

UNIVERSIDADE ESTADUAL DO MARANHÃO
PROGRAMA DE PÓS-GRADUAÇÃO EM AGROECOLOGIA
CURSO DE MESTRADO EM AGROECOLOGIA

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COMPETIÇÃO E PARTIÇÃO DE NICHOS RADICULARES ENTRE A
PALMEIRA BABAÇU (*Attalea speciosa* MART) E O CAPIM (*Urochloa brizantha*
(*Hochst.ex.A.Rich*) Stapf cv. 'marandu') EM SISTEMA SILVIPASTORIL NA
AMAZÔNIA MARANHENSE

SÃO LUÍS – MA
2021

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Engenheiro Florestal

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Dissertação apresentada ao Curso de
Mestrado do Programa de Pós-Graduação
em Agroecologia da Universidade
Estadual do Maranhão para a obtenção do
título de Mestre em Agroecologia.

Orientador: Prof. Dr. Christoph Gehring

**SÃO LUÍS – MA
2021**

Pageú, André Brenner de Alencar.

Competição e partição de nichos radiculares entre a palmeira babaçu (*Attalea speciosa* MART.) e o capim (*Urochloa brizantha* (Hochst ex. A. Rich) Stapf cv. 'marandu') em sistema silvipastoril na Amazônia maranhense / André Brenner de Alencar Pageú. – São Luís, 2022.

72

Dissertação (Mestrado) – Programa de Pós-Graduação em Agroecologia, Universidade Estadual do Maranhão, 2022.

Orientador: Prof. Dr. Christoph Gehring.

1.Ecologia. 2.Agroecossistema. 3.Solo. 4.Competição. I.Título.

CDU: 631.95(812.1)

ANDRÉ BRENNER DE ALENCAR PAGEÚ

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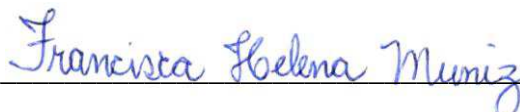
Aprovado em: 23 /12 /2021

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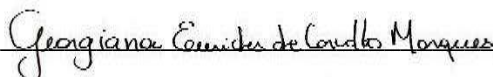
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SÃO LUÍS – MA
2021

DEDICATÓRIA

Dedico a todos os povos tradicionais do estado do Maranhão, em especial as mulheres quebradeiras de coco babaçu, verdadeiras guardiãs de nossa biodiversidade.

SUMÁRIO

LISTA DE ILUSTRAÇÕES.....	07
RESUMO.....	08
ABSTRACT.....	09
CAPITULO I: INTRODUÇÃO GERAL E REFERÊNCIAL TEÓRICO.....	10
1. INTRODUÇÃO.....	11
2. REVISÃO BIBLIOGRÁFICA.....	14
2.1. Relações Ecológicas: competição, coexistência e feedback planta-solo	14
2.2. Sistemas Silvipastoris.....	16
2.3. Palmeia Babaçu	18
2.4. Capim Marandu (<i>Urochloa brizantha</i> (Hochst.ex.A.Rich) Stapf cv. 'marandu')	20
3. REFERÊNCIAS BIBLIOGRÁFICAS.....	21
CAPITULO II – BELOWGROUND COMPETITION AND NICHE PARTITI - ONING BETWEEN THE BABASSU PALM AND UROCHLOA GRASS IN PASTURES OF THE EASTERN PERIPHERY OF AMAZONIA.....	29
ABSTRACT.....	30
I. INTRODUCTION.....	32
II. METHODS AND METHODS	35
II.1. Study region and experimental layout.....	35
II.2. Babassu and Grass Marandu root distribution.....	39
II.3 Data-processing and statistics.....	40
III. RESULTS.....	41
III.1. Impact of relative Babassu and Grass Marandu dominance on total root counts.....	41
III.2. Babassu coarse and mid-diameter horizontal and vertical profiles.....	43
III.3. Babassu and Urochloa vertical fine root profiles.....	45
III.4 Impact of relative Babassu and Urochloa dominance on vertical fine root profiles	45
III.5. Small-scale root distribution within the root walls.....	48
III.6. Relationship between bulk soil density and root counts.....	50
IV. DISCUSSION.....	50
IV.1. Babassu coarse and mid-diameter roots.....	50
IV.2. Babassu vs Urochloa fine root vertical distribution: vertical partitioning?	51
IV.3. Niche expansion under heterospecific competition.....	53
IV.4. Small-scale root variability.....	54
V. CONCLUSION	54
VI. ACKNOWLEDGEMENTS.....	55
VI. REFERENCES	55

LISTA DE ILUSTRAÇÕES

Figure – 1: Location of the three pastures (P1-P3), gray area = Pirapemas county; Green area = Legal Amazonia, and exemplary map of one of the three sites with location of the three Babassu clusters.....	35
Figure – 2: Babassu coarse and mid-diameter roots (bottom) and Babassu and Urochloa fine roots (top) in 0-50 cm soil depth. Medians, 25/75-percentiles, non-outlier range and outliers, extremes excluded. Letters refer to distance-grouping according to non-parametric Kruskal-Wallis ANOVA.....	41
Figure - 3: Relationship between metric distance from Babassu clusters and abundance of Babassu coarse and mid-diameter roots (bottom) and Babassu and Urochloa fine roots (top).....	42
Figure – 4: Coarse (>5 mm, left) and mid-diameter (2-5mm, right) root counts per 5 cm soil depth at sampling positions ‘within’ (top), at mid-distance (2.5 – 6.0 m) (middle) and ‘far’ (>6 m, bottom) from babassu clusters. Solid lines represent data interpolation, dotted lines represent 95% confidence intervals.....	43
Figure – 5: Relative vertical distribution of Babassu (left) and Urochloa (right) fine roots along the 50 cm soil profile over at all three distances: percentages of total root count per 5 cm soil layer (medians, 25 and 75 -percentiles and range).....	44
Figure – 6: Relative vertical distribution of Babassu (top) and Urochloa (bottom) fine roots down the 50 cm soil profile at distances 'within' (left) and 'far' (right). Percentages of total root counts per 5 cm soil layer (medians, 25 and 75 percentiles and range).....	45
Figura - 7: Percentage of all fine roots 0-50 cm concentrated within the top 0-10 cm soil layer for Babassu (left) and Urochloa (right), at sampling positions within, mid-distance and far from Babassu clusters. Means \pm SE and SD, letters refer to groupings according to Tukey HSD post-hoc test.....	46
Figura - 8: Exemplary root walls ‘within’ (top row), ‘mid-distance’ (center) and ‘far’ (bottom row) from Babassu palm clusters: Root counts per 5 x 5 cm grid for Babassu coarse, mid-diameter and fine roots and for Urochloa fine roots.....	48
Figure – 9: Relationship between soil bulk density and Babassu (left) and Urochloa (right) fine root counts within 5 x 5 x 3.3 cm grids / cubes containing more than zero fine roots.	49

RESUMO

Grande parte da Amazônia legal maranhense é dominada por pastagens de capim exótico do gênero (*Urochloa* spp.) com palmeira Babaçu (*Attalea speciosa* MART). Esta combinação constitui um sistema silvipastoril tradicional, que oferece a oportunidade de investigar como duas espécies muito competitivas e amplamente distribuídas interagem no solo. Este estudo mapeia perfis de raízes no solo (0,5 m x 1,0 m) em três sistemas silvipastoris na periferia oriental da Amazônia maranhense formados por Babaçu e capim (*Urochloa brizantha* (Hochst.ex.A.Rich) Stapf cv. 'marandu') em três tratamentos (distâncias) de dominância relativa ao colo da palmeira Babaçu: 'dentro' (dominância do Babaçu) (0,4 - 0,6 m); 'média distância' (2,50 - 6,0 m) e 'longe' –dominância da *Urochloa*' (8,0 - 10,00 m), contabilizando três classes de diâmetro predefinidas: 'fino' (<2 mm), 'médio' (2 - 5 mm) e 'grosso' (>5 mm) para ambas espécies. Os resultados apontaram uma prevalência de raízes finas superficiais, com 74,6% concentradas na camada (0 - 20 cm), e mais abundantes nas respectivas áreas de dominância, com 48,07% de participação de raízes finas de babaçu na posição "dentro", e 84,09 % de participação da *Urochloa* na "longe". Raízes médias e grossas de *Urochloa* foram menos expressivas em todas as posições. Mas as raízes médias e grossas de Babaçu foram significativas no enraizamento vertical na posição "próxima", com raízes grossas concentrando-se a 20-30cm ($P < 0,0001$) e médias crescendo até 50 cm de profundidade ($P < 0,0002$). Os perfis verticais de raízes finas entre Babaçu e capim *Urochloa* diferiram, apontando para partição de nicho na faixa de 0 - 10cm, com 41,9% de todas as raízes finas de *Urochloa* concentradas nos primeiros 0 - 10 cm, em oposição ao enraizamento mais profundo do Babaçu com 69,8% das raízes finas de Babaçu entre 10 – 50 cm. O perfil radicular vertical de *Urochloa* não foi afetado pelo tratamento. Já as raízes finas de Babaçu escaparam da competição por enraizamento mais profundo no ponto de dominância da *Urochloa*. Concluímos que a limitação superficial das raízes finas de *Urochloa* a ao solo indica uma redução da eficiência ecológica de pastagens monoespecíficas de *Urochloa*. Em contraste, enraizamento fino mais profundo do Babaçu indica plasticidade / expansão de nicho da palmeira quando em competição interespecífica, melhorando a eficiência ecológica do sistema. Essa característica provavelmente é um componentes-chave para o notável sucesso ecológico do Babaçu em pastagens degradadas na Amazônia oriental.

Palavras Chave: ecologia; agroecossistema; solo, competição.

ABSTRACT

Much of the Legal Amazon in Maranhão is dominated by pastures with a large presence of genus (*Urochloa* spp.) with the palm tree Babaçu (*Attalea speciosa* MART). This combination constitutes a traditional silvopastoral system that offers the opportunity to investigate how two very competitive and widely distributed species interact in the soil. This research maps soil root profiles (0.5 m x1.0 m) in three silvopastoral systems in the eastern periphery of the Maranhão Amazon formed by Babaçu and Brachiaria (*Urochloa brizantha* (Hochst.ex.A.Rich) Stapf cv. 'marandu') in three treatments (distances) of dominance relative to the neck of the Babaçu palm: 'inside' Babaçu dominance' (0.4 - 0.6 m); 'medium distance' (2.50 - 6.0 m) and 'far – dominance of *Urochloa*' (8.0 - 10.00 m), accounting for three predefined diameter classes: 'thin' (<2 mm), 'medium' (2 - 5 mm) and 'thick' (> 5 mm) for both species. The results showed a prevalence of fine superficial roots, with 74.6% concentrated in the layer (0 – 20 cm), and more abundant in the respective areas of dominance, with 48.07% of participation in the fine roots of "inside" babaçu, and 84.09% of participation of *Urochloa* in the "far" position. Medium and thick *Urochloa* roots were less expressive in all positions. But medium and thick babaçu roots were significant in vertical rooting in the “inside” position, with thick roots concentrating at 20 – 30 cm (P<0.0001) and medium ones growing up to 50 cm deep (P<0.0002). The vertical profiles of fine roots between Babaçu and Marandu grass differed, pointing to niche partitioning in the 0 – 10 cm range, with 41.9% of all *Urochloa* fine roots concentrated in the first 0 - 10 cm, as opposed to more rooting deeper of babaçu with 69.8 of the fine roots of babaçu between 10 - 50 cm. The vertical root profile of *Urochloa* was not affected by the treatment. However, the fine roots of babaçu escaped competition by rooting deeper in the *Urochloa* dominance point. It was concluded that the superficial limitation of *Urochloa* fine roots to the soil indicates a reduction in the ecological efficiency of *Urochloa* monospecific pastures. In contrast, deeper fine rooting of Babaçu indicates plasticity/niche expansion of the palm when in interspecific competition, improving the ecological efficiency of the system. This feature is likely a key component of Babaçu remarkable ecological success in degraded pastures in eastern Amazonia.

Keywords: Ecology; agroecosystem; ground, competition.

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CAPITULO I

INTRODUÇÃO GERAL E REFERÊNCIAL TEÓRICO

53 1. INTRODUÇÃO

54 A colonização da região amazônica brasileira foi centralmente moldada pela
55 conversão da floresta tropical em pastagens para bovinocultura extensiva, em sua maioria
56 com rebanhos de baixa eficiência produtiva (FEARNSIDE, 2017; ROMEIRO, 2019). O
57 desmatamento, seguido por queimadas sucessivas reduz a capacidade produtiva do
58 ecossistema (VILLA et al., 2018).

59 Anos de reprodução deste modelo de uso do solo resultaram, solos
60 desestruturados, vulneráveis a lixiviação de nutrientes e acidificação (SILVA et al., 2019;
61 OLIVEIRA et al., 2017) e redução dos estoques de carbono (BONINI et al., 2018).

62 Superar esse ciclo de desmatamento e degradação dos ecossistemas amazônicos é
63 um desafio contemporâneo mundial, que exige pôr em prática usos e manejos do solo que
64 levem em consideração as relações ecológicas e seus efeitos sobre a produção vegetal
65 (VENDRAMINI, 2019; LANGE et al., 2019).

66 Esse contexto de desequilíbrio ecológico abriu espaço para expansão geográfica
67 da dominância da palmeira Babaçu (*Attalea speciosa* Mart), uma planta nativa
68 naturalmente encontrada nas áreas de transição entre Cerrado e Amazônia, que se revelou
69 uma palmeira de habito ruderal, ocupando amplamente os nichos abertos em áreas
70 degradadas, frequentemente queimadas no arco do desmatamento da Amazônia,
71 formando extensos “babaçuais” adensados onde anteriormente coexistiam, inseridos na
72 floresta tropical pluvial densa (BARRETO et al., 2019; GEHRING et al., 2020).

73 Nas últimas décadas modelos de uso dos solos tropicais, classificados como
74 sistemas agrossilvipastoris, foram disseminados como agroecossistemas mais
75 sustentáveis por serem mais diversificados por unidade de área, incluindo componentes
76 arbóreos, forrageiros, agrícolas e animal (JOSE et al., 2019; MONTES et al., 2021) com
77 objetivo de alcançar melhores níveis de produtividade através de um manejo ecológico
78 dos recursos naturais, em especial da fertilidade do solo (SANTOS et al., 2018; ALVES
79 et al., 2017).

80 Segundo Jose et al., (2019), sistemas silvipastoris são viáveis através de
81 mecanismos ecológicos de diversificação funcional e estrutural de nichos
82 interespecíficos. São agroecossistemas que podem ser projetados para alcançar maior
83 sustentabilidade e produtividade, com a otimização dos recursos (espaciais, temporários
84 e físicos) através da maximização das interações positivas (facilitação) e minimizando a
85 ações negativas (competição), e assim buscando a coexistência interespecífica, evitando

86 exclusão competitiva postulada pela lei de Gause e (GLIESSMAN, 2001; CHESSON,
87 2000).

88 Dentre os agroecossistemas sustentáveis, no estado do Maranhão destaca-se o
89 sistema silvipastoril composto por capim (*Urochloa brizantha* cv. Marandu), com
90 diferentes densidades de palmeiras Babaçu (*A. speciosa*) aleatoriamente distribuídas no
91 pasto (GAZOLLA, 2012). Apesar de ser um modelo de baixa diversidade, o consórcio
92 desta palmeira com gramíneas atualmente é alvo de estudos sobre seus benefícios à
93 preservação das propriedades do solo (SANTOS et al., 2018), manutenção dos estoques
94 de carbono no solo (LUZ et al., 2020; RODRIGUES et al., 2015), manutenção de
95 atividades extrativistas de coco babaçu (PORRO, 2019), produção pecuária mais
96 sustentável (CARRERO, 2016) e fornecimento de serviços ecossistêmicos
97 (NICODEMO, PRIMAVESI, 2019; RODRIGUES et al., 2015).

98 Dificilmente a palmeira babaçu é plantada, normalmente neste sistema os
99 povoamentos naturais são raleados para manutenção da produção de coco e
100 sombreamento aos animais (PORRO, 2005). Regionalmente a palmeira Babaçu tem
101 grande importância socioeconômica, sendo fonte de renda de aproximadamente 13 mil
102 famílias extrativistas apenas no estado do Maranhão (IBGE, 2017). Entretanto também é
103 vista como “praga” por pecuaristas, que buscam ampliar suas pastagens, livre da
104 competição com a palmeira (PORRO, 2005).

105 O capim Marandu (*U. brizantha*) é uma gramínea de origem tropical africana, que
106 se destaca por ser bem adaptada às condições edafoclimáticas tropicais brasileiras,
107 conciliando uma vigorosa produção de fitomassa verde, para alimentação animal em solos
108 de baixa fertilidade e com baixa incidência de pragas e doenças (LIMA, 2015). Outras
109 características desejáveis do capim *Urochloa* é atribuída a tolerância ao sombreamento, o
110 que propicia melhores condições de sobrevivência e capacidade competitiva (GOMES et
111 al., 2020).

112 Apesar da difusão deste sistema nas periferias leste e sul da Amazônia, pouco se
113 sabe sobre as relações de competição e coexistência entre o babaçu e gramíneas exóticas.
114 Uma das poucas pesquisas foi realizada por May et al. (1985), apontando que a ‘expansão
115 de nichos’ (abaixo do solo) é a principal estratégia ecológica para uma relação promissora
116 no sistema silvipastoril entre babaçu com *Urochloa* corroborando com Isaac e Borden
117 (2019) que a divisão de nichos radiculares por recursos é um dos principais mecanismos
118 de promoção de uma relação interespecífica.

119 No entanto, estes mecanismos não são facilmente manejados, possui uma
120 complexa dinâmica funcional, incluindo interações multitróficas (BARTOMEUS;
121 GODOY, 2018), relações fenológicas (TANG et al., 2016) e plant-soil feedback(resposta)
122 - PSF (LEKBERG et al., 2018), em relação ao uso dos recursos e as condições ambientais
123 no tempo, requerendo uma análise agroecológica mais ampla (NICODEMO;
124 PRIMAVESI, 2019).

125 Nesse sentido, para além da competição direta por recursos, se faz necessário
126 investigar os efeitos deste consórcio sobre o solo. Plantas bem adaptada são conhecidas
127 por impactar seus arredores atuando, por exemplo, sobre a fertilidade, ciclo do carbono e
128 retenção de umidade (VAN DER PUTTEN et al., 2016). Luz et al., (2020) constataram
129 maiores teores de potássio nos arredores da palmeira babaçu, oriundos do escoamento
130 superficial do caule e folhas. Já o capim *Urochloa* realiza fixação biológica de nitrogênio
131 - FBN via associações com *Azospirillum amazonense* e *A. brasiliense* (HANISCH et al.,
132 2017).

133 Apesar dos portes contrastantes, o capim *Urochloa* e a palmeira babaçu têm
134 relações específicas em comum, são consideradas plantas com características “ruderais”,
135 com sistema radicular denso, e elevada produção/reposição de raízes finas, exercendo
136 papel estruturante ao solo e de reposição dos estoques de carbono (SILVA NETO et al.,
137 2012; RAZUK, 2002).

138 A hipótese é que os mecanismos de coexistência e competição entre a palmeira
139 babaçu e capim Marandu se manifestam na distribuição radicular no solo em diferentes
140 medidas, de acordo com o nível de dominancia. Logo o nosso objetivo foi investigar uma
141 possível partição de nichos espaciais entre as espécies, através da distribuição vertical e
142 horizontal das raízes em graus contrastantes de dominância.

143

144 2. REVISÃO BIBLIOGRÁFICA

145

146 2.1. Relações Ecológicas: competição, coexistência e feedback planta-solo.

147

148 As interações interespecíficas entre plantas e destas com o solo são um campo de
149 estudo importante de entendimento sobre os mecanismos ecológicos que determinam a
150 diversidade, persistência, abundância, invasão, competição e a formação do solo (MACK
151 et al., 2019).

152 As plantas se desenvolveram e evoluíram no ambiente natural, graças a seleção
153 natural movida em grande parte pela competição em seus respectivos nichos, por luz,
154 espaço, nutrientes no solo, portanto, a competição interespecífica é peça principal do
155 funcionamento dos ecossistemas (SCHOFIELD et al., 2018). No entanto, quando
156 abordamos a competição no solo, os sistemas radiculares das plantas interagem de muitas
157 maneiras, que variam de competição severa até uma partição de nichos em busca de uma
158 inter-relação harmônica entre si, assim, nem sempre a competição é negativa para o
159 ecossistema como um todo, pois o uso total de nutrientes e água podem ser aumentados,
160 e assim ambos são beneficiados (TSCHIRHART, 2002).

161 A exclusão competitiva, também conhecida como lei de Gause, propõe que entre
162 espécies com nichos semelhantes, a competição por recursos limitantes impossibilita a
163 coexistência. Tal teoria contribuiu decisivamente para muitas pesquisas em ecologia
164 evolutiva, entendimento da estruturação das comunidades e regulação da diversidade
165 (GLIESSMAN, 2001).

166 No entanto, as pesquisas ecológicas realizadas nas últimas décadas,
167 principalmente a partir da teoria da coexistência de Chesson (2000), identificaram que
168 nos ecossistemas naturais a resposta dominante sobre a competição, além da exclusão,
169 consiste em auto regulações em direção à coexistência interespecífica, através de
170 mecanismos de estabilização, onde espécies executam estratégias filogeneticamente
171 constituídas, que agem na diminuição dos efeitos negativos da competição e beneficiam
172 relações de facilitação, promovendo a diversidade por meio da diferenciação de nicho
173 (ADLER et al., 2018).

174 Dessa forma, compreender os diversos mecanismos de competição e coexistência
175 interespecíficos e os efeitos sobre a estrutura das comunidades é um desafio científico
176 contemporâneo (ADLER et al., 2018). O estudo desses mecanismos é pautado, como
177 forma de ajudar a resolução de problemas contemporâneos de gestão, incluindo sistemas

178 produtivos mais eficientes (THAKUR et al., 2021), manejo de espécies invasoras e
179 previsão das consequências das mudanças climáticas nos ecossistemas (WOLKOVICH;
180 CLELAND, 2014; VALLADARES et al., 2015).

181 Muitos são os mecanismos de coexistência, com diferentes respostas às
182 disponibilidades de recursos e alterações espaço-tempo do ambiente (SCHOFIELD et al.,
183 2018). Dybzinski e Tilman (2012) apontam que existe uma coexistência estável quando
184 há “invasibilidade mútua” de espécies, ou seja, quando cada espécie tem a possibilidade
185 de aumentar sua população quando rara, sobre outro nicho, se protegendo da extinção
186 local e buscando retornar a um ponto de equilíbrio de abundância.

187 No entanto, atualmente, existe uma compreensão crescente de que outras
188 interações ecológicas também afetam diretamente a estruturação das comunidades, como:
189 dinâmica temporal de recursos por adaptações fenológicas (SCHOFIELD et al., 2018);
190 partição dos nutrientes por mediação microbiana, incluindo os fungos micorrízicos
191 arbusculares (FMA) (VERESOGLOU et al., 2018); herbívoros; alelopatia entre outras
192 interações multitróficas (BARTOMEUS, GODOY, 2018).

193 Silvertown (2004) aponta que a partição de nichos em plantas acontece em dois
194 eixos: abaixo e acima do solo. No primeiro, a disputa por luz e melhores condições
195 microclimáticas é equalizada por diferenças na estratificação e dimensões da parte aérea
196 da vegetação. Abaixo do solo, a partição de nutrientes se verifica pelas segregações
197 espaciais de profundidades, enraizamento e crescimento ao longo de gradientes
198 hidrológicos.

199 As plantas podem alterar as propriedades abióticas e bióticas do solo a seu favor,
200 este processo, conhecido como Positive Feedback Plant–Soil (PSF), estabelece que as
201 plantas por meio de mecanismos como: exsudação, deposição de MOS, interações
202 simbióticas, podem alterar os componentes bióticos e abióticos do solo a seu favor
203 (CRAWFORD et al., 2019; VAN DER PUTTEN et al., 2016).

204 Nesse sentido, para além da competição interespecífica, Lekberg et al., (2018)
205 apontam que os mecanismos de PSFs são forças que podem interagir nos gradientes de
206 recursos, provavelmente fortalecendo as interações competitivas em ambientes de muitos
207 recursos e aumentando as interações facilitadoras em ambientes de poucos recursos.

208 Somado a isso, as plantas em sistemas naturais ou agroecossistemas também
209 experimentam interações complexas multitróficas e simultâneas no seu habitat, como
210 interações simbióticas, mutualísticas, de doenças e herbívora, que atuam na distribuição

211 das espécies e influenciam na coexistência entre os diferentes nichos (BARTOMEUS;
212 GODOY, 2018; LI et al., 2020). Exemplos são associações endofíticas/rizosféricas com
213 bactérias e fungos para ampliação da capacidade de absorção de nutrientes
214 (VERESOGLOU et al., 2018), mineralização do carbono (WANG et al., 2016) e a
215 diminuição de biodiversidade vegetal ao seu redor, por ação alelopática (MARTINS et
216 al., 2006)

217 A compreensão desses mecanismos pode melhorar nossa capacidade de manejar
218 agroecossistemas diversificados, permitindo o planejamento ecoeficiente da composição
219 das comunidades de plantas, bem como facilitar os mecanismos de restauração ecológica.

220

221 **2.2. Sistemas Silvipastoris**

222

223 A população mundial continua a crescer, e com ela as pressões sobre os recursos
224 naturais se aproximam dos limites físicos dos ecossistemas (GLIESSMAN, 2001). Nesse
225 contexto, Groppo et al., (2015) apontam que o desenvolvimento rural passa pelo
226 desenvolvimento de sistemas produtivos de uso do solo mais sustentáveis, adaptados às
227 condições nas vastas áreas florestais já alteradas nos últimos 30 anos.

228 Os sistemas silvipastoris vêm despontando como uma alternativa viável para
229 reverter esse quadro de crise socioambiental em grandes partes dos trópicos úmidos do
230 mundo (DOMICIANO et al., 2020). É uma modalidade de sistemas de cultivo biodiversos
231 que consistem em consorciar pastagens, animais, árvores e outras plantas forrageiras
232 (JOSE et al., 2019). Sua constituição pode se dar pela inserção das pastagens dentro de
233 povoamento arbóreo cultivados e/ou naturais raleados, ou pela inclusão de povoamentos
234 florestais em áreas de pastagens já consolidadas, definindo precisamente os arranjos
235 espaciais e espaçamentos (CARRERO, 2016; GAZOLLA, 2012). São agroecossistemas
236 que podem ser projetados para alcançar maior sustentabilidade e produtividade, através
237 da otimização dos recursos (espaciais, temporários e físicos), maximização das interações
238 positivas (facilitação) e minimizando as negativas (competição) (JOSE et al., 2019).

239 A estratégia do sistema consiste em intensificar a produção por meio da
240 diversificação de cultivos na mesma área, uso mais eficiente dos recursos naturais locais,
241 assim como usufruir dos benefícios oriundos da mitigação dos desequilíbrios ecológicos
242 dos agroecossistemas degradados (JOSE; DOLLINGER, 2019).

243 A integração de gramíneas e árvores promove modificações favoráveis nas
244 características edáficas quando comparado com sistemas tradicionais monoespecíficos,

245 os principais benefícios derivam da maior deposição de MOS; estruturação do solo,
246 contenção de erosão e translocação de nutrientes e água das camadas inferiores para
247 camadas mais próximas à superfície, favorecendo o desenvolvimento das forrageiras
248 (ALVES et al., 2017).

249 Os sistemas silvipastoris também beneficiam a produção animal com a
250 diversificação da dieta dos bovinos, que ao contrário do que a maioria dos produtores
251 específica, possuem uma dieta flexível, onde se pode incluir diversa forragens e frutos de
252 árvores como o Ingá (*Inga edulis*), palmeira macaúba (*Acrocomia sp.*), gliricídia
253 (*Gliricidia sepium*) entre outras (CARRERO, 2016). Ademais a conservação de
254 povoamentos arbóreos traz conectividade para a paisagem amazônica, com benefícios
255 diretos a estabilidade dos ciclos hídricos, ciclagem de nutrientes, biodiversidade e
256 controle natural de pragas (MELOTTO et al., 2019). Neste sentido, o uso de sistemas
257 silvipastoris pode ser uma alternativa para recuperação de pastagens degradadas, pois
258 contribuem com a conservação das propriedades do solo e diminui o estresse climático
259 sobre os animais, que conseqüentemente vão consumir uma forragem mais nutritiva com
260 melhor desempenho no ganho de peso e produção de leite (RAMOS, 2014).

261 O desenvolvimento de sistemas agropecuários menos impactantes vem se
262 ampliando quanto ao uso de estratégias de conservação do potencial produtivo do solo
263 (ALVES et al., 2017; MELADO, 2007), se somando a uma nova abordagem tecnológica,
264 que vem se popularizando como “intensificação ecológica”, onde objetiva-se aplicar
265 fundamentos ecológicos para produzir mais alimentos, na mesma área, com menor
266 impacto possível (BARROS et al., 2011). É uma quebra de paradigma, que tem como
267 desafio, popularizar fundamentos ecológicos que permitam transformar os agricultores
268 em gestores tanto da produção quanto dos ecossistemas.

269 No estado do Maranhão a introdução de capim (*Urochloa brizantha cv. Marandu*)
270 em babaçuais (*Attalea spp.*) raleados, compõem um modelo popular de sistemas
271 silvipastoris natural, onde a palmeira babaçu entra como o componente arbóreo
272 remanescente da vegetação original (GAZOLLA, 2012).

273 ARAÚJO et al., (2017) em trabalho sobre a dinâmica do pastejo bovino na
274 amazônica maranhense, concluiu que em sistemas silvipastoris compostos por palmeiras
275 de babaçu (*A. speciosa*) e capim Braquiária (*U. brizantha cv. Marandu*) proporciona um
276 ambiente estrutural mais favorável aos animais pastejarem, em uma distribuição mais
277 homogênea dos animais, em comparação com monocultivo de capim Braquiária,

278 diminuindo a incidência de áreas com sobre pastejo e beneficiando a restituição da
279 fertilidade do solo, pela melhor distribuição de fezes nas áreas.

280 De acordo com Rodrigues et al. (2015), em sistemas silvipastoris de babaçu (*A.*
281 *speciosa*) e capim Braquiária (*U. brizantha* cv. *Marandu*), existe uma relação biomassa
282 microbiana: carbono orgânico no solo, e atividade enzimática, significativa maior em
283 comparação com a monocultura de capim Braquiária, e crescente com o aumento da
284 densidade de babaçu no sistema, o que favorece a mineralização e ciclagem de nutrientes
285 no solo, e, conseqüentemente a fertilidade.

286

287 **2.3. Palmeira Babaçu**

288

289 O Babaçu (*Attalea speciosa* Mart) é uma palmeira amplamente distribuída no
290 norte do Brasil, alcançando Bolívia, Guiana e Suriname (LORENZI, 2010). No Brasil,
291 ocorre densamente na zona ecotonal da “Mata de Cocais”, localizado na transição entre
292 os Biomas Amazônia e Cerrado no estado do Maranhão. E também compõe paisagens
293 nos estados do Piauí e, em menor escala, Tocantins, Ceará, Bahia; Rondônia; Acre; Goiás,
294 Mato Grosso; Pará e sul de Minas Gerais (MAY et al., 1985; REIS et al., 2019; PORRO,
295 2019).

296

297 A palmeira babaçu ocorre inserida isoladamente na floresta tropical ou em maior
298 densidade em área abertas fortemente degradadas, colonizando antigos nichos de
299 formações florestais desmatadas, onde apresenta um habito de espécie pioneira e
300 dominante (BARRETO et al., 2019). Segundo Ribeiro; Walter (1998) a presença do
301 babaçu nos ecossistemas é associada significativamente às áreas antropizadas e sua
302 relação etnobotânica com as populações humanas nas florestas. Desta forma, a palmeira
303 babaçu foi integrada aos agroecossistemas, em especial no estado do Maranhão, porém
304 sem necessariamente ter sido feito seu plantio (PORRO, 2005). O que lhe atribui a
305 classificação como planta de habito ruderal (GEHRING et al., 2020).

306

307 O sucesso ecológico desta planta decorre da ligação de três fatores: (i) o
308 extrativismo faz uma seleção das palmeiras mais produtivas no desmatamento das
309 florestas; (ii) adaptações reprodutivas ao fogo: a ação termina funcionando como
310 mecanismo de quebra de dormência das sementes e geotropismo negativo do meristema
311 terminal nas plantas juvenis, protegido a 0,5 – 1,0 m de profundidade contra o fogo; e (iii)
comportamento de planta ruderal com forte capacidade competitiva em solos inférteis
(REIS et al, 2019; PORRO, 2019; GOUVEIA et al., 2017).

312 A sua proliferação, livre de um plano de manejo, dificulta a restauração natural
313 das florestas e conseqüentemente a biodiversidade característica do bioma amazônico
314 (SOUSA et al., 2016). Segundo Santos et al., (2015), babaçuais podem chegar a densidade
315 de até 2.000 plantas por hectare, representando uma larga produção quando investida de
316 um sistema de manejo e controle adequados para o seu crescimento e produção.

317 O fruto é do tipo drupa oblonga, com epicarpo fibroso, mesocarpo rico em amido
318 e endocarpo lignificado, constituindo um envoltório bastante resistente que guarda
319 amêndoas ricas em lipídios. Seu uso popular é para produção de farinhas, azeites/óleos e
320 carvão vegetal (PORRO, 2019; GOUVEIA et al., 2017). É o quinto produto florestal não
321 madeireiro mais explorado no Brasil, gerando em torno de 146 milhões de reais em
322 rendimentos em 2011 (NASCIMENTO et al., 2014). Seu estipe é utilizado em
323 construções rurais e também é fonte de palmito e adubo e suas folhas em coberturas,
324 artesanatos e cercas (PORRO, 2019; NASCIMENTO et al., 2014). Estima-se que a sua
325 exploração econômica beneficia direta e aproximadamente 13 mil famílias
326 quebradeiras/os de coco (IBGE, 2017). Em decorrência de sua importância
327 socioeconômica, a palmeira Babaçu foi protegida por lei (Lei nº 4734 de 18 de junho de
328 1986), tendo sua supressão regulada em favor da manutenção do potencial produtivo
329 (ARAUJO et al., 2014). No entanto, a determinação de sua densidade por hectare, ainda
330 provocando conflitos entre extrativistas e pecuaristas e carece de embasamento científico
331 (REIS et al., 2019).

332 A palmeira Babaçu é uma planta monocotiledônea, com altura média de 20 m, que
333 leva até 20 anos para chegar à fase adulta. Possui caule tipo estipe, copa em forma de
334 pirâmide invertida, composta por folhas tenras, ricas em material ligno lenhoso, entre sete
335 e 22 por planta, com 4 a 8m de comprimento e enorme capacidade regenerativa, durante
336 toda a vida da planta. A implantação das folhas aproxima-se de 45° no caule,
337 possibilitando a incidências de luz direta e difusa no solo, permitindo consorciação
338 agrícola e com pastagens (LORENZI, 2010; REIS et al., 2019; MAY et al., 1985).

339 O sistema radicular é do tipo fasciculado, próprio das Arecaceae, com um bulbo
340 radicular emitido pelo caule, composto por raízes primárias (grossas) com diâmetro de 8
341 a 10 mm, ricas em lignina, das quais derivam as raízes secundárias (médias) e destas as
342 raízes terciárias (radicelas finas), com 1 a 3 mm (CORREA et al., 2020; SOUSA et al.,
343 2016).

344 Para a palmeira Babaçu as raízes grossas tem sua máxima biomassa localizada nas
345 profundidades de 70 a 80 cm de profundidade, exercendo principalmente a função de
346 sustentação física da planta e estocagem de carboidratos e fitatos, responsáveis pelas
347 rebrotas vigorosas após o corte e queima; já as raízes finas corresponderam a 40,3% da
348 biomassa radicular, distribuídas de forma regular em todo o perfil do solo, sendo as
349 principais responsáveis pela absorção de nutrientes e água para manutenção da planta
350 (SOUSA et al., 2016).

351 Poucos estudos até agora se dedicaram a explorar as relações ecológicas do
352 Babaçu abaixo do solo, exceto sobre os impactos da palmeira babaçu na biomassa
353 microbiana do solo (RODRIGUES et al., 2015; GEHRING et al., 2020), biomassa
354 radicular e sua contribuição aos estoques de carbono do solo (SOUSA et al., 2016), as
355 influências do escoamento superficial da água da chuva sobre o caule e folhas, nos
356 nutrientes minerais sedimentados no solo (GERMER et al., 2012); relações simbióticas
357 com FMA (NOBRE et al., 2018); composição e dinâmica de mineralização da MOS
358 depositada sobre o solo (LUZ et al., 2020).

359

360 **2.4. Capim Marandu (*Urochloa brizantha* (HOCHST & A.RICH) STAPF cv. 'marandu')**

361

362 A *U.brizantha* (HOCHST & A.RICH) STAPF cv. 'marandu' é uma gramínea
363 forrageira de origem africana, mais precisamente em Zimbábue, lançada em 1983 pela
364 Embrapa Gado de Corte e Embrapa Cerrados, tornando-se largamente utilizada nas
365 pastagens no Brasil também conhecida como braquiária (DIAS-FILHO, 2014; NUNES
366 et al., 1984). Segundo Euclides et al. (2010) estima-se que existam cerca de 100 milhões
367 de hectares de pastagens no Brasil, cultivadas principalmente com *Urochloa* spp, dos
368 quais aproximadamente 45% correspondem a pastagens de *Urochloa brizantha* cv.
369 Marandu. Tornando-se atualmente um dos capins mais difundidos na pecuária extensiva
370 da Amazônia brasileira (ARAUJO et al., 2017).

371

372 Seu sucesso advém das suas características de boa adaptabilidade às condições
373 edafoclimáticas da região tropical, uma vigorosa produção de fito massa em solos de
374 baixa fertilidade, e não ser atrativa as principais doenças e pragas das culturas forrageiras,
375 por exemplo, da cigarrinha das pastagens (*Deois flavopicta*). E por sua boa palatabilidade
376 tanto para bovinos, como equinos, ovinos e caprinos, com boa rebrota ao pastejo (COSTA
et al., 2006; LIMA, 2015; NUNES et al., 1984). É considerada uma planta com habito

377 dominante de sistema radicular denso, mais amplamente distribuído nas camadas
378 superficiais do solo (0-20), exercendo papel estruturante e de estabilização de agregados
379 no solo, pela elevada deposição de MOS, pela constante renovação das raízes finas, assim
380 como emissão de exsudados ricos em carbono, que ativam as relações simbióticas com
381 microrganismos (HANISCH et al., 2017; NUNES et al., 1984).

382 A cultivar *Urochloa brizantha* cv. Marandu foi relatada com uma maior produção
383 e distribuição de biomassa radicular, nos perfis (0-10/10-20/20-40 cm) tanto em níveis de
384 baixa como de alta fertilidade, em um solo Latossolo Vermelho distrófico, quando
385 comparada a outras quatro variedades também populares no Brasil (*Brachiaria brizantha*
386 cv. Basilis; *Panicum Maximum* cv. Tanzânia e cv. Tobiata e *Andropogon gayanus* cv.
387 Baeti). Rodrigues et al., (2015) também evidencia um potencial de restabelecimento dos
388 estoques de carbono do solo, para o capim marandu.

389 Apesar de difundido em sistemas silvipastoris com palmeira babaçu, pouco se
390 sabe sobre o seu comportamento nesta relação, Andrade et al. (2004) recomendam o uso
391 do capim *Urochloa* em sistemas silvipastoris em áreas drenadas na Amazônia Ocidental,
392 com bases em respostas positivas ao sombreamento, mantendo taxas satisfatórias de
393 produção de matéria seca até um sombreamento de 30%, com tolerância até 50%.

394

395 **3. REFERÊNCIAS BIBLIOGRÁFICAS**

396

397 ADLER, P. B.; SULL, D.; BEARD, K. H.; CHOI, R. T.; FURNISS, T.;
398 KULMATISKI, A.; MEINERS, J. M.; TREDENNICK, A. T e VEBLEN, K. E.
399 Competition and coexistence in plant communities: intraspecific competition is stronger
400 than interspecific competition. **Ecology letters**, v. 21, n. 9, p. 1319-1329, 2018.

401

402 ALVES, B.; MADARI, B.; BODDEY, R. Integrated crop–livestock–forestry systems:
403 prospects for a sustainable agricultural intensification. **Nutrient Cycling in**
404 **Agroecosystems**, v. 108, n. 1, p. 1–4, 2017.

405

406 ANDRADE, C. M. S.; VALENTIM, J. F.; CARNEIRO, J. C.; VAZ, F. A. Crescimento
407 de gramíneas e leguminosas forrageiras tropicais sob sombreamento. **Pesquisa**
408 **Agropecuária Brasileira**, Brasília, v. 39, n. 3, p. 263-270, 2004.

409

410 ARAÚJO, J.; MIGUEL, E.; DMITRUK, E. J.; MOURA, J. C. C. A Lei do Babaçu Livre:
411 uma estratégia para a regulamentação e a proteção da atividade das quebraadeiras de
412 coco no Estado do Maranhão. **Sequência (Florianópolis)**, p. 129-157, 2014.

413

414 ARAÚJO, R. A. D.; RODRIGUES, R. C.; COSTA, C. D. S.; SANTOS, F. N. D. S.;
415 CUTRIM, J. A. A.; JESUS, A. P. R. D.; ARAÚJO, J. D. S. Grazing behavior and spatial
416 distribution of feces of Young bulls in silvopastoril systems and Marandu monoculture
417 in the Pre-Amazon region. **Acta Scientiarum. Animal Sciences**, v. 39, n. 1, p. 83-90,
418 2017.

419

420 BARRETO, H. N.; PARISE, C. K.A.; BEZERA, E. The Cocais Forest Landscape.
421 In: **The Physical Geography of Brazil**. Springer, Cham, p. 151-167, 2019.

422

423 BARROS, I.; MARTINS, C. R.; CINTRA, F. L. Da. Intensificação ecológica da
424 agricultura: uma opção para a preservação ambiental com lucratividade. **Embrapa**
425 **Tabuleiros Costeiros-Artigo de divulgação na mídia (INFOTECA-EMBRAPA)**,
426 Aracaju-SE, Out. 2011. Disponível em: www.agrosoft.org.br/agropag/221260.htm
427 Acessado em: 15 de junho de 2020.

428

429 BARTOMEUS, I. E.; GODOY, O. Biotic controls of plant coexistence. **Journal of**
430 **Ecology**, v.106, p.1767–1772, 2018.

431

432 CARRERO, G. C. Sistemas silvipastoris com pastejo rotacional: alternativas
433 sustentáveis para a produção pecuária na Amazônia. **Gestão e Governança Local para**
434 **a Amazônia Sustentável**; notas técnicas; PQGA/IBAM: Belém, Brasil, p. 79-91, 2016

435

436 CHESSON, P. General theory of competitive coexistence in spatially-varying
437 environments. **Theoretical population biology**, v. 58, n. 3, p. 211-237, 2000.

438
439 COSTA, N. D. L.; TOWNSEND, C. R.; MAGALHÃES, J. A.; DE A PEREIRA, R. G.;
440 AZEVEDO, D. M. M. R. Comportamento forrageiro da *Brachiaria brizantha* cv.
441 Marandu em sistema silvipastoril na Amazônia Brasileira. **Pasturas Tropicales**, v. 28,
442 n. 3, p. 22-26, 2006.
443
444 CORREA, M. M; ARAÚJO, M. G.P; MENDONÇA, M. S. Anatomical and
445 histochemical comparison of the primary and adventitious roots of *Attalea microcarpa*
446 (*Arecaceae*) at the initial growth stage. **Acta Amazonica**, v. 49, p. 311-315, 2019.
447
448 CRAWFORD, K. M.; BAUER, J. T.; COMITA, L. S.; EPPINGA, M. B.; JOHNSON,
449 D. J.; MANGAN, S. A.; BEVER, J. D. When and where plant-soil feedback may
450 promote plant coexistence: a meta-analysis. **Ecology Letters**, v. 22, n. 8, p. 1274-1284,
451 2019.
452
453 DIAS-FILHO, M. B. **Diagnóstico das pastagens no Brasil**. Embrapa Amazônia
454 Oriental-Documentos (INFOTECA-E), 2014.
455
456 DOMICIANO, L. F.; PEDREIRA, B. C.; DA SILVA, N. M.; MOMBACH, M. A.;
457 CHIZZOTTI, F. H.; BATISTA, E. D.; NASCIMENTO, H. L. Agroforestry systems: an
458 alternative to intensify forage-based livestock in the Brazilian Amazon. **Agroforestry**
459 **Systems**, v. 94, n. 5, 2020.
460
461 DYBZINSKI, R.; TILMAN, D. Competition and Coexistence in Plant Communities.
462 In:II.5 The Princeton guide to ecology. Princeton University Press, 2012.
463
464 EUCLIDES, V. P. B.; DO VALLE, C. B.; MACEDO, M. C. M.; ALMEIDA, R. G. D.;
465 MONTAGNER, D. B.; BARBOSA, R. A. Brazilian scientific progress in pasture
466 research during the first decade of XXI century. **Revista Brasileira de Zootecnia**, v.
467 39, p. 151-168, 2010.
468
469 FEARNSIDE, P. Deforestation of the Brazilian Amazon. **In: Oxford research**
470 **encyclopedia of environmental science**. 2017.
471
472 GAZOLLA, A. G. **Capim-Marandu e babaçu em sistema silvipastoril**. Tese de
473 Doutorado. UNESP, 2012.
474
475 GEHRING, C.; ZELARAYÁN, M. C.; LUZ, R. L.; ALMEIDA, R. B.; BODDEY, R.
476 M.; LEITE, M. F. A. Babassu palm (*Attalea speciosa* Mart.) super-dominance shapes its
477 surroundings via multiple biotic, soil chemical, and physical interactions and
478 accumulates soil carbon: a case study in eastern Amazonia. **Plant and Soil**, v. 454, n. 1,
479 p. 447-460, 2020.
480

481 GERMER, S.; ZIMMERMANN, A.; NEILL, C.; KRUSCHE, A.V.; ELSENBEER, H.
482 Disproportionate single-species contribution to canopy-soil nutrient flux in an
483 Amazonian rainforest. **Forest Ecology and Management**, v. 267, p. 40-49, 2012.
484
485 GLIESSMAN, S. R. **Agroecologia: processos ecológicos em agricultura sustentável**.
486 Porto Alegre: Ed. da UFRGS, 2001.
487
488 GOMES, F. J.; PEDREIRA, B. C.; SANTOS, P. M.; BOSI, C.; LULU, J.; PEDREIRA,
489 C. G. Microclimate effects on canopy characteristics of shaded palisadegrass pastures in
490 a silvopastoral system in the Amazon biome of central Brazil. **European Journal of**
491 **Agronomy**, v. 115, p. 126029, 2020.
492
493 GOUVEIA, V. M.; MATRICARDI, E. A. T; ANGELO, H. **Dinâmica espaço-**
494 **temporal da produção de amêndoas de babaçu e da utilização das terras no**
495 **Maranhão**. Embrapa Cocais-Documents (INFOTECA-E), 2017.
496
497 GROppo, J. D.; LINS, S. R. M.; CAMARGO, P. B. D.; ASSAD, E. D.; PINTO, H. S.;
498 MARTINS, S. C.; MARTINELLI, L. A. Changes in soil carbon, nitrogen, and
499 phosphorus due to land-use changes in Brazil. **Biogeosciences**, v. 12, n. 15, p. 4765-
500 4780, 2015.
501
502 HANISCH, A. L.; BALBINOT JÚNIOR, A. A.; VOGT, G. A. Desempenho produtivo
503 de *Urochloa brizantha* cv. Marandu em função da inoculação com *Azospirillum* e doses
504 de nitrogênio. **Embrapa Soja-Artigo em periódico indexado (ALICE)**, 2017.
505
506 IBGE, 2017. **Número de estabelecimentos agropecuário com produtos da extração**
507 **vegetal (Babaçu – Coco e Amêndoa) UF- Maranhão**. Acessado em 19 de setembro d
508 2021, disponível em: <https://sidra.ibge.gov.br/tabela/6949#resultado>

509 ISAAC, M.; BORDEN, K. A. Nutrient acquisition strategies in agroforestry
510 systems. **Plant and Soil**, v. 444, n. 1, p. 1-19, 2019.
511
512 JOSE, S.; DOLLINGER, J. Silvopasture: a sustainable livestock production
513 system. **Agroforestry systems**, v. 93, n. 1, p. 1-9, 2019.
514
515 JOSE, S.; WALTER, D.; KUMAR, B. MOHAN. Ecological considerations in
516 sustainable silvopasture design and management. **Agroforestry Systems**, v. 93, n. 1, p.
517 317-331, 2019.
518
519 LANGE, A.; DANTAS, J.; SILVA FREDDI, O.; BURATTO, W.; SPAZIANI, C.;
520 CAIONE, G. Degradação do solo e pecuária extensiva no norte de Mato Grosso.
521 **Nativa**, Sinop, v. 7, n. 6, p. 642-648, nov./dez. 2019.
522

523 LEKBERG, Y.; BEVER, J. D.; BUNN, R. A.; CALLAWAY, R. M.; HART, M. M.;
524 KIVLIN, S. N.; KLIRONOMOS, O.; LARKIN, B. G.; MARON, J. L.; REINHART, K.
525 O.; REMKE, M.; VAN DER PUTTEN, W. H. Relative importance of competition and
526 plant–soil feedback, their synergy, context dependency and implications for
527 coexistence. **Ecology Letters**, v. 21, n. 8, p. 1268-1281, 2018.

528

529 LI, J.; XIE, S.; WILSON, G. W.; COBB, A. B.; TANG, S.; GUO, L.; WANG, K.;
530 DENG, B. Plant–microbial interactions facilitate grassland species coexistence at the
531 community level. **Oikos**, v. 129, n. 4, p. 533-543, 2020.

532

533 LIMA, A. J. T. **Características agronômicas, morfogênicas, estruturais e**
534 **demográficas do capim-Marandu em sistemas silvipastoris e monocultura na**
535 **região PréAmazônica**. Dissertação (Mestrado em Ciência Animal). UFMA,
536 Chapadinha-MA. 82f. 2015.

537

538 LORENZI, H. **Flora Brasileira: Arecaceae (palmeiras)**. 1º ed. Nova Odessa, SP.
539 Instituto Plantarum, 2010, 376p.

540

541 LUZ, R. L., LEITE, M. F. A., ZELARAYÁN, M. C., BODDEY, R. M., GEHRING, C.
542 Litter decomposition and nutrient release dynamics of leaves and roots of the Babassu
543 palm in eastern Amazonia. **Acta Amazonica**, v. 50, p. 213-222, 2020.

544

545 MACK, K. M. L.; EPPINGA, M. B.; BEVER, J. D. Plant-soil feedbacks promote
546 coexistence and resilience in multi-species communities. **Plos one**, v. 14, n. 2, p.
547 e0211572, 2019.

548

549 MARTINS, D.; MARTINS, C. C.; COSTA, N. V. Allelopathic potential of solutions of
550 soils cultivated with *Brachiaria brizantha*: effects on some pasture grass and weeds
551 seeds. **Planta Daninha**, v. 24, n. 1, p. 61-70, 2006.

552

553 MAY, P. H.; ANDERSON, A. B.; FRAZÃO, J. M. F.; BALICK, M. J. Babassu palm in
554 the agroforestry systems in Brazil's Mid-North region. **Agrof Syst** v. 3, p. 275-295,
555 1985.

556

557 MELADO, J. Pastagem Ecológica e serviços ambientais da pecuária
558 sustentável. **Revista de Política Agrícola**, v. 16, n. 3, p. 113-118, 2007.

559

560 MELOTTO, A. M.; LAURA, V. A.; BUNGENSTAB, D. J.; FERREIRA, A. D.
561 **Espécies florestais em sistemas de produção em integração**. Embrapa Gado de
562 Corte-Capítulo em livro científico (ALICE), 2019.

563

564 MONTES, A. O.; LLANOS-CABRERA, M. P.; CHERUBIN, M. R.; HERRERA-
565 VALENCIA, W.; ORTIZ-MOREA, F. A.; SILVA-OLAYA, A. M. Restoring soil

566 carbon and chemical properties through silvopastoral adoption in the Colombian
567 Amazon region. **Land Degradation & Development**, v. 32, n. 13, p. 3720-3730, 2021.
568
569 NASCIMENTO, M. D. D. S. B.; LEITÃO, V. M. S.; SILVA, M. A. C. N. D.;
570 MACIEL, L. B.; MUNIZ, W. E.; VIANA, G. M. D. C.; BEZERRA, G. F. D. B. Eco-
571 epidemiologic study of emerging fungi related to the work of babaçu coconut breakers
572 in the State of Maranhão, Brazil. **Revista da Sociedade Brasileira de Medicina**
573 **Tropical**, v. 47, n. 1, p. 74-78, 2014
574
575 NICODEMO, M.L.F.; PRIMAVERSI, O. Serviços ambientais em sistemas
576 silvopastoris. **Embrapa Pecuária Sudeste-Capítulo em livro científico (ALICE)**,
577 2019.
578
579 NOBRE, C. P.; COSTA, M. G. D.; GOTO, B. T.; GEHRING, C. Arbuscular
580 mycorrhizal fungi associated with the Babassu palm (*Attalea speciosa*) in the eastern
581 periphery of Amazonia, Brazil. **Acta Amazonica**, v. 48, p. 321-329, 2018.
582
583 NUNES, S. G.; BOOCK, A.; PENTEADO, M. D. O.; GOMES, D. T. **Brachiaria**
584 **brizantha cv. Marandu**. Embrapa Gado de Corte-Documents (INFOTECA-E), 1984
585
586 OLIVEIRA, A. N.; DE OLIVEIRA, A. N.; DA SILVA, K. R.; DA SILVA, L. J. D. A.
587 MELLO, A. H. Atributos químicos de solo sob diferentes sistemas de uso e manejo no
588 projeto de assentamento veneza-São Domingos do Araguaia, PA. **Revista**
589 **Agroecossistemas**, v. 9, n. 1, p. 170-179, 2017.
590
591 PORRO, R. A economia invisível do babaçu e sua importância para meios de vida em
592 comunidades agroextrativistas. **Bol. Mus. Para. Emílio Goeldi. Ciênc. hum**, p. 169-
593 188, 2019.
594
595 PORRO, R. Palms, pastures, and swidden fields: the grounded political ecology of
596 “agro-extractive/shifting-cultivator peasants” in Maranhão, Brazil. **Human ecology**, v.
597 33, n. 1, p. 17-56, 2005.
598
599 RAMOS, L. M. Estudo de variáveis ecofisiológicas de *Brachiaria decumbens* em
600 diferentes sistemas de manejo de pecuária. Tese de Doutorado. UEMA, 2014.
601
602 RAZUK, R. B. Avaliação do sistema radicular de acessos de *Brachiaria brizantha* e suas
603 relações com atributos químicos e físicos do solo. Tese de Doutorado. UFMT, 2002.
604
605 REIS et al. Dinâmica populacional de babaçu (*Attalea speciosa* Mart. ex. Spreng.) em
606 pastagens na Amazônia Oriental. Tese de Doutorado. UFRA/Campus Belém, 2019.
607

608 RIBEIRO, J. F.; WALTER, B. M. T. Fitofisionomias do bioma Cerrado. Cerrado:
609 ambiente e flora. Planaltina: **Embrapa Cerrados-Capítulo em livro científico**
610 **(ALICE)**, 1998, p. 87-166
611
612 RODRIGUES, R. C.; ARAÚJO, R. A.; COSTA, C. S.; LIMA, A. J.; OLIVEIRA, M. E.;
613 CUTRIM JR, J. A.; FRANCISCO NS SANTOS, F. N. S.; JOCÉLIO S. A.; VILMA, M.
614 S. E.; ARAÚJO, A. S. Soil microbial biomass in an agroforestry system of Northeast
615 Brazil. **Tropical Grasslands-Forrajes Tropicales**, v. 3, n. 1, p. 41-48, 2015.
616
617 ROMEIRO, A. R. Meio ambiente e produção agropecuária na Amazônia. **Revista de**
618 **Economia e Sociologia Rural**, v. 37, n. 1, p. 9-34, 2019.
619
620 SANTOS, A. M. S.; GHOSH, A.; NETO, B. C. V.; FERREIRA, O. P. Carbonização de
621 biomassa de babaçu e suas potenciais aplicações: uma prospecção tecnológica. **R**
622 **GEINTEC-Gestão, Inovação e Tecnologias**, v. 5, n. 4, p. 2619-2631, 2015.
623
624 SANTOS, P. M.; SANTOS, A. C.; NETO, D. N. N.; OLIVEIRA, W. H.; SOUSA, L. F.
625 E OLIVEIRA, L. B. T Implementation of Silvopastoral Systems under Nutrient Cycling
626 in Secondary Vegetation in the Amazon. **Journal of Agricultural Science**, v. 10, n. 4,
627 2018.
628
629 SCHOFIELD, E. J.; ROWNTREE, J. K.; PATERSON, E.; BROOKER, R. W.
630 Temporal dynamism of resource capture: a missing factor in ecology?. **Trends in**
631 **ecology & evolution**, v. 33, n. 4, p. 277-286, 2018.
632
633 SILVA NETO, S. P.; SANTOS, A. C.; LIMA LEITE, R. L.; DIM, V. P.; NEVES
634 NETO, D. N.; SILVA, J. E. C. Variação espacial do teor de matéria orgânica do solo e
635 produção de gramínea em pastagens de capim-marandu. **Bioscience Journal**, v. 28, n.
636 1, 2012.
637
638 SILVA, E. C. D.; PEREIRA, M. G.; FRADE, E. F.; SILVA, S. B. D.; CARVALHO, J.
639 A. D.; SANTOS, J. C. D. Temporal evaluation of soil chemical attributes after slash-
640 and-burn agriculture in the Western Brazilian Amazon. **Acta Scientiarum. Agronomy**,
641 v. 41, 2019.
642
643 SILVERTOWN, J. Plant coexistence and the niche. **Trends in Ecology & evolution**, v.
644 19, n. 11, p. 605-611, 2004.
645
646 SOUSA, J. T. R; MORAES, F. H. R; GEHRING, C. Root biomass in a shifting cultivation
647 system in the eastern periphery of Amazonia, and contribution of the Babassu
648 palm. **Agroforestry systems**, v. 90, n. 2, p. 351-360, 2016.
649

650 TANG, J.; KÖRNER, C.; MURAOKA, H.; PIAO, S.; SHEN, M.; THACKERAY, S. J.;
651 YANG, X. Special feature: international LTER emerging opportunities and challenges
652 in phenology: a review. **Ecosphere**, v. 7, n. 8, p. 1-17, e01436, 2016.
653

654 THAKUR, M. P.; VAN DER PUTTEN, W. H.; WILSCHUT, R. A.; VEEN, G. C.;
655 KARDOL, P.; VAN RUIJVEN, J.; ALLAN, E. ; KLEUNEN, M.; BEZEMER, T. M.
656 Plant–Soil Feedbacks and Temporal Dynamics of Plant Diversity–Productivity
657 Relationships. **Trends in ecology & evolution**, 2021.
658

659 TSCHIRHART, J. Resource competition among plants: from maximizing individuals to
660 community structure. **Ecological Modelling**, v. 148, n. 2, p. 191-212, 2002.
661

662 VALLADARES, F.; BASTIAS, C. C.; GODOY, O.; GRANDA, E.; ESCUDERO, A.
663 VAN DER PUTTEN, W. H.; BRADFORD, M. A.; PERNILLA BRINKMAN, E.; VAN
664 DE VOORDE, T. F.; VEEN, G. F. Where, when and how plant–soil feedback matters in
665 a changing world. **Functional Ecology**, v. 30, n. 7, p. 1109-1121, 2016.
666

667 VENDRAMINI, T. Um novo olhar para a pecuária brasileira. **AgroANALYSIS**, v. 39,
668 n. 5, p. 47, 2019.
669

670 VERESOGLOU, S. D.; RILLIG, M. C.; JOHNSON, D. Responsiveness of plants to
671 mycorrhiza regulates coexistence. **Journal of Ecology**, v. 106, n. 5, p. 1864-1875,
672 2018.
673

674 VILLA, P. M.; MARTINS, S. V.; NETO, S. N. O.; RODRIGUES, A. C.;
675 MARTORANO, L. G.; MONSANTO, L. D.; CANCIO, N. M.; GASTAUER, M.
676 Intensification of shifting cultivation reduces forest resilience in the northern
677 Amazon. **Forest Ecology and Management**, v. 430, p. 312-320, 2018.
678

679 WANG, X.; TANG, C.; SEVERI, J.; BUTTERLY, C. R.; BALDOCK, J. A.
680 Rhizosphere priming effect on soil organic carbon decomposition under plant species
681 differing in soil acidification and root exudation. **New Phytologist**, v. 211, n. 3, p. 864-
682 873, 2016.
683

684 WOLKOVICH, E. M.; CLELAND, E. E. Phenological niches and the future of invaded
685 ecosystems with climate change. **Plantas AoB**, v.6, p1-16, 2014.
686

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CAPITULO II

700

701 **BELOWGROUND COMPETITION AND NICHE PARTITIONING BETWEEN**
702 **THE BABASSU PALM AND UROCHLOA GRASS IN PASTURES OF THE**
703 **EASTERN PERIPHERY OF AMAZONIA**

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717 **Belowground Competition and niche partitioning between the Babassu palm and**
718 **Urochloa grass in eastern Amazonia pastures**

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726

727 **Abstract**

728 Much of deforested Amazonia is dominated by pastures planted with exotic *Urochloa*
729 (syn *Brachiaria*) grass, containing interspersed the ruderal Babassu palm (*Attalea*
730 *speciosa*). This two-species system offers the opportunity to investigate how two very
731 competitive species interact. Research was conducted in the eastern periphery of
732 Amazonia in three monospecific *Urochloa* pastures (*U.brizantha* cv. 'marandu')
733 containing dispersed Babassu palm clusters. We mapped 0-50 cm root profiles of Babassu
734 and *Urochloa* at three distances representing contrasting relative dominance: 'within
735 clusters' (0.4-0.6 m from adult palm, Babassu-dominated); 'mid-distance' (at 2.5-6.0 m)
736 and 'far' (at >8.0-10.0 m, *Urochloa*-dominated). Babassu coarse and mid-diameter roots
737 concentrated within clusters at 20 – 50 cm depth, well protected against disturbance, but
738 Babassu mid-diameter roots did extend up to 10 m from clusters, indicating active
739 foraging at mid and long distances. Fine roots predominated root counts throughout all
740 soil profiles, with 74.6% concentrated in the 0-20 cm topsoil. Fine-scale variability of
741 fine roots was high, with high density hotspots of both species in the topsoil. Babassu fine

742 root share was 48.1% within clusters, as opposed to 84.1% Urochloa fine root share far
743 from clusters, and the metric distance from Babassu clusters was a significant predictor
744 of root abundance in all diameter classes. Vertical fine root profiles of Babassu and
745 Urochloa differed systematically, with 41.9% of all Urochloa fine roots concentrated
746 within the first 0-10 cm, as opposed to deeper rooting Babassu (69.8% of all fine roots
747 below 10 cm). Urochloa vertical root profile was unaffected by the degree of interspecific
748 competitive confrontation and possibly limited by physical or chemical soil rootability
749 constraints. By contrast, Babassu fine roots escaped competition from Urochloa by
750 rooting significantly deeper in grass-dominated sampling points. Limitation of Urochloa
751 fine roots to the topsoil reduces the ecological efficiency of pure Urochloa pastures. By
752 contrast, deeper fine rooting and high plasticity under interspecific competitive
753 confrontation are likely key components for Babassu's outstanding ecological success in
754 degraded pastures throughout Amazonia. In practical terms, our findings call for an
755 optimized Babassu palm management and for the diversification of Amazonian pastures
756 in order to increase their ecological efficiency and productivity.

757

758 **Keywords:** *Attalea speciosa*; *Brachiaria*; fine roots; coarse roots; dominance effects;
759 signal grass; silvopasture; niche expansion; root competition; plasticity.

760 **I. Introduction**

761 Competition is at its maximum when occurring between ecologically similar
762 species exploiting the same resources, and either causes the elimination of the
763 competitively inferior species (law of Gause), or it results in a dynamic state of
764 coexistence under high competition maintained by ‘mutual invasability’ (Dybinski and
765 Tilman 2012). More stable species coexistence turns possible by the occupation of
766 different niches / niche partitioning (Chesson 2009, Andrea et al. 2020). This reduces
767 competition and maximizes resource exploitation, the basis of overyielding reported in
768 many multi-species agroforestry systems (Isaac and Borden 2019). On the other hand,
769 competitively very successful ‘invasive’ species are known to be able to monopolize
770 resource exploitation via positive plant:soil feedbacks (Crawford et al. 2019). Depending
771 on their plasticity, different species will or will not adapt their resource acquisition
772 strategies in order to avoid competition by increasing niche segregation under
773 heterospecific - as opposed to conspecific - competition (Adler et al. 2018). Belowground,
774 strong competition between two similarly competitive species (but not under asymmetric
775 competitive settings) can cause fine root aggregation and segregation as a strategy for the
776 consolidation of foraging area under competitive pressure (Leipik et al. 2021).
777 Unsustainable land-use intensification in human-transformed landscapes (frequent burns
778 and short fallow periods) reduces overall biodiversity and increases the dominance of
779 aggressive ruderal species (Jakovach et al. 2016, Villa et al. 2018). This study compares
780 the case of the competitive confrontation between two ecologically very successful
781 species, the native but ‘superdominant’ babassu palm (*Attalea speciosa* MART.) and the
782 exotic and invasive pasture grass ‘Urochloa’ (*Urochloa brizantha* (HOCHST & A.RICH)
783 STAPF cv. ‘marandu’).

784 An estimated 116 Mio hectares of Brazil have been converted to planted pastures,
785 85% of which planted with *Urochloa* species, next to palisade grass (*U.brizantha*) also
786 signal grass (*U.decumbens*) and ruzigrass (*U.ruziziensis*). The ‘Marandu’ variety of
787 palisade grass, released by Embrapa in 1984, still occupies most of these pastures (~50
788 Mio ha) and is considered the world’s largest monoculture in terms of area (Low 2015).
789 Exotic *Urochloa* is highly invasive into native Brazilian savannas, with strong
790 suppression of both early and late-successional neighboring vegetation (Zangaro et al.
791 2016), likely due to strong phytotoxic or plant allelopathic effects (Kato-Noguchi et al.
792 2014).

793 The ruderal Babassu palm is omnipresent throughout the landscapes of deforested
794 Amazonia, on an estimated 200.000 km² in Brazil alone (May et al. 1985). Although
795 Babassu occurs in low abundance in mature rainforests, its dominance increases
796 dramatically after repeated burns and reduced fallow periods both in the extensive
797 pastures and in shifting cultivation fields and fallows, in some cases forming near
798 monospecific stands (Anderson et al. 1991; Santos Filho et al. 2013). There are many
799 reasons for the outstanding ecological success of the Babassu palm in such degraded
800 lands, next to the (initial) selective sparing of productive adult palms for palm oil
801 production (see below) its adaptation to frequent fires (fire-induced germination, well
802 protected belowground meristem of stemless juvenile, vigorous resprouting capacity
803 following slash&burn (Mitia and Ferraz 2001), as well as its adaptation to abiotically
804 stressed degraded lands (Sampaio et al. 2012). Gehring et al. (2020) show the Babassu
805 palm to simplify vegetation:litter:topsoil interactions in eastern Amazonian secondary
806 regrowth, suggesting positive plant:soil feedback as a further pathway for the dominance-
807 increase of this palm.

808 The sustainability (or lack thereof) of *Urochloa* pastures with differing portions
809 of Babassu infestation is of great concern both from ecological and socioeconomic
810 perspectives. This silvopastoral system combines frequently conflicting interests between
811 the large-scale cattle ranchers and Babassu nut extractivists (mainly women), granted free
812 access to these lands for palm oil extraction. Babassu is one of the world's top-ranking
813 non-cultivated species used for extractivism, with its palm oil and charcoal providing a
814 vital income-source for an estimated 300,000 babassu extractivists in Maranhão state
815 alone (Almeida et al. 2001). Stakeholder's perceptions of both species also contrast
816 markedly (Almeida et al. 2016), with cattle ranchers considering the Babassu palm an
817 aggressive 'pest', difficult to control with (legal) herbicides, as pasture grass productivity
818 declines with increasing palm densities (Rodrigues et al. 2016), whereas Babassu
819 extractivists complain of *Urochloa* grass impeding Babassu germination, growth and
820 development (Porro 2019), supposedly via allelopathic effects.

821 Though Babassu and *Urochloa* are from different growth forms and contrasting
822 (aboveground) plant size, they also have many characteristics in common. Both species
823 are known to invest heavily in their root systems, with – relative to aboveground biomass
824 shares - disproportionately high Babassu root biomass shares in secondary forests (Sousa
825 et al. 2015), and above-average investment of *Urochloa* species in their abundant fine /
826 'graminoid' root system (Huot et al. 2020). Both are also known to strongly associate
827 with arbuscular mycorrhizal fungi, Glomerospore density increases and species
828 composition changes with Babassu dominance (Nobre et al. 2018), and *Urochloa* grasses
829 are likewise strongly mycorrhizal (Teutscherova et al. 2019) and due to their generalist
830 mycorrhizal associations frequently used as 'trap plants' (Leal et al. 2009). Both Babassu
831 (Gehring et al. 2012) and *Urochloa* grass (Kato-Noguchi et al. 2014) also exert
832 allelopathic effects on other plants in their surroundings.

833 Babassu and Urochloa have in common an accumulation of soil organic matter
834 in their surroundings, reported for Babassu by Gehring et al. (2020), and in Urochloa
835 pastures by (Silva Neto et al. 2012, Santos et al. 2013). The pathways for such SOM-
836 buildup, however, likely differ between the two, with high root exudation from the C4
837 grass Urochloa (Louw-Gaume et al. 2017), as opposed to high Babassu litter inputs with
838 high C:N-ratios (Gehring et al. 2020) and slow litter decomposition (Luz et al. 2020).

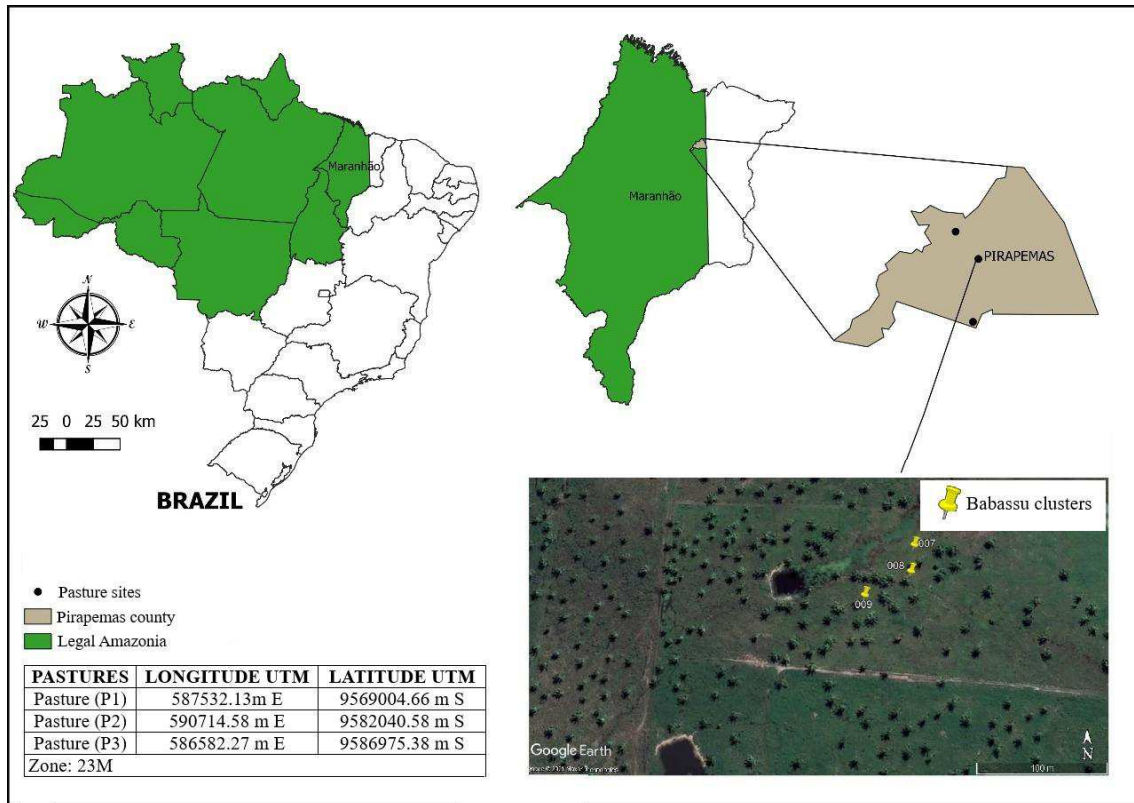
839 This study investigates the direct confrontation between the two species in
840 monospecific Urochloa pastures containing Babassu clusters in the eastern periphery of
841 Amazonia. We capture the relative dominance of Babassu and Urochloa in a horizontal
842 dominance gradient ranging from within the Babassu clusters (Babassu dominated) to far
843 from any Babassu palm (Urochloa dominated), and vertical rooting profiles of Babassu
844 and Urochloa in 0-50 cm root walls. We explore the degree of niche overlap vs. niche
845 partitioning between these two ruderal species and hypothesize that interspecific
846 competitive confrontation may increase niche partitioning as a strategy of competitive
847 avoidance. We strive to advance both theoretical understanding of interspecific
848 competition strategies, and provide a basis for a more ecoefficient management of
849 degraded pastures of eastern Amazonia and beyond.

850

851 **II. METHODS AND METHODS**

852 **II.1. Study region and experimental layout**

853 Research was conducted in the eastern periphery of Amazonia (transition-zone to
854 Cerrado savannas), in Pirapemas county, Maranhão State, Brazil (UTM 585905.12 m E;
855 9587870.75 m S., 40 m a.s.l.) (Figure 1).



856

857 **Figure 1.** Location of the three pastures (P1-P3), gray area = Pirapemas county; Green
 858 area = Legal Amazonia, and exemplary map of one of the three sites with location of the
 859 three Babassu clusters

860 Climate according to the Köppen-classification is wet tropical (*Aw*), with an average
 861 1580 mm precipitation concentrated in a 6-month rainy season (InMet 2021: 10 yr.-
 862 average of meteorological station at <100 km distance, precipitation in the 2019 study
 863 year: 1724 mm). Soils are classified Ultisols, plintic subgroup according to the US soil
 864 taxonomy (SANTOS et al., 2018). Are deeply-weathered, acid and nutrient-poor, with
 865 likely problems of strong P-fixation and possible Al-toxicity especially in the subsoil
 866 (Souza et al. 2018). Table 1 depicts average soil physical and chemical indicators of the
 867 three study sites.

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871 **Table 1.** Topsoil physical and chemical indicators of the three study sites (means \pm SE,
 872 total n=27 sampling points).

PHYSICAL AND CHEMICAL INDICATORS	0-10 cm	10-20 cm	METHOD
% Fine sand	50.21 (\pm 1.08)	49.65 (\pm 1.28)	wet sieving ¹⁾
% Coarse sand	37.78 (\pm 1.48)	38.40 (\pm 1.69)	wet sieving ¹⁾
% Silt	5.23 (\pm 0.49)	5.13 (\pm 0.36)	wet sieving ¹⁾
% Clay	6.89 (\pm 0.27)	6.89 (\pm 0.25)	wet sieving ¹⁾
Microporosity ($\text{m}^3 \text{m}^{-3}$)	0.26 (\pm 0.01)	0.24 (\pm 0.01)	Suction table at 6 kPa ¹⁾
Macroporosity ($\text{m}^3 \text{m}^{-3}$)	0.14 (\pm 0.01)	0.16 (\pm 0.01)	Difference between total porosity (saturated water content) and microporosity ¹⁾
bulk soil density (g cm^{-3})	1.64 (\pm 0.03)	1.63 (\pm 0.03)	Average of two 5cm depths per sample in root walls (see chap. II.2)
Particulate Organic C (POC) (g kg^{-1})	3.62 (\pm 0.28)	4.51 (\pm 0.36)	Granulometric fractionation ²⁾ and Walkley&Black digestion ³⁾
MOC (g kg^{-1})	8.85 (\pm 0.60)	4.22 (\pm 0.66)	Granulometric fractionation ²⁾
TOC (g/kg^{-1})	12.48 (\pm 0.59)	8.73 (\pm 0.57)	Walkley&Black digestion ³⁾
pH (CaCl_2)	4.12 (\pm 0.04)	4.05 (\pm 0.05)	

873

total N (%)	0.06 (±0.01)	0.05 (±0.01)	Kjeldåhl digestion ¹⁾
available P (mg kg ⁻¹)	4.31 (±0.38)	3.02 (±0.42)	Mehlich 1 extraction ⁴⁾
K mg kg ⁻¹	23.77 (±4.03)	15.18 (±2.75)	Mehlich 1 extraction ⁴⁾
Ca (cmolc dm ⁻³)	0.98 (±0.08)	0.55 (±0.04)	1M KCl-extraction ⁵⁾
Mg (cmolc dm ⁻³)	0.77 (±0.08)	0.41 (±0.06)	1M KCl-extraction ⁵⁾
effective CEC (cmolc dm ⁻³)	2.05 (±0.11)	1.36 (±0.09)	Exchangeable bases +Al ³⁺
total CEC (cmolc dm ⁻³)	4.68 (±0.24)	3.58 (±0.23)	Exchangeable bases + potential acidity (H+Al) ¹⁾
H+Al (cmolc dm ⁻³)	2.78 (±0.19)	2.51 (±0.19)	Potential acidity via Ca-acetate extraction at pH 7 ¹⁾
Aluminum saturation (m%)	9.08 (±1.11)	24.51 (±3.20)	Portion of 1M-extractable Al in relation to exchangeable bases+Al ¹⁾

874 ¹⁾ Teixeira et al. 2017; ²⁾ adapted from Cambardella & Elliott (1992); ³⁾ Walkley&Black
875 (1934); ⁴⁾ Mehlich (1953); ⁵⁾ Raij et al. (2001)

876

877 We selected three pastures located at 3 - 9 km distance from another (points P1, P2
878 and P3 in Figure 1). All three sites had been planted between 5 and 8 years ago with
879 *Urochloa palisade* grass (*Urochloa brizantha* cv. 'marandu') containing clusters of an

880 adult Babassu palm and surrounding juvenile (stemless) palms. We estimate average adult
881 Babassu palm density of the three sites at $\sim 25 \text{ ha}^{-1}$. All three pasture sites had been under
882 extensive grazing ($2\text{-}3 \text{ cattle ha}^{-1}$), but in a resting phase (no grazing) for more than four
883 months prior to sampling, thus avoiding short-term artefacts caused by grazing. None of
884 the pastures had previously received any application of fertilizers or lime, representing
885 the prevailing practice throughout Amazonian pastures. In each site we selected three
886 such Babassu-islands clusters with $>30 \text{ m}$ distance between another, and for each cluster
887 we selected three contrasting sampling positions (at $0.4 - 0.6 \text{ m}$ ‘within-cluster’: high
888 Babassu dominance – ‘mid-distance’ (at $2.5\text{-}6 \text{ m}$ distance from the adult palm):
889 confrontation-zone – ‘far’ (at $>8\text{-}10 \text{ m}$ distance from the adult palm): high Urochloa grass
890 dominance, total of 27 sampling points. Aboveground Urochloa biomass (sampled in 1 m^2
891 squares per sampling point was estimated at 2.23 Mg ha^{-1} , 27.2% of which was classified
892 as dead. All 27 sampling-locations were specifically visually scrutinized for the absence
893 of any other (gramineous or herbaceous) species in their surroundings, thus guaranteeing
894 the pure confrontation of our two model-species. All field work was conducted in
895 May/June of 2019 (end of rainy season) within a time-span of 2 weeks.

896

897 **II.2. Babassu and Urochloa root distribution**

898 We used ‘root walls’ (Böhm 1979) to evaluate Babassu and Urochloa root
899 distribution. Each root wall was 1 meter-wide and 50 cm deep, with orientation parallel
900 to the Babassu-island borders. Each root wall was sub-divided into 200 $5 \times 5 \text{ cm}$ grids,
901 and we counted in each grid Babassu and Urochloa roots in three predefined diameter
902 classes: ‘fine’ ($<2 \text{ mm}$), mid-diameter ($2\text{-}5 \text{ mm}$) and ‘coarse’ ($>5 \text{ mm}$).

903 The definition of ‘fine roots’ (as opposed to mid-diameter and coarse roots) is a
904 compromise between inherent species / growth-form specific differences in specific root

905 diameter (i.e. thin graminoid Urochloa grass roots vs. coarser lignified Babassu roots) and
906 within-species physiological/functional distinction (fast-growing and shorter-lived fine
907 roots for water- and nutrient-uptake vs. slow turnover/'long-lived' mid-sized and coarse
908 roots for transport and storage) (McCormack et al. 2015, Freshet et al. 2021). Our
909 definition of a 2 mm threshold for 'fine' roots is in accordance with some studies (Sanford
910 and Cuevas, 1996), though thicker than in others (Castellanos et al. 2001, Huot et al.
911 2020), and is designed to account for the coarser fine roots (lowest branching-levels) of
912 the Babassu palm, typical also for other palms (Nitta et al. 2002).

913 Distinction between Babassu and Urochloa roots is unambiguous; due to their
914 contrasting color and structure, (orange lignified Babassu roots vs. white flexible almost
915 exclusively fine Urochloa roots). We limit statistical analysis of Urochloa roots to their
916 fine roots, as we registered only very few mid-diameter and coarse Urochloa roots (chap.
917 III.1).

918 We furthermore estimated soil bulk density in one selected / 'representative' 5 x 5
919 cm grid at each 5 cm depth of each root wall in 5 x 5 x 3.3 cm cubic samples, permitting
920 the analysis of the immediate impact of bulk soil density on root distributions in the
921 selected grids (chap. III.5).

922

923 **II.3 Data-processing and statistics**

924 The root wall counts both visually and statistically. For statistical processing, we
925 (i) analyzed grid-data as a total, and (ii) summed root-counts in the 20 5 cm grids per soil
926 depth, thus reducing the problem of zero-inflation. We checked data for normality of
927 distribution via Kolmogorow-Smirnov and Lilliefors' tests, and also checked for
928 homogeneity of variance (Levene test). We explore the effects of our relative dominance

929 gradient (distance from Babassu clusters) with both distance classes as a categorical
930 variable and with continuous metric distance.

931 We used Generalized Additive Mixed Models (GAMM) for estimation of
932 regression parameters, based on log10-transformed variables corrected for dispersion and
933 spatial autocorrelation, in order to control residual variance. We selected the best
934 likelihood model based on lowest AIC values. Statistical analyses were carried out in R
935 studio Version 4.1.0 (R Core Team, 2021) using the package “mgcv” (Wood 2003, 2004,
936 2011, Wood et al. 2016) to run models. Steps for model selection were carried out as
937 suggested by Zuur et al. (2009) and Zuur (2012), accepting p-values <0.001 as
938 precondition for parameter selection.

939

940 **III. RESULTS**

941 **III.1. Impact of relative Babassu and Urochloa dominance on root counts**

942 We counted a total of 10.409 Babassu and 10.326 Urochloa roots in the 27 root
943 walls. 69.1% of all roots were fine (>2 mm) roots but root diameter composition differed
944 strongly between the two species: Babassu with 24.9% coarse root, 19.7% mid-diameter
945 root and 55.4% fine root counts, as opposed to Urochloa with 6.5% coarse root, 10.5%
946 mid-diameter root and 83.0% fine root counts.

947 Figure 2 compares the four main root categories between distance categories, and
948 Figure 3 depicts the respective relationships with metric distance from the Babassu
949 clusters. The strong differences in all root categories between sampling positions and their
950 significant relationships with metric distance of sampling points from the Babassu
951 clusters confirm our experimental layout which takes horizontal distance from the
952 Babassu clusters as a proxy for relative Babassu / Urochloa dominance.

953 Coarse root counts were 4.7-fold higher within the Babassu clusters ('within-
 954 cluster') than at mid-distance and 12-fold higher than far from the Babassu clusters. Mid-
 955 diameter Babassu roots were less horizontally concentrated within the Babassu clusters.
 956 Of their total of 2046 mid-sized roots, 1460 were within clusters and 394 at mid-distance,
 957 but a further 162 were 'far' (at >8.0 - 10.0 m distance from the Babassu clusters), pointing
 958 to a significant horizontal extension of the Babassu root system and root Babassu foraging
 959 at far distances / within the Urochloa pasture. Contrary to Babassu coarse and mid-
 960 diameter roots, Babassu fine root counts were less than double within the Babassu clusters
 961 than at mid- and long distances. Urochloa fine root counts were maximum far from
 962 Babassu clusters, similar at mid-distance (14.4% lower) but 59.3% lower within Babassu
 963 clusters.

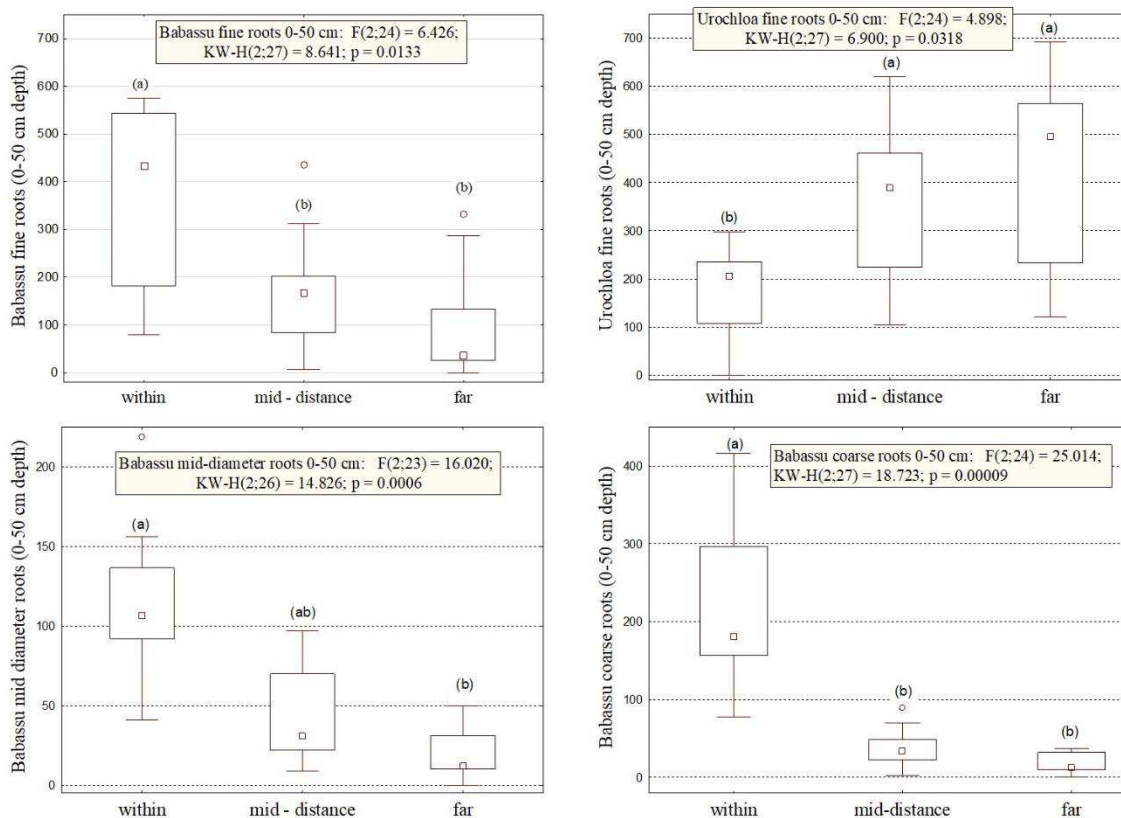
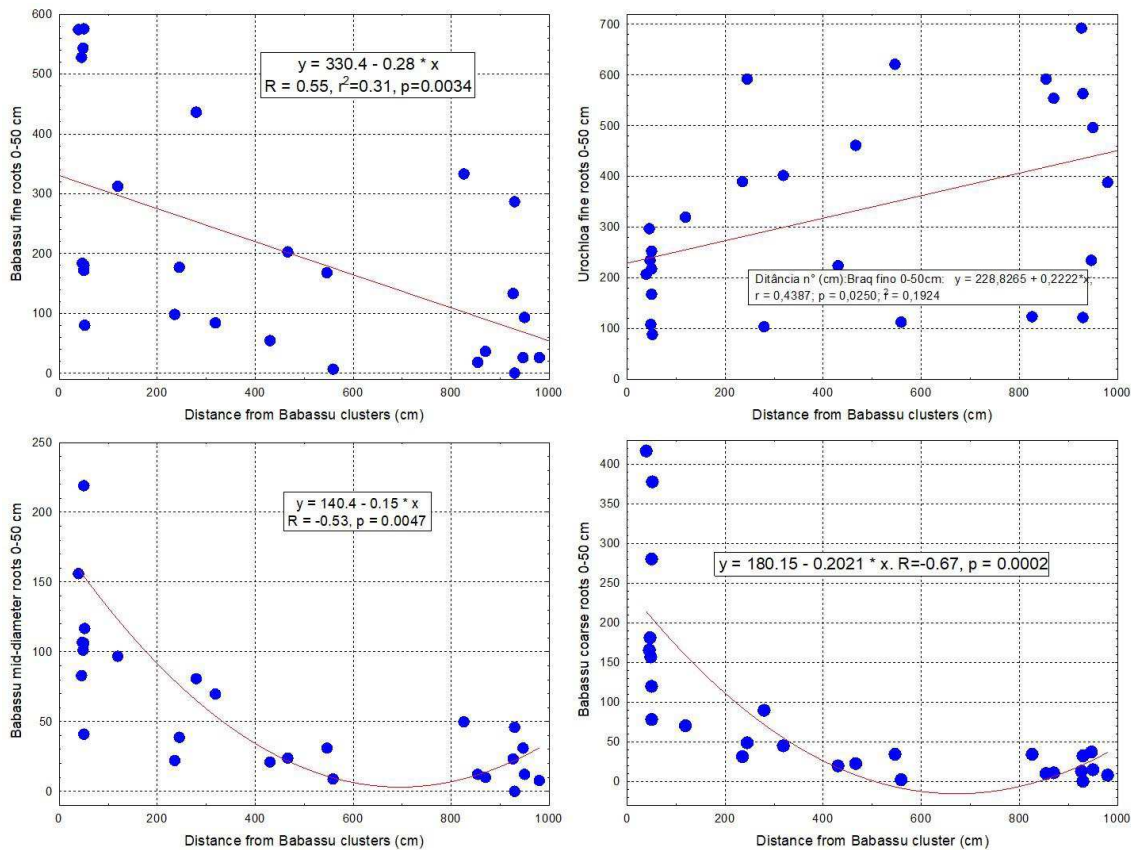


Figure 2. Babassu and Urochloa fine roots (top) and Babassu mid-diameter and coarse roots (bottom) in 0-50 cm soil depth. Medians, 25/75-percentiles, non-outlier range and outliers, extremes excluded. Letters refer to distance-grouping according to non-parametric Kruskal-Wallis ANOVA.



964

965 **Figure 3.** Relationship between metric distance from Babassu clusters and abundance
 966 of Babassu and Urochloa fine roots (top, linear fits) and of Babassu coarse and mid-
 967 diameter roots (bottom, negative exponential fit).

968

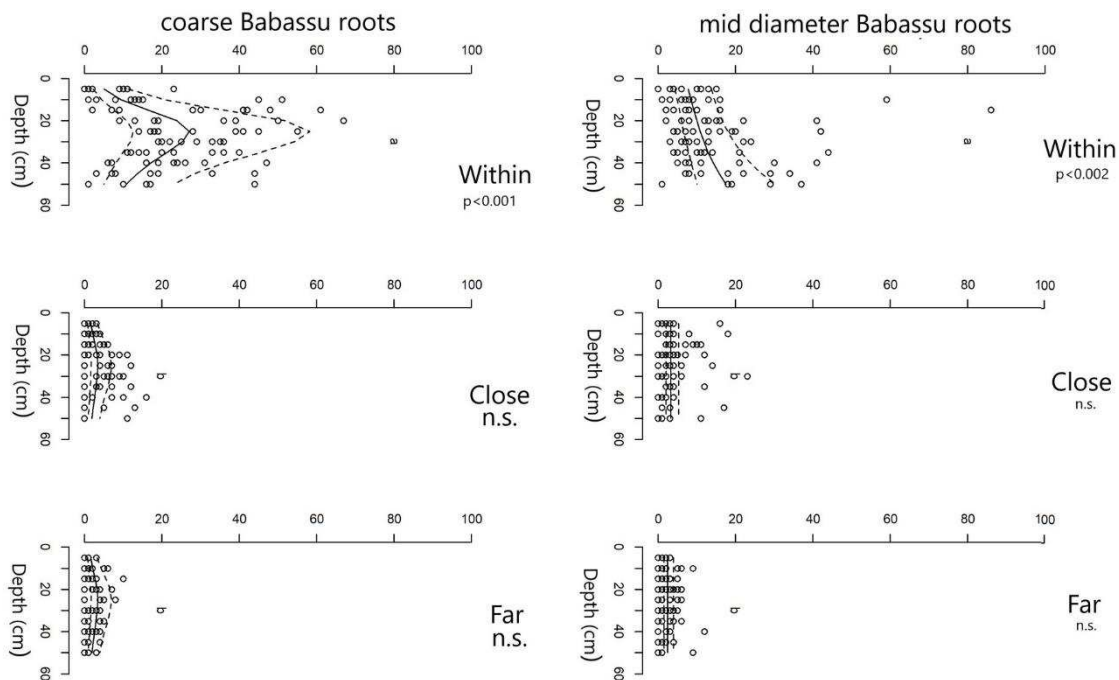
969 III.2. Babassu coarse and mid-diameter horizontal and vertical profiles

970 Figure 4 depicts coarse and mid-sized Babassu root vertical distribution at three
 971 distances from Babassu clusters. Coarse root counts were 4.7-fold higher within the
 972 Babassu clusters than at mid-distance and 12-fold higher than at long distance from the
 973 Babassu clusters, pointing to a very limited horizontal dispersal of Babassu coarse roots
 974 and their concentration directly beneath the palms within the Babassu clusters.
 975 Curvilinear relationships between root counts and soil depth were significant within
 976 Babassu clusters, both for coarse and mid-diameter roots, but – due to small densities –
 977 failed to be significant at mid-distance and far from Babassu clusters. Coarse root counts

978 peaked at approximately 30 cm depth in all three sampling distances, but the peak was
 979 far more expressed within the Babassu clusters.

980 Mid-diameter roots likewise were concentrated within the Babassu clusters but to a
 981 lesser degree. Mid-diameter Babassu root counts were 3.7-fold higher within the Babassu
 982 clusters than at mid-distance and 7.6-fold higher within the Babassu clusters than far from
 983 Babassu clusters. The occurrence of an average 43.7 mid-diameter Babassu roots at mid-
 984 distance and of 21.3 far (8-10 m distance) from Babassu palms is indicative of a wide
 985 spatial range of the Babassu rooting system and root foraging well within the Urochloa
 986 pastures.

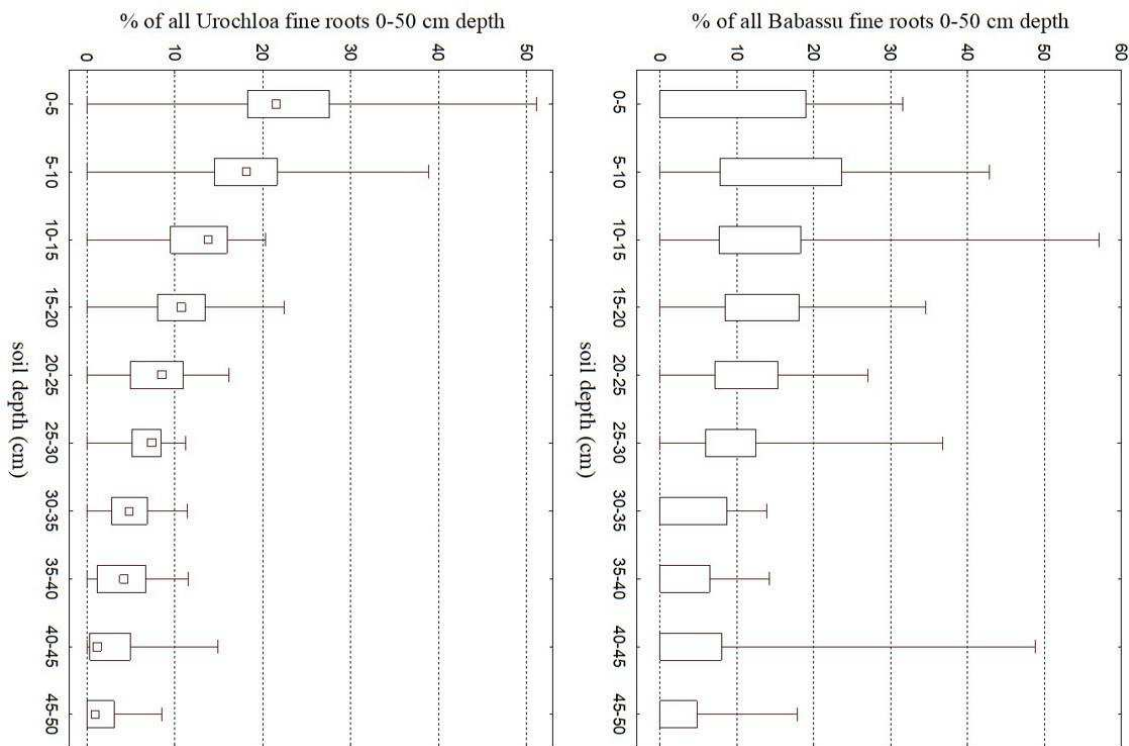
987 Contrary to the coarse root counts, Babassu mid-diameter counts within the Babassu
 988 clusters didn't exhibit a clear peak at 30 cm soil depth, but rather continuously increased
 989 down to the 50 cm maximum sampling-depth (Figure 4 right).



990
 991 **Figure 4.** Coarse (>5 mm, left) and mid-diameter (2-5mm, right) root counts per 5 cm
 992 soil depth at sampling positions ‘within’ (top), at mid-distance (2.5 – 6.0 m) (middle) and
 993 ‘far’ (>6 m, bottom) from babassu clusters. Solid lines represent data interpolation, dotted
 994 lines represent 95% confidence intervals.

995 **III.3. Babassu and Urochloa vertical fine root profiles**

996 Figure 5 depicts the vertical distribution of Babassu and Urochloa fine roots down
 997 the 0-50 cm soil profile. Surface rooting was expressive, 74.6% of all fine roots occurred
 998 in the upper 20 cm, but the relative vertical distribution below the 0-50 cm soil profile
 999 differed between Babassu and Urochloa - Urochloa fine roots were more concentrated in
 1000 the topsoil layer (on average 41.9% of all Urochloa fine roots were concentrated in the
 1001 upper 0-10 cm layer, compared to only 30.1% of Babassu fine roots) 22.5% of all Babassu
 1002 fine roots were below 30 cm, as opposed to only 14.8% of Urochloa roots.



1003
 1004 **Figure 5.** Relative vertical distribution of Urochloa (left) and Babassu (right) fine roots
 1005 along the 50 cm soil profile over at all three distances: percentages of total root count per
 1006 5 cm soil layer (medians, 25- and 75-percentiles and range).

1007 **III.4 Impact of relative Babassu and Urochloa dominance on vertical fine root**
 1008 **profiles**

1009 Vertical distribution differed significantly between distance / relative dominance
 1010 (Figure 6). Topsoil concentration of Urochloa fine root counts was maximum in the first

1011 10 cm, with (50.6%) far from Babassu clusters, (41.9%) at mid-distance and (38.3%)
 1012 within the Babassu clusters, with no significant differences in their vertical profile
 1013 between distances classes. In marked contrast, the vertical profile of Babassu fine roots
 1014 differed significantly between distance classes, with 37.5% of all Babassu fine roots
 1015 concentrated in the top 0-10 cm within Babassu clusters, as opposed to only 20.3% at
 1016 mid-distance and 20.8% at far sampling distance dominated by Urochloa.

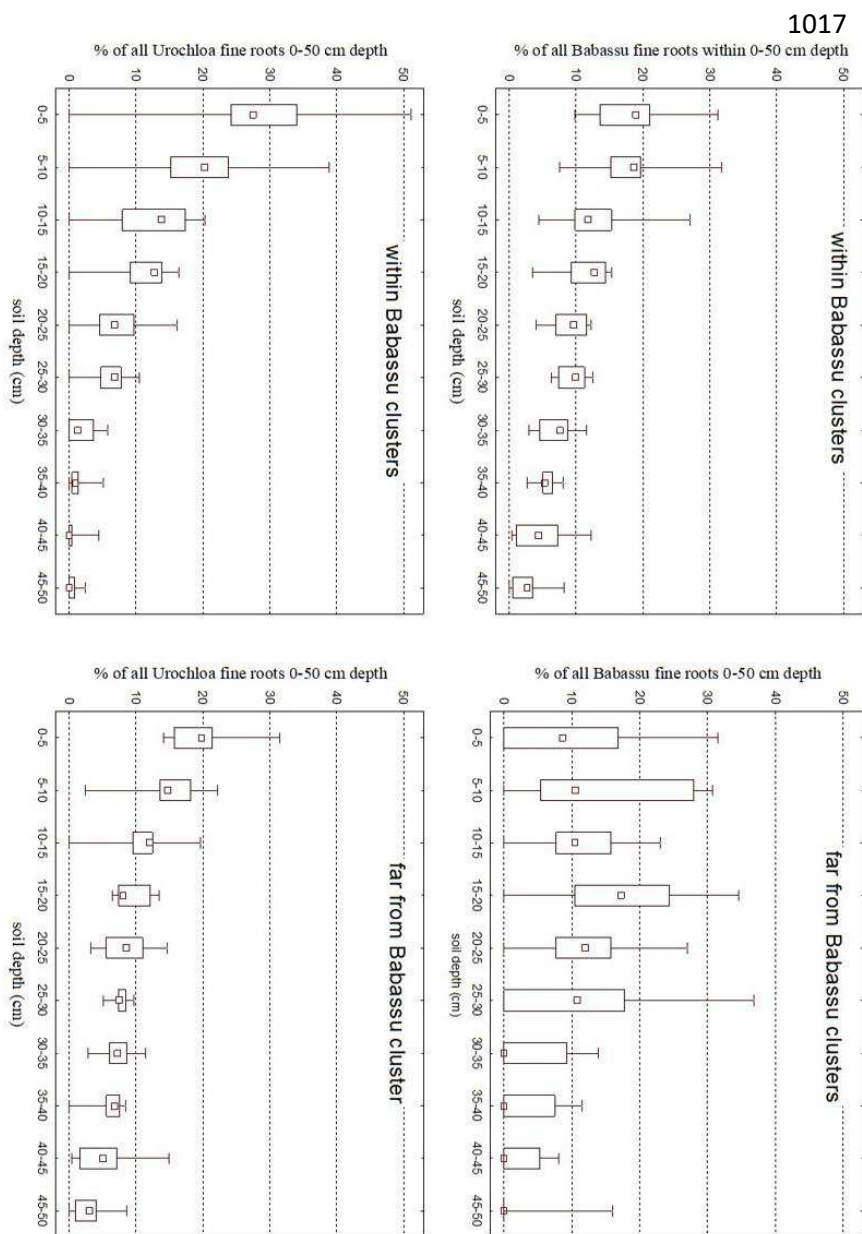
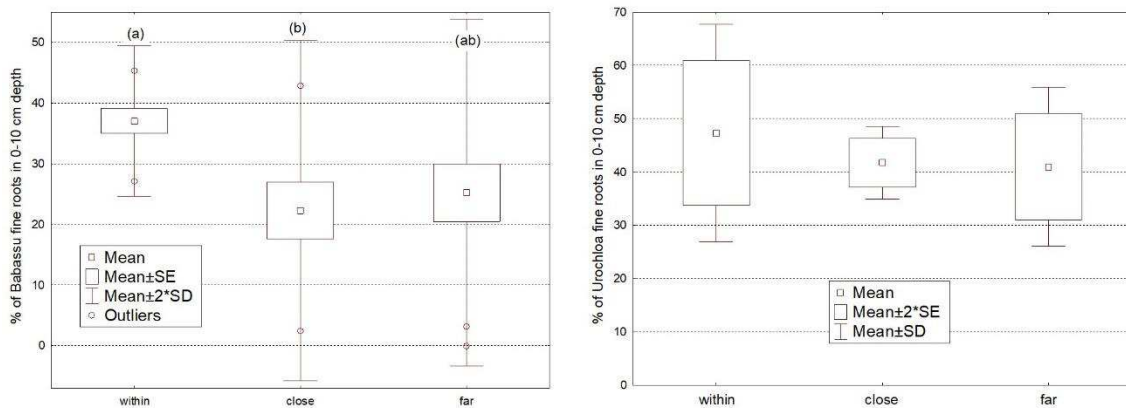


Figure 6. Relative vertical distribution of Babassu (top) and Urochloa (bottom) fine roots down the 50 cm soil profile at distances 'within' (left) and 'far' (right). Percentages of total root counts per 5 cm soil layer (medians, 25 and 75 percentiles and range).

1020 Figure 7 compares the vertical fine root distribution of Babassu and Urochloa
 1021 under monospecific vs. heterospecific competition. Whereas Babassu fine root
 1022 distribution within Babassu clusters was strongly concentrated in the top 15 cm soil, its
 1023 vertical profile changed systematically under conditions of Urochloa dominance (far from
 1024 Babassu clusters), with significantly lower fine roots in the topsoil and fine root density
 1025 peak at 15-20 cm soil depth. By contrast, Urochloa fine root vertical profile was
 1026 unchanged between sampling positions ‘within’ vs. ‘far’ from Babassu clusters.
 1027 Concomitantly, the portion of fine root counts concentrated in the first 10 cm topsoil
 1028 (relative to 0-50 cm total profile) was significantly lower for Babassu fine roots in
 1029 Urochloa-dominated ‘mid-distance’ and ‘far’ sampling positions (Figure 7 left), whereas
 1030 Urochloa fine root shallowness remained unchanged by sampling distances / relative
 1031 dominances (Figure 7, right).

1032



1033

1034 **Figure 7.** Percentage of all fine roots 0-50 cm concentrated within the top 0-10 cm soil
 1035 layer for Babassu (left) and Urochloa (right), at sampling positions within, mid-distance
 1036 and far from Babassu clusters. Means \pm SE and SD, letters refer to groupings according
 1037 to Tukey HSD post-hoc test.

1038

1039

1040

1041 **III.5. Small-scale root distribution within the root walls**

1042 Figure 8 depicts exemplary root walls of the four main root fractions at three
1043 different distances from the Babassu clusters. Next to the – expected – differences in total
1044 root counts (see previous chapters) a large small-scale variability in root count densities
1045 turns apparent. Root distribution between the 5401 5 x 5 cm grids was strongly skewed.
1046 For Urochloa fine roots, the densest 10% of all Urochloa grids (≥ 6 roots 25 cm^{-2})
1047 combined 40.3% of all fine roots, whereas the top 10-percentile of Babassu fine roots (≥ 5
1048 roots 25 cm^{-2}) only 38.4% of all fine roots. Our findings point to 'hotspots' of fine root
1049 proliferation and soil exploration of both species.
1050 We searched for but did not find any significant correlations between root counts of
1051 Babassu and Urochloa fine roots in each 5 x 5 cm grid for any soil horizon (data not
1052 shown).
1053

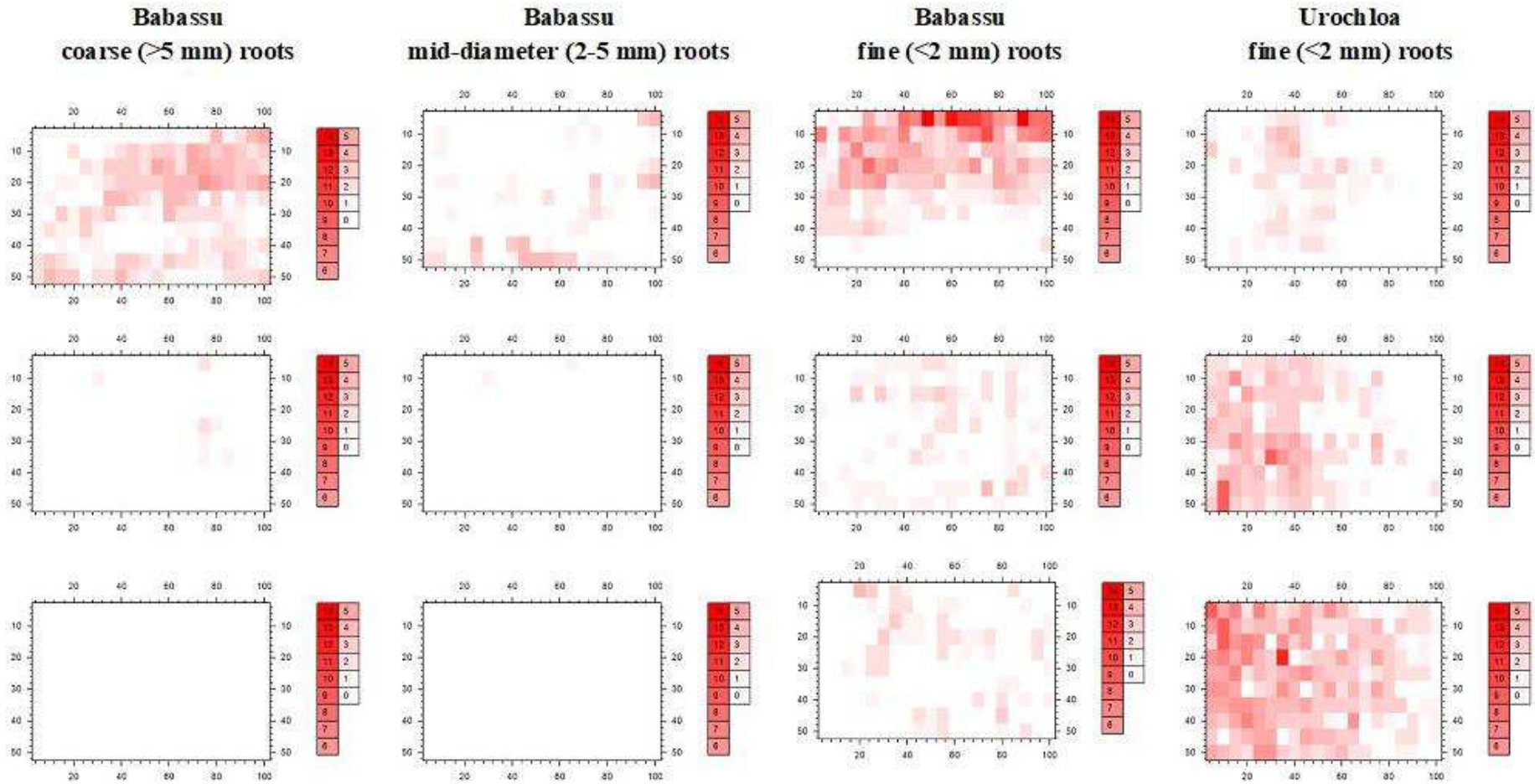


Figure 8. Exemplary root walls ‘within’ (top row), ‘mid-distance’ (center) and ‘far’ (bottom row) from Babassu palm clusters: Root counts per 5 x 5 cm grid for Babassu coarse, mid-diameter and fine roots and for Urochloa fine roots.

III.6. Relationship between bulk soil density and root counts

We found significant relationships between soil density and Babassu and Urochloa fine root counts, both determined in the same 5 x 5 x 3.3 cm grids of the root walls (see chap. II.2). The relationships were weak, but significant for both species, but with contrasting signs (positive relationship for Babassu, negative relationship for Urochloa) (Figure 9). Relationships were not systematically affected by soil depth.

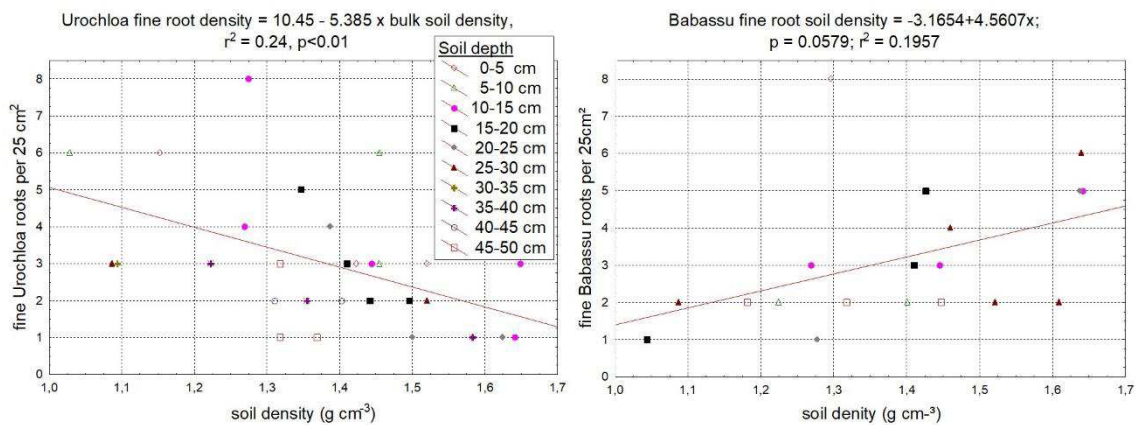


Figure 9. Relationship between soil bulk density and Urochloa (left) and Babassu (right) fine root counts within 5 x 5 x 3.3 cm grids / cubes containing more than zero fine roots.

IV. DISCUSSION

IV. 1. Babassu coarse and mid-diameter roots

Vertical profiles likewise differed between coarse and mid-diameter Babassu roots. Coarse root counts peaked at about 30 cm depth, followed by a reduction with depth. By contrast, mid-diameter Babassu roots increased in density with depth throughout the 50 cm profile. This pattern applied at all three sampling distances, but was more evident within the Babassu clusters, due to the overall greater abundance of coarse roots. Such massive coarse root concentrations within-clusters / directly below the palms in deeper soil layers confirms the results of a previous study on Babassu roots in shifting cultivation fields (SOUSA et al., 2016) pointing to a limited horizontal dispersal of

Babassu coarse roots / their concentration within the Babassu clusters / directly beneath the palms. These coarse roots are the basis for the high reporting ability of Babassu palms even after repeated slash-and-burn losses, likely due to abundant reserves of labile carbohydrates and phytates (Ashworth 2021). Their deep location was previously also reported by Sousa et al. (2016), rendering high protection of these coarse root reserves and posing serious problems for efforts of controlling juvenile (stemless) Babassu palm density.

Babassu coarse roots were strongly concentrated within Babassu clusters and strongly reduced at distances >1 m. Though mid-diameter Babassu roots likewise declined with distance, we still counted an average 43.7 mid-diameter roots / soil profile at 2.5–6 m and 21.3 mid-diameter roots / soil profile at 8-10 m distance from the Babassu clusters. The main function of mid-diameter roots is to serve as ligand for fine roots (Freshet et al., 2021), though mid-diameter roots also are important for short-term carbohydrate storage (Signori-Müller et al. 2021). Our finding points to significant Babassu root foraging at mid- to long distances, well within the *Urochloa* pastures.

IV.2. Babassu vs *Urochloa* fine root vertical distribution: vertical partitioning?

We counted overall 48.6% more *Urochloa* than Babassu fine roots. Over both species and all sampling points, 37.2% of all fine root counts within the 0-50 cm profile walls were registered in the top 0-10 cm, and 62.9% top 0-20 cm, reflecting the shallow distribution of soil organic matter and nutrients over an acid and nutrient-poor weathered subsoil typical for the humid tropics (SOUZA et al., 2018).

Compared with Babassu fine roots, *Urochloa* graminoid fine roots were more shallowly distributed: 43.3% of all 0-50 cm *Urochloa* fine roots concentrated in the top 10 cm and 67.0% in the top 20 cm, as opposed to only 28.2% and 57.7% of all Babassu

fine roots. Our study confirms previous studies reporting on a shallow root system of *Urochloa* grass (Huot et al. 2020, Santos et al. 2013). Failure of *Urochloa* fine roots to penetrate deeper down the soil may have been partially caused by limitation of rootability caused by higher bulk soil density (negative correlation found in this study, Figure 10). *Urochloa* fine root sensitivity to bulk soil density has also been reported by Pacheco et al. (2016). As Al-saturation is high already in the 10-20 cm soil layer (Table 1), Al-toxicity may be a further impeding factor. The graminoid roots of *Urochloa* spp. are known to be sensitive against Al-toxicity (Ramos et al. 2012; Furlan et al. 2020, Li et al. 2020). Shallow *Urochloa* rooting brings risks concerning losses via leaching of mobile nutrient ions (Bowman et al. 1998, Lehmann and Schroth 2003). On the other hand, shallow rooting has been shown to be advantageous for capturing intermittent dry season precipitation (De Deurwaerder et al. 2018).

By contrast, Babassu fine roots were significantly deeper rooted, with a more homogenous distribution down the first 20 cm and significant root counts even in the lowest horizons (43.7% of all fine roots in the 20-50 cm layer). Deeper rooting Babassu can be expected to explore more soil volume and resources, thus conferring this species a competitive advantage in temporarily water-stressed and nutrient-poor environments. The contrasting vertical fine root profiles of Babassu and *Urochloa* suggest that the two species occupy different belowground ecological niches and confirms the existence of (vertical) niche partitioning. The combination of both within a 'silvopastoral system' may therefore be expected to result in higher productivity than pure *Urochloa* pastures. The ecological and socioeconomic efficiency of *Urochloa* pastures with interspersed Babassu is nevertheless likely low, due to still very incomplete niche partitioning of this two-species 'silvopastoral system' and significant vertical niche overlap. Diversification of *Urochloa* pastures with further deeper-rooting components (e.g. fruit or timber trees) will

be key for the transformation of low-efficiency pure pastures into more productive silvopastoral systems throughout Amazonia.

IV.3. Niche expansion under heterospecific competition

Though conspecific competition generally outweighs heterospecific competition (Adler et al. 2018, Lak et al. 2020), heterospecific competition frequently comes at a high cost for plant fitness. Plants under heterospecific competitive stress therefore tend to seek reduction of competition via niche segregation, both horizontally via spatial clustering (Lepik et al. 2021) and vertically via altered rooting depth (Dawson et al. 2001, Rolo and Moreno 2012). The ability of species to avoid interspecific competitive stress via niche segregation constitutes a form of plasticity and is likely a key component of species survival and success in stressed ecosystems (Callaway et al. 2003).

Vertical fine root distribution is a function of both intrinsic species-specific differences, and the plastic response of plants to their environment (Weiser et al. 2016). The vertical profile of Babassu fine roots strongly adapted to interspecific competition and partially escaped direct competition with dominant *Urochloa* at sampling positions far from the Babassu clusters by increasing their fine roots further down the soil profile. By contrast, *Urochloa* relative fine root vertical distribution was unaffected by sampling positions and similarly shallow (topsoil-dominated) within Babassu-dominated Babassu clusters as in *Urochloa*-dominated sampling position far from the Babassu clusters. Thus, Babassu exhibits significant plasticity to interspecific competitive pressure, whereas *Urochloa* apparently lacks such plasticity. Babassu's high plasticity confirms results of Semchenko et al. (2017) on a higher tolerance of deeper-rooted species to interspecific competition stress, and low *Urochloa* vertical fine root plasticity confirms results of low vertical plasticity of graminoid fine roots to interspecific competition in montane

grasslands (Herben et al. 2017), but contrasts high vertical fine root plasticity in an arid savanna (Chen et al. 2020).

IV.4. Small-scale root variability

Horizontal variability within the analyzed soil profiles (1.0 m x 0.5 m) was high, and some ‘hotspots’ with high fine root densities both of *Babassu* and *Urochloa* were apparent in all root walls and is confirmed in the strongly skewed root density frequency distributions. Skewness was higher for *Babassu* than for *Urochloa* fine roots, pointing to a patchier distribution and hotspots of *Babassu* fine roots. Hodge (2009) and Wang et al. (2017) have shown the importance of rooting hotspots / plasticity as key attributes for efficient accessing and exploration of heterogeneous soil resources. This could indicate superior foraging ability of *Babassu* in heterogeneous soils with high small-scale spatial variability (Freshet et al. 2021). Interspecific interaction between fine-root systems occurs at the cm-level. Herben et al. (2020) report both between-species aggregation (common foraging of resources) and fine-root segregation. Contrary to our initial expectations, we did not find either positive or negative correlations between *Babassu* and *Urochloa* fine root counts within the 5 x 5 cm grids, possibly the net (mixed) outcome of foraging for the same small-scale distributed resources and mutual competitive exclusion / avoidance.

V. CONCLUSIONS

Fine root vertical distribution of *Urochloa* is shallower than that of *Babassu*, indicating belowground niche-partitioning. The more homogeneous and deeper profile of *Babassu* fine roots gives this palm access to more soil volume. However, considerable vertical niche overlap and wide-reaching *Babassu* mid-diameter roots both suggest that

interspecific competition between these two ruderal species is nevertheless high. Thus, niche partitioning and overyielding is likely limited in this species-poor silvopastoral system, calling for the expansion of more diversified land-use models including more deeper-rooting species, in order to increase productivity and ecological efficiency.

Interspecific competitive stress provoked niche expansion of Babassu (increased fine rooting depth) but not of Urochloa, point to a higher plasticity of the Babassu rooting system. The lacking plasticity of Urochloa fine roots adds a further aspect to the low ecological efficiency of Urochloa-based pastures. By contrast, Babassu fine root plastic response to interspecific competition is a further feature of its optimum adaptation to biotic and abiotic stress in degraded lands, providing the foundation for the outstanding ecological success and expansion of this super-dominant palm throughout Amazonia. Controlling Babassu density / dominance is a difficult task, as large coarse root stocks well protected in deeper soil horizons guarantee vigorous resprouting.

VI. ACKNOWLEDGEMENTS

We are grateful for the financial support of the Foundation of Support for Scientific Research and Development and Technological of Maranhão – FAPEMA (Nº 028/2018 - IECT Babassu) and for the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES, by granting scholarship to the first author.

VII. REFERENCES

Adler, P. B.; Sull, D.; Beard, K. H.; Choi, R. T.; Furniss, T.; Kulmatiski, A.; Meiners, J. M.; Trennick, A. T.; Veblen, K. E. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology*, v. 21, n. 9, p. 1319-1329, 2018.

- Almeida, A. W.; Shiraishi Neto, J.; Mesquita, B. A. Economia do babaçu: levantamento preliminar de dados. MIQCB. Balaios Typografia; São Luís – MA, 2 ed; p. 294 2001.
- Almeida, G.; Ramos, M. A.; Araújo, E. L.; Baldauf, C.; Albuquerque, U. P. Human perceptions of landscape change: The case of a monodominant forest of *Attalea speciosa* Mart ex. Spreng (Northeast Brazil). *Ambio*, v. 45, n. 4, p. 458-467, 2016.
- Anderson, A. B.; May, P. H.; Balick, M. The subsidy from nature: Palm forests, peasantry, and development on an Amazon frontier. Columbia University Press, 1991.
- Andrea, R.; Guitar, J.; O'Dwyer, J. P.; Figueroa, H.; Wright, S. J.; Condit, R.; Ostling, A. Counting niches: Abundance-by-trait patterns reveal niche partitioning in a neotropical forest. *Ecology*, v. 101, n. 6, p. e03019, 2020.
- Ashworth, A. J., Adams, T., Kharel, T., Phillip, D., Owens, P., Sauer, T. Root decomposition in silvopastures is influenced by grazing, fertility, and grass species. *Agrosystems, Geosciences & Environment*, v. 4, n. 3, p. e20190, 2021.
- Bartolomeus, I. E.; Godoy, O. Biotic controls of plant coexistence. *Journal of Ecology*, v.106, p.1767–1772, 2018.
- Böhm. W. Methods of studying root systems. *Ecological Studies Vol 33*, Springer-Verlag, Heidelberg, 1979.
- Bowman, D.C; Bowman, D.C.; Devitt, D.A.; Engelke, M.C; Rufty Jr, T.W. Root architecture affects nitrate leaching from bentgrass turf. *Crop Science*, v. 38, n. 6, p. 1633-1639, 1998.
- Callaway, R.M.; Pennings, S.C.; Richards, C.L. Phenotypic plasticity and interactions among plants. *Ecology*, v. 84, n. 5, p. 1115-1128, 2003.

- Cambardella, C. A.; Elliott, E.T. Carbon and nitrogen distributions in aggregates from cultivated and native grassland soils. *Soil Science Society of America Journal* v. 57, p. 1071–1076, 1992.
- Castellanos, J.; Jaramillo, V. J.; Sanford J.R.; Kauffman, J. B. Slash-and-burn effects on fine root biomass and productivity in a tropical dry forest ecosystem in Mexico. *Forest Ecology and Management*, v. 148, n. 1-3, p. 41-50, 2001.
- Chen, B.J.W.; Xu, C.; Liu, M.-S.; Huang, Z.Y.X.; Jian, M.J.S.; Anten, T.P.R. Neighbourhood-dependent root distributions and the consequences on root separation in arid ecosystems. *Journal of Ecology* v. 108, n. 4, p. 1635-1648.
- Chesson, P. General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology*, v. 58, n. 3, p. 211-237, 2000.
- Claessen, Marie Elisabeth Christine. Manual de métodos de análise de solo. Embrapa Solos-Documentos (INFOTECA-E), 1997.
- Costa, N.D.L.; Paulino, V.T.; Da Costa, R.S.C.; Pereira, R.D.A.; Townsend, C.R.; Magalhães, J.A. Effect of arbuscular mycorrhiza on growth and mineral nutrition of *Brachiaria brizantha* cv. Marandú. *Ciência Animal Brasileira*, v. 13, n. 4, p. 406-411, 2012.
- Crawford, K.M.; Bauer, J.T.; Comita, L.S.; Eppinga, M.B.; Johnson, D.J.; Mangan, S.A.; Bever, J.D. When and where plant-soil feedback may promote plant coexistence: a meta-analysis. *Ecology Letters*, v. 22, n. 8, p. 1274-1284, 2019.
- Dawson, L.A.; Duff, E.I.; Campbell, C.D.; Hirst, D.J. Depth distribution of cherry (*Prunus avium* L.) tree roots as influenced by grass root competition. *Plant and Soil*, v. 231, n. 1, p. 11-19, 2001.
- De Deurwaerder, H.; Hervé-Fernández, P.; Stahl, C.; Burban, B.; Petronelli, P.; Hoffman, B.; Bonal, D.; Boeckx, P.; Verbeeck, H. Liana and tree below-ground water competition—

- evidence for water resource partitioning during the dry season. *Tree Physiology* v.38, n. 7, p. 1071-1083, 2018.
- Dybinski, R.; Tilman, D. Competition and Coexistence in Plant Communities. In:II.5 The Princeton guide to ecology. Princeton University Press, 2012.
- Freshet, G.T.; Pagès, L.; Iversen, C.M.; Comas, L.H; Rewald, B.; Roumet, C.; McCormack, M.L. A starting guide to root ecology: strengthening ecological concepts and standardizing root classification, sampling, processing and trait measurements. *New Phytologist*, v. 232, n. 3, p. 973-1122, 2021.
- Furlan, F.; Borgo, L.; Rabêlo, F.H.S.; Rossi, M.L.; Linhares, F.S.; Martinelli, A.P.; Lavres, J. Aluminum-induced toxicity in *Urochloa brizantha* genotypes: A first glance into root Al-apoplastic and-symplastic compartmentation, Al-translocation and antioxidant performance. *Chemosphere*, v. 243, p. 125362, 2020.
- Gehring, C.; Leite, M.F.A.; Moraes, F.H.R. Allelopathic effects of the babassu palm on crops, pasture-grasses and key soil fungi. In: Resilience of agricultural systems against crises (Book of abstracts), p.97, Tropentag, Göttingen, 2012.
- Gehring, C.; Zelarayán, M. C.; Luz, R.L.; Almeida, R.B.; Boddey, R.M.; Leite, M.F.A. Babassu palm (*Attalea speciosa* Mart.) super-dominance shapes its surroundings via multiple biotic, soil chemical, and physical interactions and accumulates soil carbon: a case study in eastern Amazonia. *Plant and Soil*, v. 454, n. 1, p. 447-460, 2020.
- Gichangi, E. M.; Njarui, D. M.; Ghimre, S. R.; Gatheru, M.; Magirol, K. W. Effects of cultivated *Brachiaria* grasses on soil aggregation and stability in the semi-arid tropics of Kenya. *Tropical and Subtropical Agroecosystems*, v. 19, n. 2, p. 205-217, 2016.
- Groppo, J.D.; Lins, S.R.M.; Camargo, P.B.; Assad, E.D.; Pinto, H.S.; Martins, S.C.; Salgado, P.R.; Evangelista, B.; Vasconcellos, E.; Sano, EE; Pavão, E .; Luna, R.; Martinelli, LA. Mudanças no carbono, nitrogênio e fósforo do solo devido a

- mudanças no uso da terra no Brasil. *Biogeosciences Discussions*, v. 12, n.3, p. 2533–2571.
- Herben, T.; Vozábová, T.; Hadincová, V.; Krahulec, F.; Mayerová, H.; Pecháčková, S.; Skálová, H.; Krak, K. Vertical root distribution of individual species in a mountain grassland community: Does it respond to neighbours? *Journal of Ecology*, v. 106, n. 3, p. 1083-1095, 2017.
- Hernem, T.; Balsankova, T.; Hadincová, V.; Krahulek, F.; Perchasková, S.; Skalová, H.; Krak, K. Fine-scale root community structure in the field: Species aggregations change with root density. *Journal of Ecology*, v. 108, n. 4, pp. 1738-1749, 2020.
- Hodge, A. Root decisions. *Plant, Cell & Environment*, v. 32, n. 6, p. 628-640, 2009.
- Holdo, R.M. Revisiting the two-layer hypothesis: coexistence of alternative functional rooting strategies in savannas. *PLoS One*, v. 8, n. 8, p. e69625, 2013.
- Huot, C.; Zhou, Y.; Philip, J. N.; Denton, M. D. Root depth development in tropical perennial forage grasses is related to root angle, root diameter and leaf area. *Plant and Soil*, v. 456, n. 1, p. 145-158, 2020.
- InMet (Brazilian National Meteorological Institute) Rainfall data of the meteorological station of Chapadinha (MA), 2021. Available at <https://bdmep.inmet.gov.br/>
- Isaac, M.; Borden, K. A. Nutrient acquisition strategies in agroforestry systems. *Plant and Soil*, v. 444, n. 1, p. 1-19, 2019.
- Jakovac, C.C.; Peña-Claros, M.; Mesquita, R.C.; Bongers, F.; Kuyper, T.W. Swiddens under transition: consequences of agricultural intensification in the Amazon. *Agriculture, Ecosystems and Environment*, v. 218, p. 116-125, 2016.
- Kato-Noguchi, H., Kobayashi, A., Ohno, O., Kimura, F., Fuji, Y., Suenaga, K. Substâncias fitotóxicas com atividade alelopática podem ser centrais para o forte

- potencial invasivo de *Brachiaria brizantha*. *Journal of Plant Physiology*, v. 171, n. 7, p. 525-530, 2014.
- Lak, Z.A.; Sandén, H.; Mayer, M.; Godbold, D.L.; Rewald, B. Plasticity of root traits under competition for a nutrient-rich patch depends on tree species and possesses a large congruency between intra-and interspecific situations. *Forests*, v. 11, n. 5, p. 528, 2020.
- Leal, L.P.; Stürmer, S.L.; Siqueira, J.O. Occurrence and diversity of arbuscular micorrhizal fungi in trap cultures from soils under different land use systems in the Amazon, Brazil. *Brazilian Journal of Microbiology* v. 40, p.111-121, 2009.
- Lehmann, J.; Schroth, G. Nutrient leaching. *Trees, Crops and Soil Fertility*, p. 151-166, 2003.
- Lepik, A.; Abakumova, M.; Davidson, J.; Zobel, K.; Semchenko, M. Spatial mapping of root systems reveals diverse strategies of soil exploration and resource contest in grassland plants. *Journal of Ecology*, v. 109, n. 2, p. 652-663, 2021.
- Li, Z.; Wehr, J.B.; Wang, P.; Menzies, N.W.; Kopittke, P.M. Understanding the delayed expression of Al resistance in signal grass (*Urochloa decumbens*). *Annals of Botany*, v. 125, n. 5, p. 841-850, 2020.
- Lima, R.L.F. Micorrizas arbusculares e absorção de fósforo em função da capacidade de fixação de fósforo do solo e da competição com a microbiota. *Revista Brasileira de Geografia Física*, v. 13, n. 03, p. 1062-1079, 2020.
- Louw-Gaume, A.E.; Schweizer, N.; Rao, I.M.; Gaume, A.J.; Frossard, E. Temporal differences in plant growth and root exudation of two *Brachiaria* grasses in response to low phosphorus supply. *Tropical Grasslands* v. 5, n. 3, p. 103-116, 2017.
- Low, S.G. Signal grass (*Brachiaria decumbens*) toxicity in grazing ruminants. *Agriculture*, v. 5, n. 4, p. 971-990, 2015.

- Luz, R. L.; Leite, M.F.A.; Zelarayán, M. C.; Boddey, R.M.; Gehring, C. Litter decomposition and nutrient release dynamics of leaves and roots of the Babassu palm in eastern Amazonia. *Acta Amazonica*, v. 50, p. 213-222, 2020.
- Martins, D.; Martins, C.C.; Costa, N.V. Allelopathic potential of solutions of soils cultivated with *Brachiaria brizantha*: effects on some pasture grass and weeds seeds. *Planta Daninha*, v. 24, n. 1, p. 61-70, 2006.
- May, P.H. ; Anderson, A.B. ; Frazão, J.M.F.; Balick, M.J. Babassu palm in the agroforestry systems in Brazil's Mid-North region. *Agroforestry Systems*, v.3, n.3, p. 275-295, 1985.
- McCormack, M.L.; Dickie, I.A.; Eissenstat, D.M.; Fahey, T.J.; Fernandez, C.W.; Guo, D.; Helmisaari, H.S.; Hobbie, E.A.; Iversen, C.M.; Jackson, R.B.; Leppälmy-Kujansuu, J.; Norby, R.J.; Philips, R.P.; Pregitzer, K.S.; Prichard, S.G.; Rewald, B.; Zadworny, M. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist*, v. 207, n. 3, p. 505-518, 2015.
- Mehlich, A. Determination of P, Ca, Mg, K, Na, and NH₄. North Carolina Soil Test Division (Mimeo 1953), p. 23-89, 1953.
- Mitja, D.; Ferraz, I. D. Establishment of babassu in pasture in Para, Brazil. *Palms*, v. 45, n. 3, p. 138-147, 2001.
- Nitta, Y.; Goto, Y.; Kakuda, K.I.; Ehara, H.; Ando, H.; Yoshida, T.; Yamamoto, Y.; Matsuda, T.; Jong, F.S.; Hassan, A.H. Morphological and anatomical observations of adventitious and lateral roots of sago palms. *Plant Production Science*, v. 5, n. 2, p. 139-145, 2002.
- Nobre, C.P.; Costa, M.G.; Goto, B.T.; Gehring, C. Arbuscular mycorrhizal fungi associated with the Babassu palm (*Attalea speciosa*) in the eastern periphery of Amazonia, Brazil. *Acta Amazonica*, v. 48, p. 321-329, 2018.

- Pacheco, L.P.; São Miguel, A.S.D.; de Souza, E.D.; de Carvalho, I.C.; Petter, F.A.; da Silva, R.G.; da Silva, C.M.R. Shoot and root development of brachiaria grass (*Urochloa ruziziensis*) under different levels of soil density. *Australian Journal of Crop Science* v. 10, n. 10, p. 1424-1428, 2016.
- Porro, R. A economia invisível do babaçu e sua importância para meios de vida em comunidades agroextrativistas. *Boletim do Museu Paraense Emílio Goeldi*, p. 169-188, 2019.
- Raij, B.V.; Andrade, J.C.; Cantarella, H.; Quaggio, J.A. Análise química para avaliação da fertilidade de solos tropicais. Campinas, Instituto Agronômico, 285p. 2001.
- Ramos, F.T.; França, M. G.; Alvim, M. N.; Rosiello, R.O.; Zonta, E. Aluminum tolerance measured by root growth and mucilage protection in *Urochloa brizantha* and *Urochloa decumbens*. *Journal of Plant Interactions*, v. 7, n. 3, p. 225-229, 2012.
- Rodrigues, R. C.; Lima, A. J. T.; De Araújo, R. A.; De Jesus, A. P. R.; Costa, C. D. S.; Santos, F. N. S.; Costa, F. L.; Júnior, J. A. A. C.; Shigaki, J. F; Azevêdo, D. M. M. Agronomic, morphogenic and structural characteristics of Marandu grass in silvopastoral systems composed of babassu palm and grass monoculture. *Semina: Ciências Agrárias*, v. 37, n. 4, p. 2331-2341, 2016.
- Rolo, V.; Moreno, G. Interspecific competition induces asymmetrical rooting profile adjustments in shrub-encroached open oak woodlands. *Trees* v. 26, p. 997-1006, 2012.
- Sampaio, S.M.N.; Kingo, A.; Laques, A.E.; de Souza Miranda, I.; Mitja, D. Formation of Babassu in degraded areas by human action in southeast Para, Brazil: its importance for recovery of legal reserve areas. *Proceedings of The International Society for Ecological Economics*, ISEE Conference 16-19 June, 2012, Rio de Janeiro, Brazil.

- Sanford, R. L.; Cuevas, E. Crescimento da raiz e interações da rizosfera em florestas tropicais (Root growth and rhizosphere interactions in tropical forests). In: *Ecofisiologia de plantas florestais tropicais*. Springer, Boston, MA, p. 268-300, 1996.
- Santos, H. G.; Jacomime, P. K. T.; Dos Anjos, L. H. C.; De Oliveira, V. A.; Lumbreras, J. F.; Coelho, M. R.; Cunha, T. J. F. Sistema brasileiro de classificação de solos (Brazilian Soil Taxonomy). Brasília, DF: Embrapa, 2018.
- Santos, P. M.; Cruz, P. G. D.; Araujo, L. C. D.; Pezzopane, J. R. M.; Valle, C. B. D.; Pezzopane, C. D. G. Response mechanisms of *Brachiaria brizantha* cultivars to water deficit stress. *Revista Brasileira de Zootecnia*, v. 42, n. 11, p. 767-773, 2013.
- Santos-Filho, F.S.; Júnior, E,B,A.; Soares, C,J,R. Cocais: zona ecotonal natural ou artificial?. *Revista Equador*, v. 2, n. 1, p. 02-13, 2013.
- Schofield, E.J.; Rowntree, J.K.; Paterson, E.; Brooker, R.W. Temporal dynamism of resource capture: a missing factor in ecology? *Trends in Ecology & Evolution*, v. 33, n. 4, p. 277-286, 2018.
- Schroth, G. A review of belowground interactions in agroforestry, focussing on mechanisms and management options. *Agroforestry systems*, v. 43, n. 1, p. 5-34, 1998.
- Semchenko, M.; Lepik, A.; Abakumova, M.; Zobel, K. Different sets of belowground traits predict the ability of plant species to suppress and tolerate their competitors. *Plant and Soil*, v. 424, p. 157-169, 2018.
- Signori-Müller, C.; Oliveira, R. S.; Valentim Tavares, J.; Carvalho Diniz, F.; Gilpin, M.; Barros, F.; Zevallos, M.J.M.; Yupaycana, C.S.A.; Brum, M.; Baker, T.R.; Cosio, E.G.; Mahli, Y.; Mendoza, A.B.; Oliver, L.; Philips, O.L.; Rowland, L.; Salinas, N.; Vásques, R.; Mencuccini, M.D. Variation of non-structural carbohydrates across the fast–slow continuum in Amazon Forest canopy trees. *Functional Ecology*, v. 36, n. 2, p. 341-355, 2022.

- Silva Neto, S.P.; Santos, A.C.; Lima Leite, R.L.; Dim, V.P.; Neves Neto, D.N.; Silva, J.E.C. Variação espacial do teor de matéria orgânica do solo e produção de gramínea em pastagens de capim-marandu. *Bioscience Journal*, v. 28, n. 1, 2012.
- Sousa, J.T.R; Moraes, F.H.R; Gehring, C. Root biomass in a shifting cultivation system in the eastern periphery of Amazonia, and contribution of the Babassu palm. *Agroforestry Systems*, v. 90, n. 2, p. 351-360, 2016.
- Souza, E.S.D.; Fernandes, A.R.; De Souza Braz, A.M.; Oliveira, F.J.D., Alleoni, L.R.F.; Campos, M.C.C. Physical, chemical, and mineralogical attributes of a representative group of soils from the eastern Amazon region in Brazil. *Soil*, v. 4, n. 3, p. 195-212, 2018.
- Sumarsih, E.; Nugroho, B.; Widyastuti, R. Study of root exudate organic acids and microbial population in the rhizosphere of oil palm seedlings. *Journal of Tropical Soils*, v. 22, n. 1, p. 29-36, 2017.
- Teixeira, P.C.; Donagemma, G.K.; Fontana, A.; Teixeira, W.G. Manual de métodos de análise de solo. Brasília: Embrapa, p. 573, 2017.
- Teutscherova, N.; Vazques, E.; Arevalo, A.; Pulleman, M.; Rao, I.; Arango, J. Differences in arbuscular mycorrhizal colonization and P acquisition between genotypes of the tropical *Brachiaria* grasses: is there a relation with BNI activity? *Biology and Fertility of Soils*, v. 55, n. 4, p. 325-337, 2019.
- Vendramini, T. Um novo olhar para a pecuária brasileira. *AgroANALYSIS*, v. 39, n. 5, p. 47, 2019.
- Villa, P. M.; Martins, S. V.; Neto, S. N. O.; Rofdrigues, A. C.; Martorano, L. G.; Monsanto, L. D.; Cancio, N. M.; Gastauer, M. Intensification of shifting cultivation reduces forest resilience in the northern Amazon. *Forest Ecology and Management*, v. 430, p. 312-320, 2018.

- Walkley, A.; Black, I.A. An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. *Soil Science*, v. 37, n. 1, p. 29-38, Jan. 1934.
- Wang, P.; Shu, M.; Mou, P.; Weiner, J. Fine root responses to temporal nutrient heterogeneity and competition in seedlings of two tree species with different rooting strategies. *Ecology and Evolution*, v. 8, n. 6, p. 3367-3375, 2018.
- Weiser, M.; Koubek, T.; Herben, T. Root foraging performance and life-history traits. *Frontiers in Plant Science* v. 7, p. 779, 2016.
- Wood, S.N. Thin plate regression splines. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, v. 65, n. 1, p. 95-114, 2003.
- Wood, S.N. Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association*, v. 99, n. 467, p. 673-686, 2004.
- Wood, S.N. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, v. 73, n. 1, p. 3-36, 2011.
- Wood, S.N.; Pya, N.; Säfken, B. Smoothing parameter and model selection for general smooth models. *Journal of the American Statistical Association*, v. 111, n. 516, p. 1548-1563, 2016.
- Zangaro, W.; Lescano, L.E.; Matsuura, E.M.; Rondina, A.B.L.; Nogueira, M.A. Differences between root traits of early- and late-successional trees influence below-ground competition and seedling establishment. *Journal of Tropical Ecology*, v. 32, n. 4, p. 300-313, 2016.
- Zuur A.F.; Ieno, E.N.; Walker, N.; Saveliev, A.A.; Smith, G.M. *Mixed effects models and extensions in ecology with R*. New York: Springer, 2009.
- Zuur, A. F. *A beginner's guide to generalized additive models with R*. Newburgh, NY, USA: Highland Statistics Limited, 2012.

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Assembly. Assemble the parts of the main manuscript in this order: title page, abstract, key words, text, acknowledgments, literature cited, tables, figure legends. Figures can be provided as the last pages of the main manuscript or as separate files. Appendices and Supplements should follow in a separate file or files. Number all pages of the main manuscript file consecutively.

All papers must be in English. Use American spellings (e.g., behavior, not behaviour). The CBE Style Manual, Fifth Edition, is recommended for details of style.

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All title pages should contain the following elements:

- **Running Head.** A running head of no longer than 40 letters and spaces should be provided at the top of the title page.

- **Title.** Titles should be concise, informative, tell what the paper is about and what it found. It should contain key words necessary for digital search and retrieval methods. Avoid vague declarations (e.g., "effects of ..."); strive for information content (e.g., "fungi kill tardigrades"). The maximum length is 120 characters, including spaces. Do not include the authority for taxonomic names in the title or in the abstract. Titles may not include numerical series designations. The first letter of the first word in the title is capitalized. All other words, except for proper nouns, are lowercase.
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Abstract

The abstract should explain to the general reader why the research was done and why the results should be viewed as important. It should provide a brief summary of the research, including the purpose, methods, results, and major conclusions. Do not include literature citations in the Abstract. Avoid long lists of common methods or discursive explanations of what you set out to accomplish.

The primary purpose of an abstract is to allow readers to determine quickly and easily the content and results of a paper. Abstracts should not exceed 200 words for Reports and Statistical Reports, and 350 words for Articles and for Data Papers.

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Following the Abstract, list between 6–12 key words/phrases. Each key word should be useful as an entry point for a literature search.

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Results generally should be stated concisely and without interpretation, though in complex studies modest interpretation of individual parts can provide context helpful for understanding subsequent parts. The

Discussion should explain the significance of the results. Distinguish factual results from speculation and interpretation. Avoid excessive review.

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