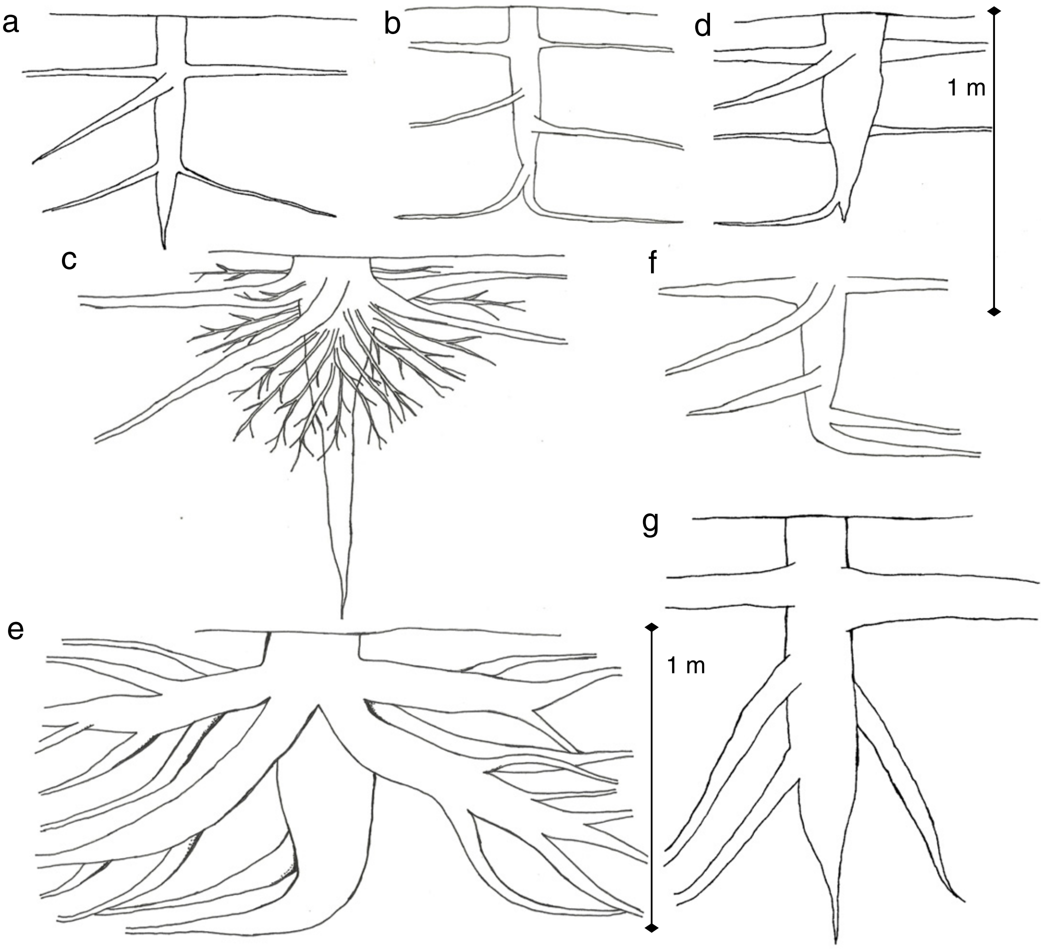

Fig. 2. Schematic drawings of root systems of savanna species in the Pantanal wetland: *Annona dioica* (a), *Byrsonima cydoniifolia* (b), *Cecropia pachystachya* (c), *Curatella americana* (d), *Dipteryx alata* (e), *Mouriri elliptica* (f), and *Zanthoxylum rigidum* (g).

lateral roots reaching up to 20 m in length, but in the Pantanal we found the same species with roots reaching up to 4 m, while individuals of *Cecropia pachystachya* had longer root, reaching up to 8 m.

The average percentage of root biomass relative to total plant biomass in both savanna physiognomies in Pantanal is low (35%–40%) when compared with percentages in similar savanna physiognomies in Venezuela (Sarmiento and Vera, 1979), Africa (Rutherford, 1983) and in central-western Brazilian (Castro and Kauffman, 1998), which are 62%–78%, 54% and 71%, respectively. Thus, the root behavior of savanna species in the Pantanal differs from that found in other savannas around the world. Such differences in root behavior have implications, for instance, in the accurate calculation of carbon stocks in national and global inventories of savanna regions.

Stem diameter at ground level is commonly used as a representative measure in Brazilian savanna surveys (Barbosa and Fearnside, 2004; Saporetti Jr. et al., 2003), and we confirm it as a useful parameter for estimating root biomass in the Pantanal, assuming the observed valid diameter ranges. The allometric power-law $Y = aX^b$ represents satisfactorily the relationship between stem diameter at ground level (X) and root biomass (Y), as also reported by Niklas (1994).

5. Conclusions

The root systems of woody species in savanna physiognomies in the Pantanal are shorter and lighter than those observed in other savannas, due to the singular effect of the higher water table level in relation to the soil surface. The root behavior of woody plants in the Pantanal, which may be analogous to that found in other wetlands around the world that have high water table, such as the Llanos, has important implications for accurately computing the carbon stocks of these ecosystems.

The stem diameter at ground level is a useful parameter for estimating the root biomass of savanna woody species in the Pantanal wetland, and the allometric power-law $Y = aX^b$ best represents this relationship for all species.

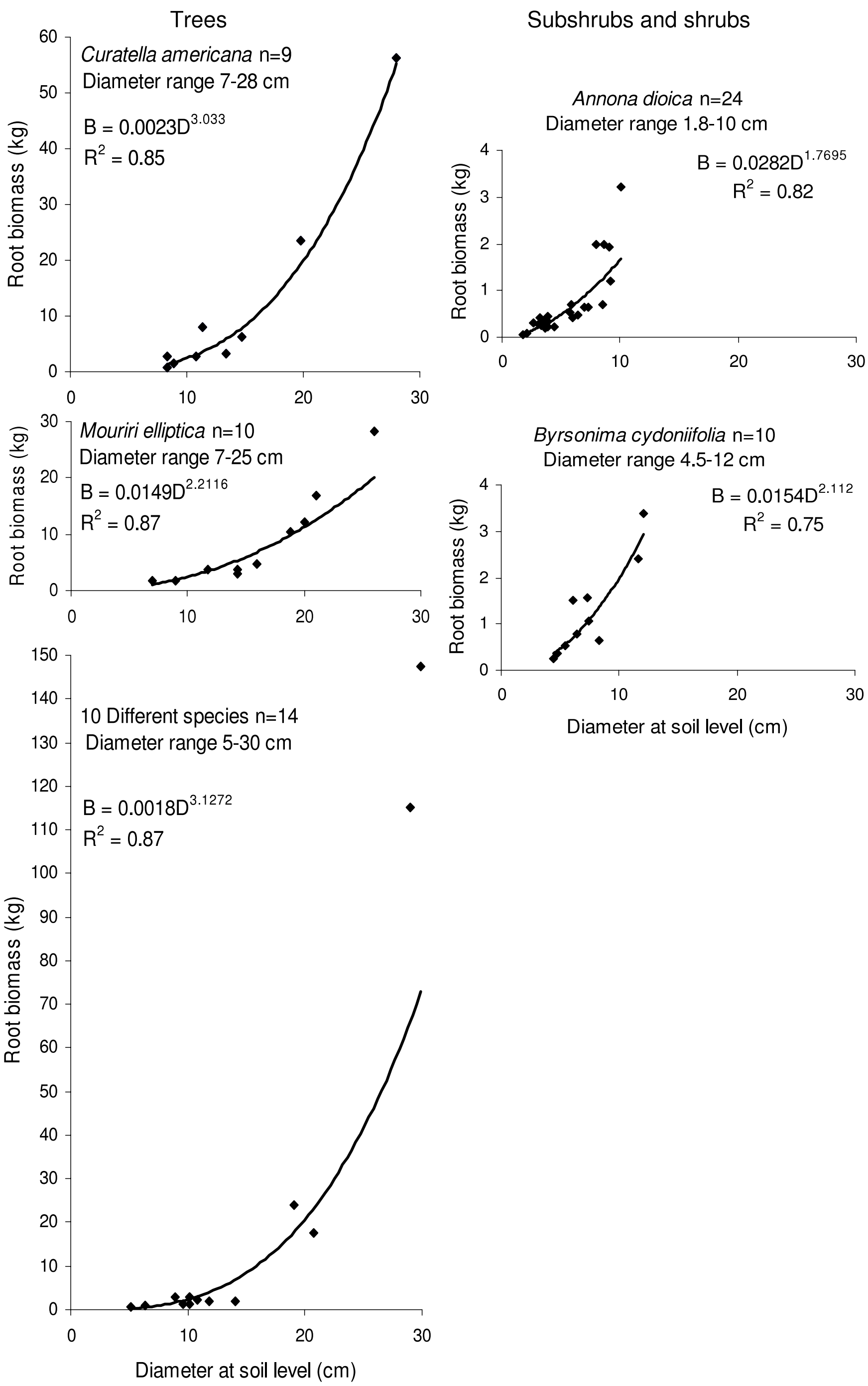

Fig. 3. Equations and curves obtained by nonlinear regression to estimate root biomass of woody species in the Pantanal savanna. B = root biomass, D = stem diameter at ground level, R^2 = square of the correlation coefficient and n = number of individuals sampled of 10 different species = *Bowdichia virgilioides*, *Caryocar brasiliense*, *Casearia sylvestris*, *Cecropia pachystachya*, *Dipteryx alata*, *Sapium haematospermum*, *Simarouba versicolor*, *Stryphnodendron*, *adstringens*, *Tabebuia aurea* and *Zanthoxylum rigidum*.

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