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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

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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

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DEDICATÓRIA

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

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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 raizes 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´dominancia do Babaçú’ (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) paras 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 Babaçú 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 monoespecificas 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 caracteristica provavelmente é um componentes-chave para o notável sucesso ecológico do Babaçu em pastagens degradadas na Amazônia oriental.

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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.

CAPITULO I

INTRODUÇÃO GERAL E REFERÊNCIAL TEÓRICO

1. INTRODUÇÃO

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

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

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

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

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

Segundo Jose et al., (2019), sistemas silvipastoris são viáveis através de mecanismos ecológicos de diversificação funcional e estrutural de nichos interespecíficos. São agroecossistemas que podem ser projetados para alcançar maior sustentabilidade e produtividade, com a otimização dos recursos (espaciais, temporários e físicos) através da maximização das interações positivas (facilitação) e minimizando a ações negativas (competição), e assim buscando a coexistência interespecífica, evitando exclusão competitiva postulada pela lei de Gause e (GLIESSMAN, 2001; CHESSON, 2000).

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

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

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

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

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

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

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

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

2. REVISÃO BIBLIOGRÁFICA

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

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

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

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

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

Dessa forma, compreender os diversos mecanismos de competição e coexistência interespecíficos e os efeitos sobre a estrutura das comunidades é um desafio científico comptemporâneo (ADLER et al., 2018). O estudo desses mecanismos é pautado, como forma de ajudar a resolução de problemas contemporâneos de gestão, incluindo sistemas produtivos mais eficientes (THAKUR et al., 2021), manejo de espécies invasoras e previsão das consequências das mudanças climáticas nos ecossistemas (WOLKOVICH; CLELAND, 2014; VALLADARES et al., 2015).

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

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

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

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

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

Somado a isso, as plantas em sistemas naturais ou agroecossistemas também experimentam interações complexas multitróficas e simultâneas no seu habitat, como interações simbióticas, mutualísticas, de doenças e herbívora, que atuam na distribuição das espécies e influenciam na coexistência entre os diferentes nichos (BARTOMEUS; GODOY, 2018; LI et al., 2020). Exemplos são associações endofíticas/rizosféricas com bactérias e fungos para ampliação da capacidade de absorção de nutrientes (VERESOGLOU et al., 2018), mineralização do carbono (WANG et al., 2016) e a diminuição de biodiversidade vegetal ao seu redor, por ação alelopática (MARTINS et al., 2006)

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

2.2. Sistemas Silvipastoris

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

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

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

A integração de gramíneas e árvores promove modificações favoráveis nas características edáficas quando comparado com sistemas tradicionais monoespecíficos, os principais benefícios derivam da maior deposição de MOS; estruturação do solo, contenção de erosão e translocação de nutrientes e água das camadas inferiores para camadas mais próximas à superfície, favorecendo o desenvolvimento das forrageiras (ALVES et al., 2017).

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

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

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

ARAÚJO et al., (2017) em trabalho sobre a dinâmica do pastejo bovino na amazônica maranhense, concluiu que em sistemas silvipastoris compostos por palmeiras de babaçu (*A. speciosa*) e capim Braquiária (*U. brizantha cv. Marandu*) proporciona um ambiente estrutural mais favorável aos animais pastejarem, em uma distribuição mais homogênea dos animais, em comparação com monocultivo de capim Braquiária, diminuindo a incidência de áreas com sobre pastejo e beneficiando a restituição da fertilidade do solo, pela melhor distribuição de fezes nas áreas.

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

2.3. Palmeira Babaçu

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

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

O sucesso ecológico desta planta decorre da ligação de três fatores: (i) o extrativismo faz uma seleção das palmeiras mais produtivas no desmatamento das florestas; (ii) adaptações reprodutivas ao fogo: a ação termina funcionando como mecanismo de quebra de dormência das sementes e geotropismo negativo do meristema 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).

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

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

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

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

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

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

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

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

Seu sucesso advém das suas características de boa adaptabilidade às condições edafoclimáticas da região tropical, uma vigorosa produção de fito massa em solos de baixa fertilidade, e não ser atrativa as principais doenças e pragas das culturas forrageiras, por exemplo, da cigarrinha das pastagens (*Deois flavopicta).* E por sua boa palatabilidade 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 dominante de sistema radicular denso, mais amplamente distribuído nas camadas superficiais do solo (0-20), exercendo papel estruturante e de estabilização de agregados no solo, pela elevada deposição de MOS, pela constante renovação das raízes finas, assim como emissão de exsudados ricos em carbono, que ativam as relações simbióticas com microrganismos (HANISCH et al., 2017; NUNES et al., 1984).

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

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

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CAPITULO II

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

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

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Abstract

Much of deforested Amazonia is dominated by pastures planted with exotic *Urochloa* (syn *Brachiaria)* grass, containing interspersed the ruderal Babassu palm (*Attalea speciosa*). This two-species system offers the opportunity to investigate how two very competitive species interact. Research was conducted in the eastern periphery of Amazonia in three monospecific Urochloa pastures (*U.brizantha* cv. ‘marandu’) containing dispersed Babassu palm clusters. We mapped 0-50 cm root profiles of Babassu and Urochloa at three distances representing contrasting relative dominance: 'within clusters' (0.4-0.6 m from adult palm, Babassu-dominated); 'mid-distance' (at 2.5-6.0 m) and 'far' (at >8.0-10.0 m, Urochloa-dominated). Babassu coarse and mid-diameter roots concentrated within clusters at 20 – 50 cm depth, well protected against disturbance, but Babassu mid-diameter roots did extend up to 10 m from clusters, indicating active foraging at mid and long distances. Fine roots predominated root counts throughout all soil profiles, with 74.6% concentrated in the 0-20 cm topsoil. Fine-scale variability of fine roots was high, with high density hotspots of both species in the topsoil. Babassu fine root share was 48.1% within clusters, as opposed to 84.1% Urochloa fine root share far from clusters, and the metric distance from Babassu clusters was a significant predictor of root abundance in all diameter classes. Vertical fine root profiles of Babassu and Urochloa differed systematically, with 41.9% of all Urochloa fine roots concentrated within the first 0-10 cm, as opposed to deeper rooting Babassu (69.8% of all fine roots below 10 cm). Urochloa vertical root profile was unaffected by the degree of interspecific competitive confrontation and possibly limited by physical or chemical soil rootability constraints. By contrast, Babassu fine roots escaped competition from Urochloa by rooting significantly deeper in grass-dominated sampling points. Limitation of Urochloa fine roots to the topsoil reduces the ecological efficiency of pure Urochloa pastures. By contrast, deeper fine rooting and high plasticity under interspecific competitive confrontation are likely key components for Babassu´s outstanding ecological success in degraded pastures throughout Amazonia. In practical terms, our findings call for an optimized Babassu palm management and for the diversification of Amazonian pastures in order to increase their ecological efficiency and productivity.

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

I. Introduction

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

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

The ruderal Babassu palm is omnipresent throughout the landscapes of deforested Amazonia, on an estimated 200.000 km^2 in Brazil alone (May et al. 1985). Although Babassu occurs in low abundance in mature rainforests, its dominance increases dramatically after repeated burns and reduced fallow periods both in the extensive pastures and in shifting cultivation fields and fallows, in some cases forming near monospecific stands (Anderson et al. 1991; Santos Filho et al. 2013). There are many reasons for the outstanding ecological success of the Babassu palm in such degraded lands, next to the (initial) selective sparing of productive adult palms for palm oil production (see below) its adaptation to frequent fires (fire-induced germination, well protected belowground meristem of stemless juvenile, vigorous resprouting capacity following slash&burn (Mitia and Ferraz 2001), as well as its adaptation to abiotically stressed degraded lands (Sampaio et al. 2012). Gehring et al. (2020) show the Babassu palm to simplify vegetation:litter:topsoil interactions in eastern Amazonian secondary regrowth, suggesting positive plant:soil feedback as a further pathway for the dominance-increase of this palm.

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

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

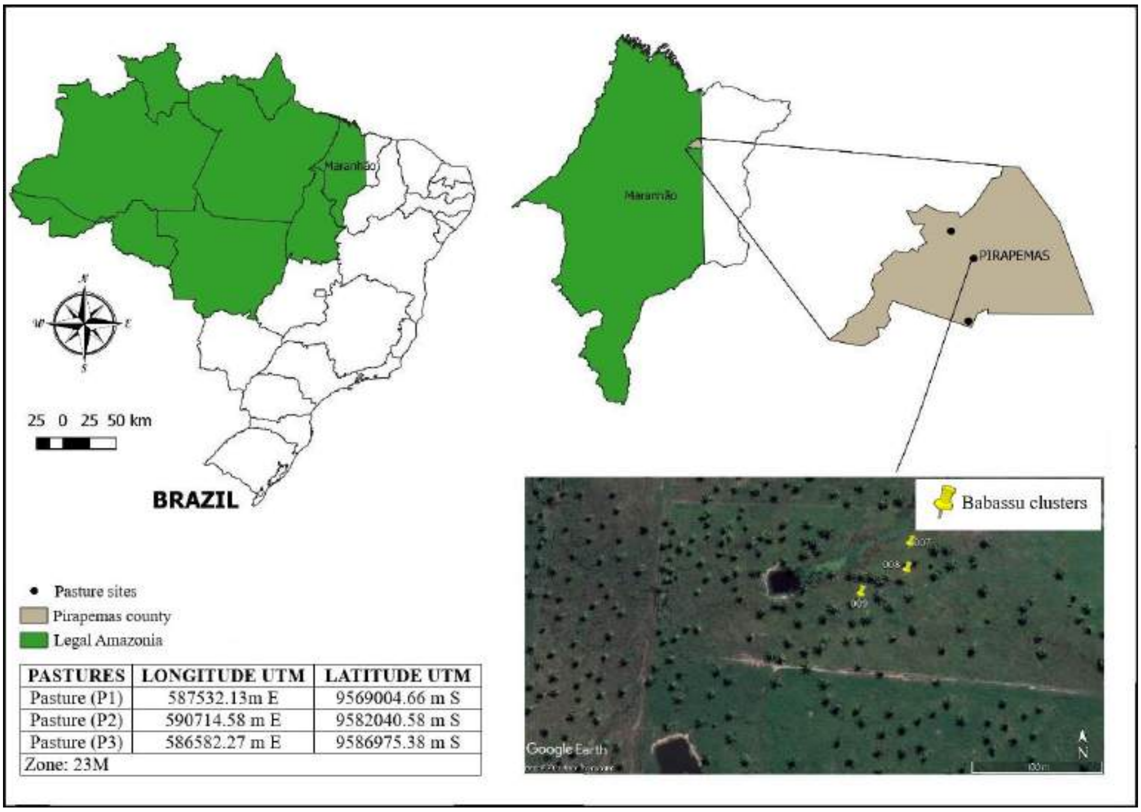
Babassu and Urochloa have in common an accumulation of soil organic matter in their surroundings, reported for Babassu by Gehring et al. (2020), and in Urochloa pastures by (Silva Neto et al. 2012, Santos et al. 2013). The pathways for such SOM-buildup, however, likely differ between the two, with high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

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

II. METHODS AND METHODS

II.1. Study region and experimental layout

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



PASTURES	LONGITUDE UTM	LATITUDE UTM
Pasture (P1)	587532.13m E	9569004.66 m S
Pasture (P2)	590714.58 m E	9582040.58 m S
Pasture (P3)	586582.27 m E	9586975.38 m S
Zone: 23M		

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

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

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

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

total N (%)	0.06 (±0.01)	0.05 (±0.01)	Kjeldåhl digestion1)
available P (mg kg^{-1})	4.31 (±0.38)	3.02 (±0.42)	Mehlich 1 extraction4)
K mg kg^{-1}	23.77 (±4.03)	15.18 (±2.75)	Mehlich 1 extraction4)
Ca (cmolc dm^{-3})	0.98 (±0.08)	0.55 (±0.04)	1M KCl-extraction5)
Mg (cmolc dm^{-3})	0.77 (±0.08)	0.41 (±0.06)	1M KCl-extraction5)
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-exctractable Al in relation to exchangeable bases+Al1)

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

We selected three pastures located at 3 - 9 km distance from another (points P1, P2 and P3 in Figure 1). All three sites had been planted between 5 and 8 years ago with Urochloa palisade grass (*Urochloa brizantha* cv. 'marandu') containing clusters of an adult Babassu palm and surrounding juvenile (stemless) palms. We estimate average adult Babassu palm density of the three sites at ~25 ha^{-1}. All three pasture sites had been under extensive grazing (2-3 cattle ha^{-1}), but in a resting phase (no grazing) for more than four months prior to sampling, thus avoiding short-term artefacts caused by grazing. None of the pastures had previously received any application of fertilizers or lime, representing the prevailing practice throughout Amazonian pastures. In each site we selected three such Babassu-islands clusters with >30 m distance between another, and for each cluster we selected three contrasting sampling positions (at 0.4 – 0.6 m 'within-cluster': high Babassu dominance – 'mid-distance' (at 2.5- 6 m distance from the adult palm): confrontation-zone – 'far' (at >8-10 m distance from the adult palm): high Urochloa grass dominance, total of 27 sampling points. Aboveground Urochloa biomass (sampled in 1m^2 squares per sampling point was estimated at 2.23 Mg ha^{-1}, 27.2% of which was classified as dead. All 27 sampling-locations were specifically visually scrutinized for the absence of any other (gramineous or herbaceous) species in their surroundings, thus guaranteeing the pure confrontation of our two model-species. All field work was conducted in May/June of 2019 (end of rainy season) within a time-span of 2 weeks.

II.2. Babassu and Urochloa root distribution

We used 'root walls' (Böhm 1979) to evaluate Babassu and Urochloa root distribution. Each root wall was 1 meter-wide and 50 cm deep, with orientation parallel to the Babassu-island boarders. Each root wall was sub-divided into 200 5 x 5 cm grids, and we counted in each grid Babassu and Urochloa roots in three predefined diameter classes: 'fine' (<2 mm), mid-diameter (2-5 mm) and 'coarse' (>5 mm).

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

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

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

II.3 Data-processing and statistics

The root wall counts both visually and statistically. For statistical processing, we (i) analyzed grid-data as a total, and (ii) summed root-counts in the 20 5 cm grids per soil depth, thus reducing the problem of zero-inflation. We checked data for normality of distribution via Kolmogorow-Smirnov and Lilliefor´s tests, and also checked for homogeneity of variance (Levene test). We explore the effects of our relative dominance gradient (distance from Babassu clusters) with both distance classes as a categorical variable and with continuous metric distance.

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

III. RESULTS

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

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

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

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

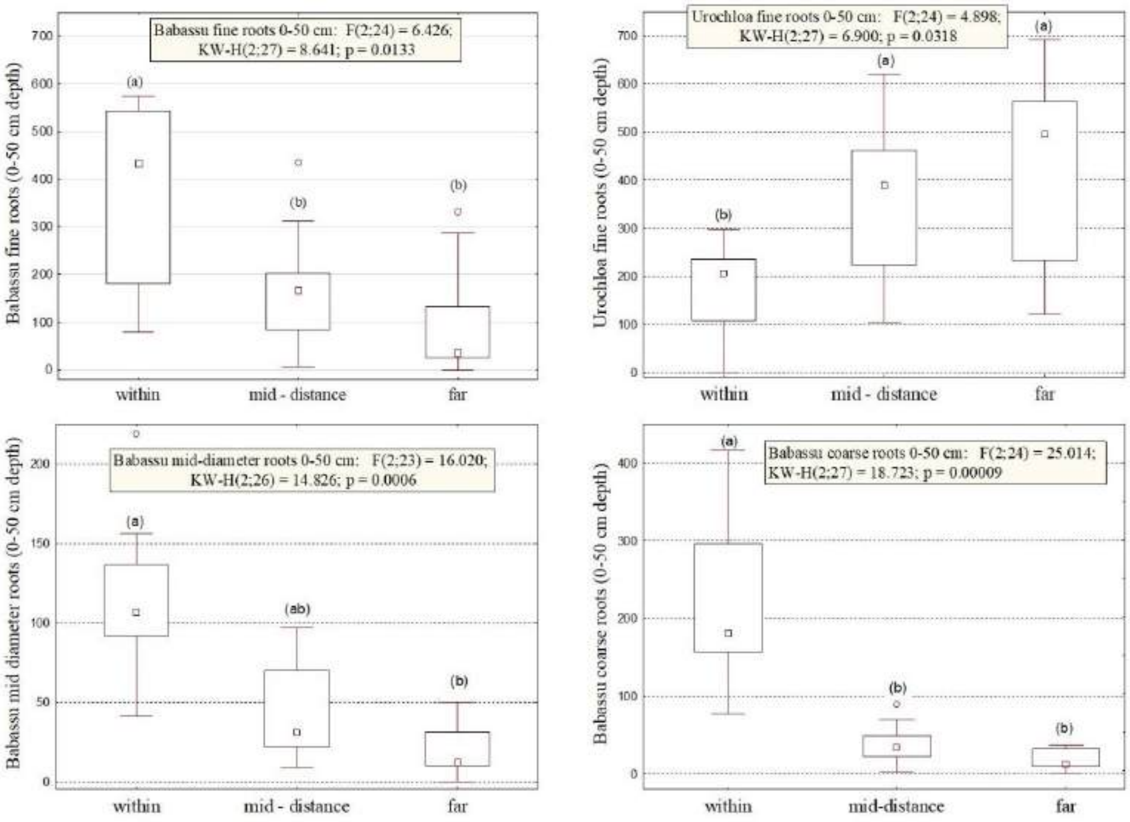


Figure 2. Babassu and Urochloa fine roots (top) and Babassu mid-diameter and coarse roots (bottom) in 0-50 cm soil depth. Medians, 25/75-percentiles, non-outlier range and outliers, extremes excluded. Letters refer to distance-grouping according to non-parametric Kruskall-Wallis ANOVA.

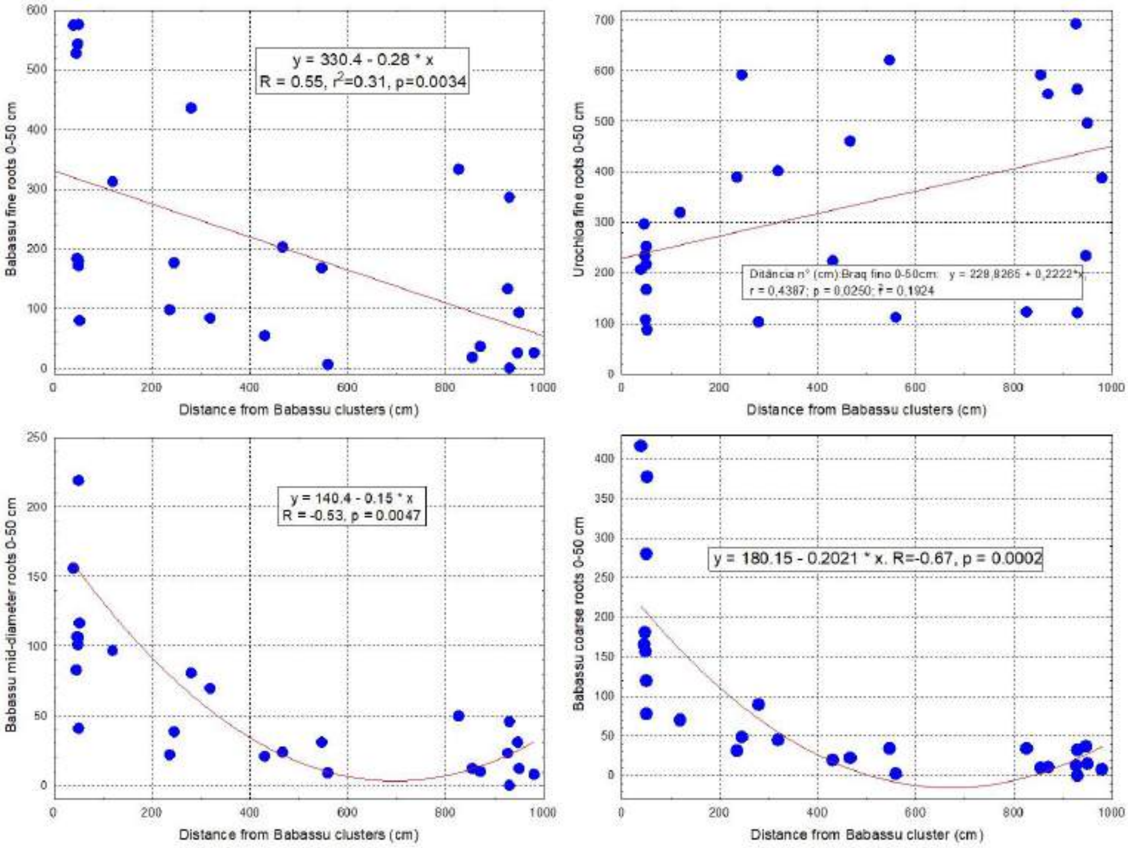


Figure 3. Relationship between metric distance from Babassu clusters and abundance of Babassu and Urochloa fine roots (top, linear fits) and of Babassu coarse and mid-diameter roots (bottom, negative exponential fit).

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

Figure 4 depicts coarse and mid-sized Babassu root vertical distribution at three distances from Babassu clusters. Coarse root counts were 4.7-fold higher within the Babassu clusters than at mid-distance and 12-fold higher than at long distance from the Babassu clusters, pointing to a very limited horizontal dispersal of Babassu coarse roots and their concentration directly beneath the palms within the Babassu clusters. Curvilinear relationships between root counts and soil depth were significant within Babassu clusters, both for coarse and mid-diameter roots, but – due to small densities - failed to be significant at mid-distance and far from Babassu clusters. Coarse root counts peaked at approximately 30 cm depth in all three sampling distances, but the peak was far more expressed within the Babassu clusters.

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

Contrary to the coarse root counts, Babassu mid-diameter counts within the Babassu clusters didn´t exhibit a clear peak at 30 cm soil depth, but rather continuously increased down to the 50 cm maximum sampling-depth (Figure 4 right).

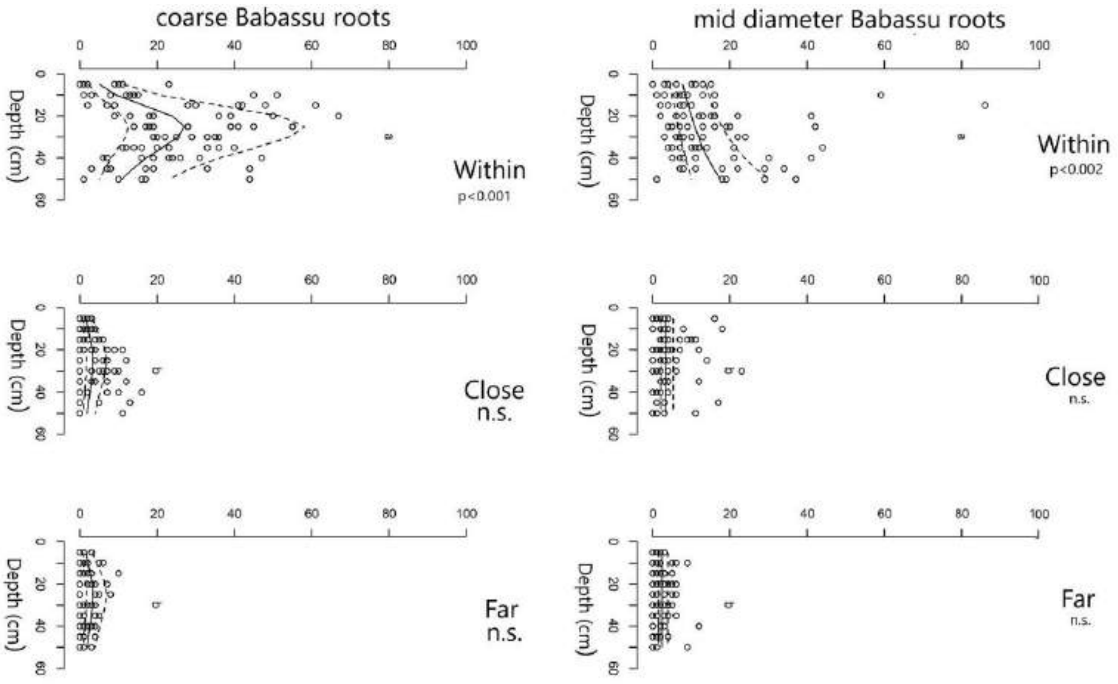


Figure 4. Coarse (>5 mm, left) and mid-diameter (2-5mm, right) root counts per 5 cm soil depth at sampling positions ‘within’ (top), at mid-distance (2.5 – 6.0 m) (middle) and ‘far’ (>6 m, bottom) from babassu clusters. Solid lines represent data interpolation, dotted lines represent 95% confidence intervals.

III.3. Babassu and Urochloa vertical fine root profiles

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

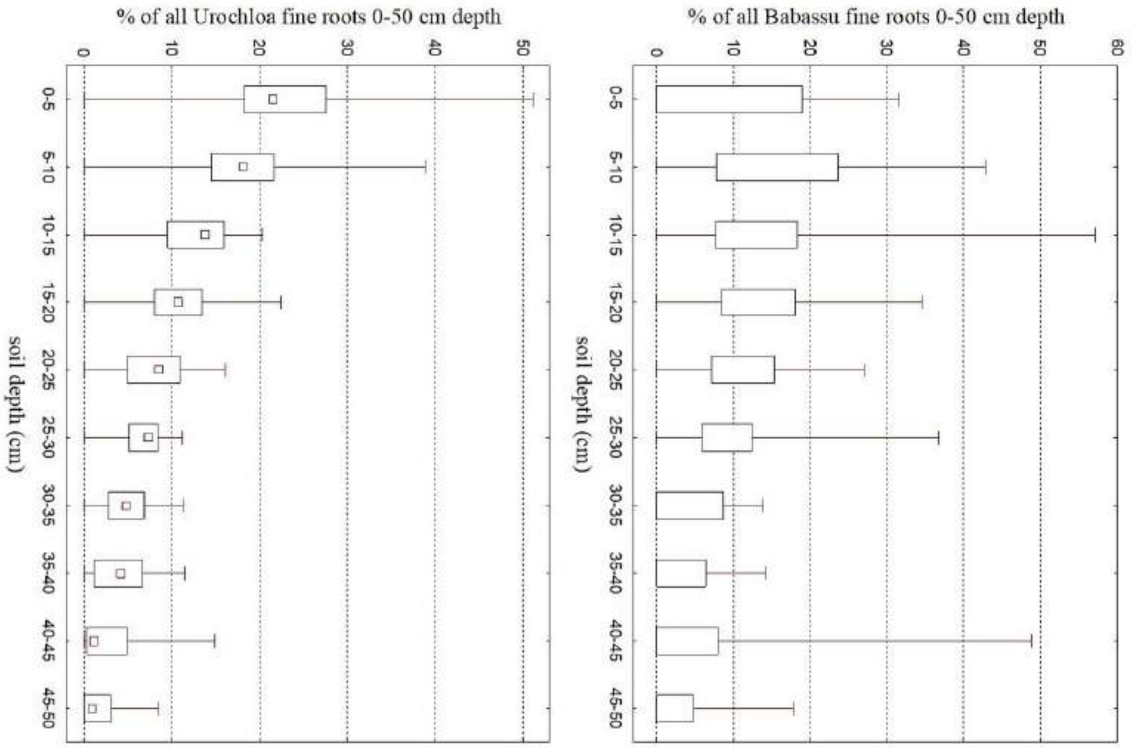


Figure 5. Relative vertical distribution of Urochloa (left) and Babassu (right) fine roots along the 50 cm soil profile over at all three distances: percentages of total root count per 5 cm soil layer (medians, 25- and 75-percentiles and range).

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

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

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

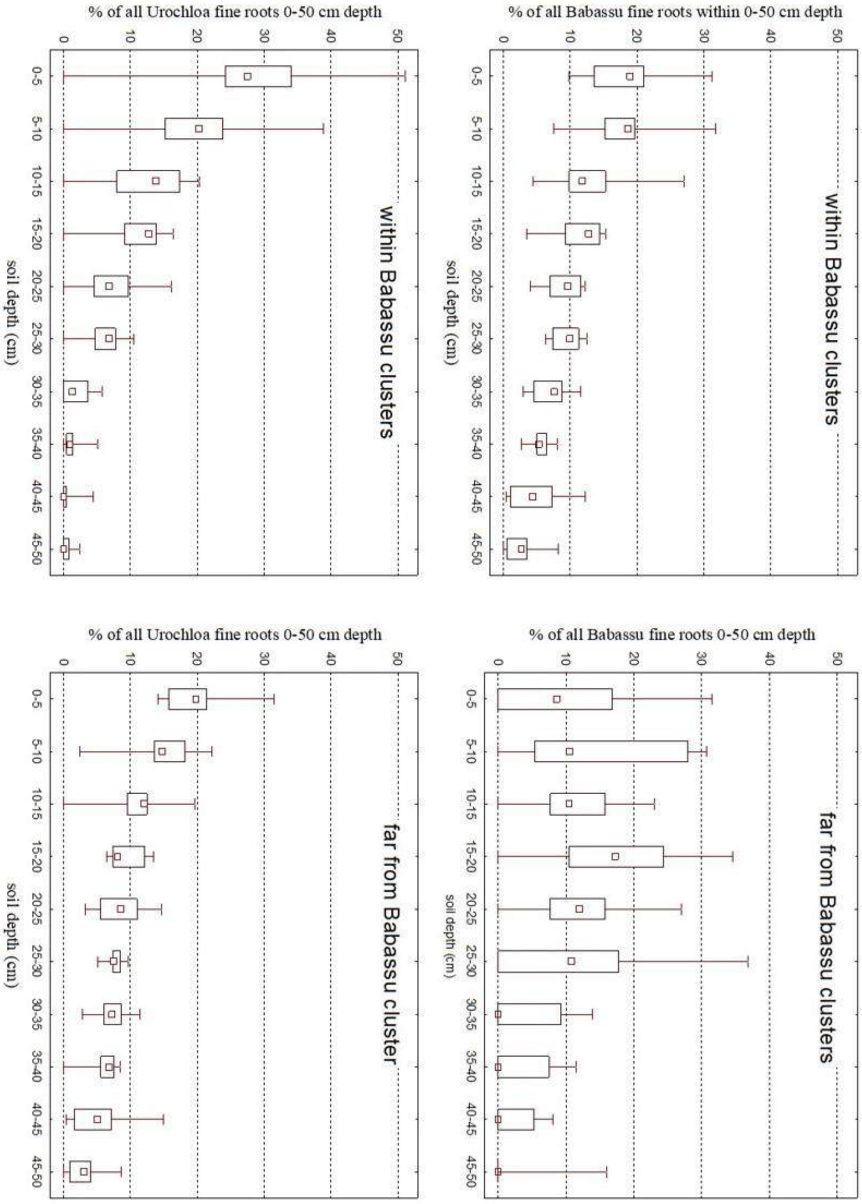


Figure 6. Relative vertical distribution of Babassu (top) and Urochloa (bottom) fine roots down the 50 cm soil profile at distances 'within' (left) and ‘far' (right). Percentages of total root counts per 5 cm soil layer (medians, 25 and 75 percentiles and range).

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

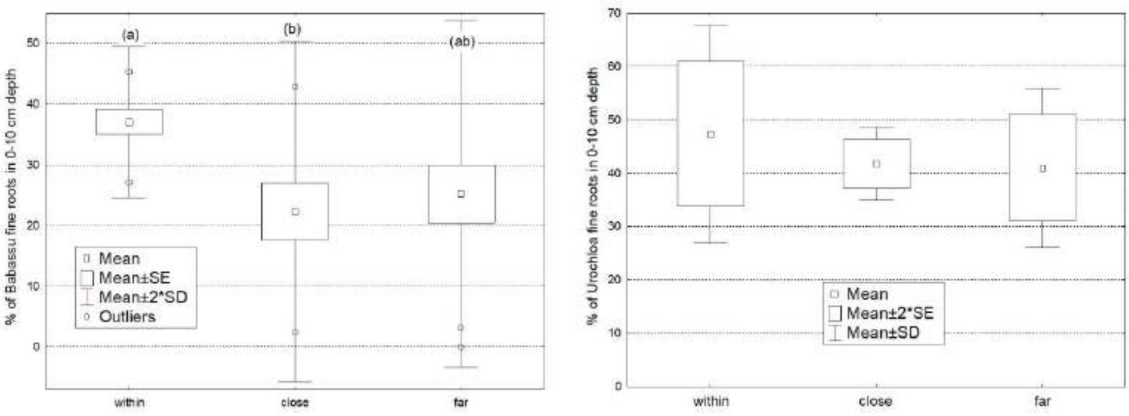
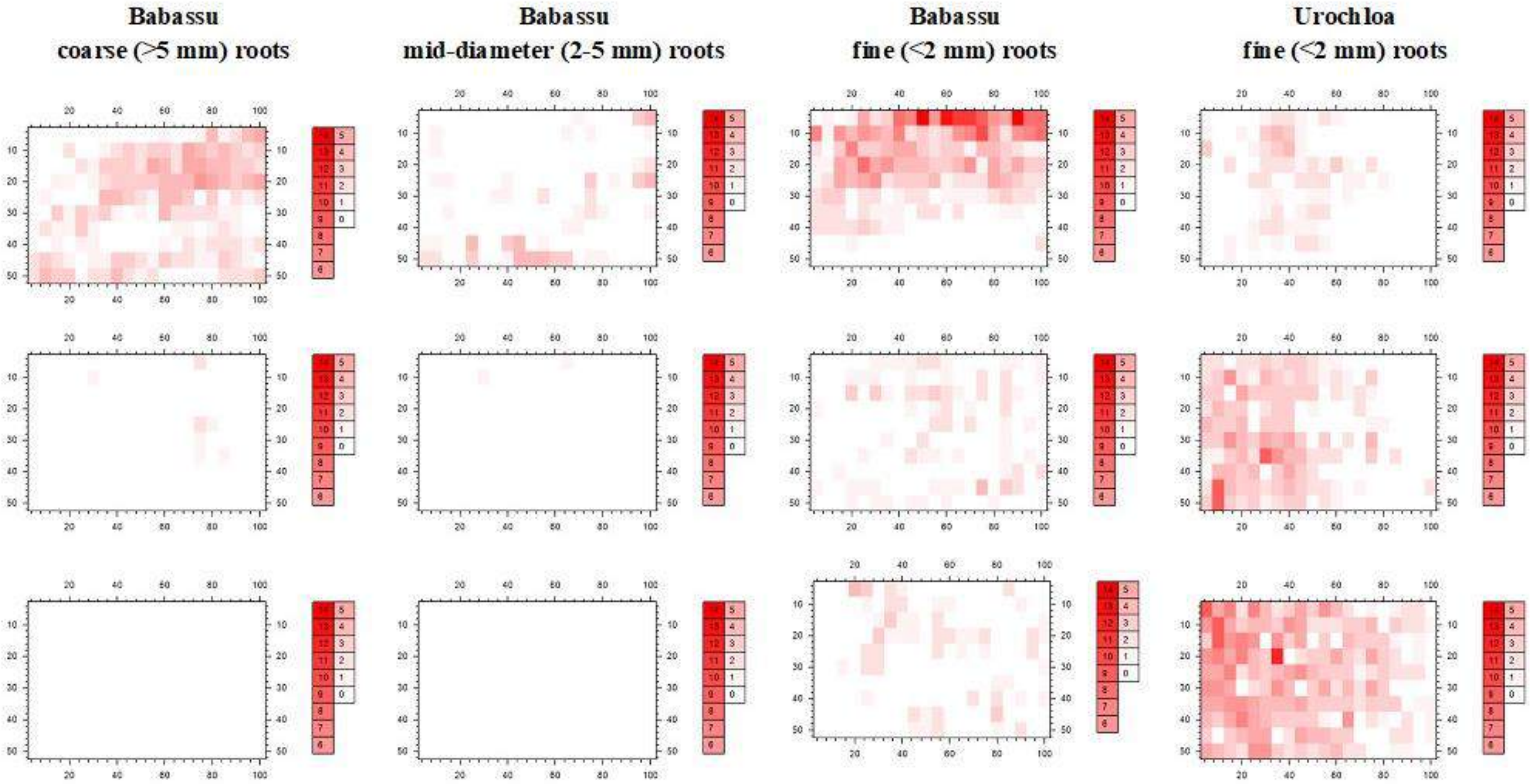


Figure 7. Percentage of all fine roots 0-50 cm concentrated within the top 0-10 cm soil layer for Babassu (left) and Urochloa (right), at sampling positions within, mid-distance and far from Babassu clusters. Means ±SE and SD, letters refer to groupings according to Tukey HSD post-hoc test.

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

Figure 8 depicts exemplary root walls of the four main root fractions at three different distances from the Babassu clusters. Next to the – expected – differences in total root counts (see previous chapters) a large small-scale variability in root count densities turns apparent. Root distribution between the 5401 5 x 5 cm grids was strongly skewed. For Urochloa fine roots, the densest 10% of all Urochloa grids (≥6 roots 25 cm^{-2}) combined 40.3% of all fine roots, whereas the top 10-percentile of Babassu fine roots (≥5 roots 25 cm^{-2}) only 38.4% of all fine roots. Our findings point to 'hotspots' of fine root proliferation and soil exploration of both species.

We searched for but did not find any significant correlations between root counts of Babassu and Urochloa fine roots in each 5 x 5 cm grid for any soil horizon (data not shown).



Babassu
coarse (>5 mm) roots

Babassu
mid-diameter (2-5 mm) roots

Babassu
fine (<2 mm) roots

Urochloa
fine (<2 mm) roots

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.

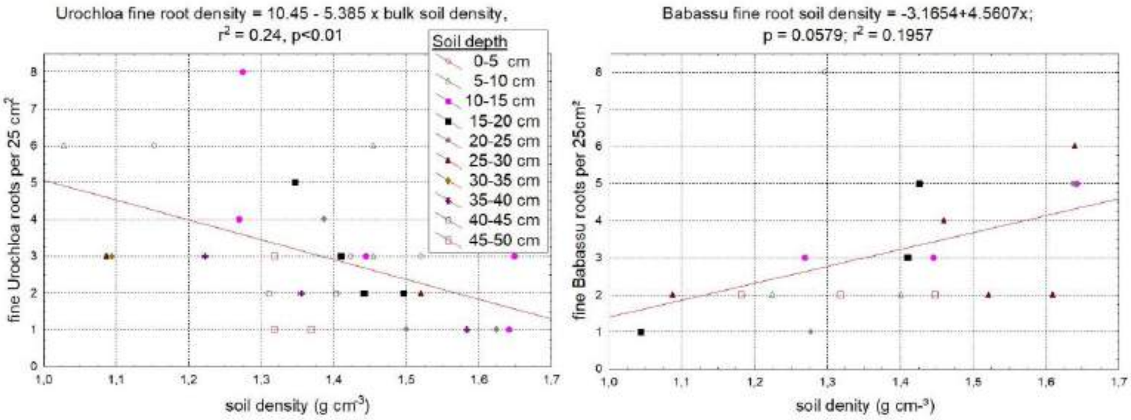


Figure 9. Relationship between soil bulk density and Urochloa (left) and Babassu (right) fine root counts within 5 x 5 x 3.3 cm grids / cubes containing more than zero fine roots.

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 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 therefor 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 distrtibution 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 heterogenous 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.

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