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A IMPORTÂNCIA DAS CONDIÇÕES HIDROLÓGICAS LOCAIS PARA A PRODUTIVIDADE ARBÓREA DAS FLORESTAS DE TERRA-FIRME NA AMAZÔNIA CENTRAL

Erick Jonathan Lavado Esteban

Manaus, Amazonas

Julho – 2025

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Orientadora:
Dra. Flavia Costa

Coorientadores:
Dra. Maquelle Garcia,
Dra. Loren P. Albert,
Dr. Sean McMahon

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Ata da Defesa REMOTA de **ERICK JONATHAN LAVADO ESTEBAN,** ocorrida no dia 24 de julho de 2025, via plataforma de videoconferência Zoom.

Aos 24 dias de abril de 2025, às 09:h00 (horário de Manaus/AM), realizou-se a Defesa Pública de tese de **ERICK JONATHAN LAVADO ESTEBAN**, aluno do Programa de Pós-Graduação *Stricto sensu* em Ciências de Florestas Tropicais, intitulada **"**A importância das condições hidrológicas locais para a produtividade arbórea das florestas de terra-firme na Amazônia Central," sob a orientação da Dra. Flávia Regina Capellotto (INPA) e coorientação: Dra. Maquelle Neves Garcia, Dra. Loren P. Albert, Dr. Sean McMahon. em conformidade com o Art. 52 do Regimento Geral da Pós-Graduação do Instituto Nacional de Pesquisas da Amazônia (MCTI/INPA) e Art. 67 do Regimento Interno do Programa de Pós-Graduação em Ciências de Florestas Tropicais, como parte das atividades para conclusão e obtenção do Título de Doutor(a) em Ciências de Florestas Tropicais. A **Banca Examinadora** foi constituída pelos seguintes membros: Dr. David Galbraith (University of Leeds (UK), Dr. Tomas Ferreira Domingues (USP), Dra. Marina Hirota (UFSC), Dra. Thaise Emilio (IB-UNESP), Dr. Jochen Schongart (INPA), e tendo como suplentes os seguintes membros: Dr. Ben Hur Marimon (UNEMAT), Dr. Peter Groenendijk (UNICAMP), Dra. Carolina Castilho (EMBRAPA CPAFRR). O Presidente da Banca Examinadora deu início à seção e informou os procedimentos do exame. O aluno fez uma exposição do seu estudo e ao término foi arguido oralmente pelos membros da Comissão. Após as arguições os membros da banca se reuniram para avaliação e chegaram ao seguinte parecer:

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Adriano José Nogueira Lima
Coordenador do PPG-CFT
PO. Nº 392/2023

Dedico

A Antonio Esteban, toñito,
siempre guiando mi camino,
y a Gloria Esteban,
mi motor y mi motivo.

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RESUMO GERAL

O destino das florestas tropicais frente às mudanças do clima ainda está cheio de incertezas. Alguns estudos de modelagem preveem que as florestas irão sucumbir ao clima, e outros sugerem uma resiliência desses ecossistemas no futuro. Tais debates tornam-se evidentes nos estudos relatando os impactos de eventos de secas *severas* no maior ecossistema florestal do planeta, a Amazônia. Enquanto dados de monitoramento a longo prazo -por parcelas permanentes- mostram um declínio na produtividade da floresta (efeito negativo), dados de sensoriamento remoto reportam um *esverdeamento*, relacionado a uma maior capacidade da floresta para fazer fotossíntese (efeito positivo) em várias partes da Amazônia. Essas observações, que parecem contraditórias, podem apenas ser o reflexo da baixa representatividade -em dados de parcelas permanentes em relação aos dados de satélite-, que têm recebido um tipo particular de ambientes hidrológicos na Amazônia: as áreas de floresta de terra-firme com lençol freático superficial. Embora esses ambientes representem uma importante extensão da bacia (ca. 40% com profundidade do lençol < 5m), nosso conhecimento sobre como a vegetação nesses ambientes responde ao clima e, portanto, a importância das condições hidrológicas locais na produtividade da floresta, ainda é bastante limitado. Diante disso, surge a questão: é possível um único efeito (positivo ou negativo) da variação do clima na produtividade das florestas da Amazônia? Ou a resposta total do ecossistema dependeria não só da variação climática, mas também das condições hidrológicas locais? Meu objetivo nesta tese foi analisar as variações que ocorrem na produtividade arbórea em áreas de floresta madura de terra-firme com condições hidrológicas contrastantes: áreas com lençol freático profundo (>20m) vs. áreas com lençol freático superficial (<5m). Para ter um entendimento geral da influência da profundidade do lençol freático, neste estudo analisei como as diferenças na escala local do acesso a água para as plantas (via lençol freático) modula a produtividade arbórea no nível da folha (na capacidade fotossintética e taxa de assimilação do carbono), no tronco (na taxa de crescimento diamétrico), e na biomassa e estrutura vertical das raízes finas.

No primeiro capítulo, investiguei como a produtividade das árvores -no nível da folha e madeira- varia ao longo de gradientes de disponibilidade de água no solo e de nutrientes em uma floresta de terra-firme na Amazônia central. Com medições de fotossíntese, crescimento do tronco, traços funcionais e distribuição ao longo do gradiente hidro-edáfico de 23 espécies arbóreas abundantes, encontrei que, em áreas com lençol freático profundo—com menor disponibilidade de água, mas

maior teor de nitrogênio no solo—, as árvores desenvolvem maior capacidade fotossintética por meio de ajustes na estrutura foliar. Já em áreas com lençol freático superficial, as árvores mantêm maior condutância estomática e crescimento do tronco, favorecidas pela maior disponibilidade de água no solo. Ainda com tais estratégias contrastantes, as espécies dominantes alcançam produtividades similares entre folhas e tronco ao longo do gradiente hidro-edáfico, sugerindo um efeito compensatório que pode ajudar a estabilizar a produtividade da floresta frente às mudanças climáticas.

No segundo capítulo, analisei como a disponibilidade de água no solo e de nutrientes influencia a distribuição da biomassa de raízes finas e o particionamento (alocação) entre biomassa acima e abaixo do solo (relação BGB:AGB) em áreas de floresta com lençol freático superficial. Usando dados de nutrientes do solo, monitoramento da flutuação do lençol freático, e medições diretas de biomassa de raízes e do tronco ao longo de um transecto de 600 km na Amazônia central, observei que o excesso de água no solo -seja pelo clima mais úmido ou pela presença constante de lençol freático muito raso (<2m) -restringe a distribuição da biomassa das raízes finas às camadas mais superficiais do solo. Essa limitação, isolada ou somada à baixa disponibilidade de fósforo, resulta em maior alocação de biomassa abaixo do solo (maior BGB:AGB) levando a uma floresta com maior densidade de arvores de menor diâmetro. Em áreas onde o excesso de água no solo é ausente ou pouco frequente, ocorre o padrão oposto. A disponibilidade de fosforo também influencia a alocação da biomassa, mas com os regimes do lençol freático modulando fortemente esses efeitos. Os resultados desse capítulo destacam a importância do regime hídrico do solo na estrutura das florestas de lençol freático superficial, desafiando a visão tradicional de que a alocação da biomassa é controlada apenas por nutrientes e clima, e trazendo implicações importantes para a modelagem do funcionamento da Amazônia e seu papel no ciclo global de carbono.

No terceiro capítulo (ainda não finalizado), analisei os padrões espaço-temporais do crescimento diamétrico do tronco em árvores estabelecidas em áreas de floresta com lençol freático superficial e profundo. Utilizando dados mensais de mais de mil árvores monitoradas com bandas dendrométricas desde fevereiro de 2022 até dezembro de 2024, avaliei como a taxa de crescimento do tronco variou entre ano de sazonalidade climática normal (2022) e durante anos com eventos de seca severa (2023 e 2024). Em 2022, as taxas de crescimento foram semelhantes entre os ambientes. Contudo, durante os anos de secas, as árvores em áreas de lençol freático superficial

mantiveram -e até aumentaram- as suas taxas de crescimento, enquanto nas áreas de lençol profundo tal crescimento caiu significativamente, sem recuperação dos padrões esperados até o fim de 2024. Além disso, usando modelos bayesianos integrados a diagramas causais (DAG), analisei quais são os principais fatores que modulam o crescimento dentro de cada ambiente. Os resultados mostram que a disponibilidade de água no solo, via lençol freático (profundo vs superficial), modula fortemente o efeito da chuva e o impacto dos eventos de seca, com resultados contrastantes entre ambientes: nas áreas de lençol profundo, o crescimento do tronco depende fortemente da precipitação anterior, enquanto nas áreas de lençol superficial, o crescimento é mais associado à interação entre quantidade de luz (radiação) e disponibilidade de água e oxigênio no solo. Este capítulo contribui para um melhor entendimento da vulnerabilidade (ou resiliência) da floresta amazônica a mudança do clima, reforçando a importância das áreas com lençol freático superficial, atuando como potenciais refúgios hidrológicos para o funcionamento da floresta (absorção e alocação do carbono) durante eventos de seca.

De forma integrada, os resultados da minha tese revelam que as condições hidrológicas locais, representadas pela profundidade do lençol freático, são determinantes para o funcionamento das florestas amazônicas, modulando desde traços funcionais e estratégias fotossintéticas até o particionamento da biomassa e o crescimento do tronco em diferentes escalas temporais. Enquanto o funcionamento arbóreo em áreas com lençol freático profundo apresenta uma forte dependência da precipitação e do nitrogênio do solo para sustentar a produtividade, as arvores estabelecidas em áreas com lençol freático superficial se destacam pela maior estabilidade no crescimento e na produtividade, mesmo durante eventos de seca, devido ao acesso constante à água no solo. Esses ambientes atuam como refúgios hidrológicos, compensando, ao menos parcialmente, as perdas de produtividade em outras partes da floresta durante períodos climáticos adversos. Assim, nesta tese evidencio que a resposta da floresta amazônica às mudanças climáticas não é uniforme, mas sim fortemente condicionada pela interação entre clima e hidrologia local, ressaltando a importância de incluir os gradientes hidrológicos nos modelos de vegetação e nas estratégias de conservação visando a manutenção do funcionamento e dos serviços ecossistêmicos da Amazônia.

Palavras-chave: Ambientes hidrológicos, disponibilidade de água no solo, estresse hídrico, eventos de seca, floresta de terra-firme, lençol freático, sazonalidade climática.

SUMARIO

INTRODUÇÃO

A produtividade das florestais tropicais está diminuindo (Anderegg *et al*., 2015; Sullivan *et al*., 2020), com a mortalidade das árvores aumentando drasticamente (Hartmann *et al*., 2018; McDowell *et al*., 2018). Tais mudanças estão gerando alterações em larga escala na estrutura e composição das florestas (e.g. Allen & Breshears, 1998; Bennett *et al*., 2015; Laurance *et al*., 2004; Sande *et al*., 2016), afetando o efeito mitigador desses ecossistemas nos impactos da mudança do clima -como sumidouros do carbono-, e com consequentes feedbacks negativos do clima na escala local e global (Cox *et al*., 2000).

Essa situação, atribuída à mudança climática global e aos eventos extremos de secas, ondas de calor, e inundações (Cook *et al*., 2014; Dai, 2013; Hirabayashi *et al*., 2008; IPCC, 2012), gera grande preocupação sobre o destino das florestas (Friend *et al*., 2014; Gloor, 2019; Trumbore *et al*., 2015). Contudo, ainda existe muita incerteza sobre os efeitos da mudança do clima nos ecossistemas tropicais (Cox *et al*., 2013), dificultando prever os impactos futuros no planeta (Booth *et al*., 2012).

Temperaturas mais altas, mudanças nos regimes de precipitação, e aumento na frequência e intensidade de eventos de seca, são apontadas como os principais fatores climáticos causantes de mudanças nas florestas (e.g., Allen *et al*., 2010; Anderegg *et al*., 2013; Erfanian *et al*., 2017; Holmgren *et al*., 2013). Tais efeitos negativos são reportados nas florestas da Amazônia, resultado do monitoramento ao longo do tempo da vegetação no nível do chão (remedições de parcelas permanentes). Maior mortalidade e menor produtividade arbórea têm sido associados a condições climáticas extremas (Aleixo *et al*., 2019; Phillips *et al*., 2009), com um declínio de longo prazo na absorção do carbono (Brienen *et al*., 2015), e com mudanças de composição taxonômica e funcional (Costa *et al*., 2020; Esquivel-Muelbert *et al*., 2019). Condições severas de seca, com aumento da temperatura e redução da quantidade de chuva, como nos eventos extremos de 2005, 2009-2010 e 2015-2016, são apontadas como principais causantes de alta mortalidade e baixa produtividade arbórea na Amazônia (e.g. Feldspauch *et al*., 2016; Gatti *et al*., 2014; Leitold *et al*., 2018). Todo esse conjunto de fatores -em sinergia com o efeito antrópico- tem levado a diversos cientistas argumentar a possibilidade da Amazônia estar prestes a atingir um ponto de não retorno, gerando um colapso de grande escala (Flores *et al*., 2024; IPCC, 2021; SPA, 2021).

Entretanto, usando diferentes índices de vegetação extraídos de imagens de satélite (e.g. EVI, NDVI), e confirmando os resultados com dados de torres de fluxo, estudos de sensoriamento remoto têm demostrado que algumas áreas de floresta na Amazônia tendem a responder, tanto a condições sazonais como a eventos de seca, com um *esverdeamento* (green-up) das copas do dossel (e.g. Huete *et al*., 2006; Saleska *et al*., 2007, 2016). Esse *esverdeamento*, que estaria refletindo maior capacidade da floresta para realizar fotossíntese (Myneni *et al*., 1995), e sugerindo à disponibilidade de luz como fator mais limitante do que a água nesses ecossistemas (Nemani *et al*., 2003), resulta mais evidente em áreas de floresta onde o lençol freático é superficial. Entretanto, embora ca. 50% das florestas de terra-firme da Amazônia estão em ambientes onde o lençol freático tem profundidade menor a 5m (Costa et al., 2022; Fan e Miguez-Macho, 2010, Nobre *et al.*, 2011), os esforços de monitorar a floresta por meio de parcelas permanentes (nos quais a maioria dos estudos relatando os impactos negativos da seca são baseados) têm negligenciado e sub-representado esse tipo de ambientes hidrológicos contrastantes (Costa *et al*., 2022). Nesse contexto, maior representação e estudo desse tipo particular de ambientes hidrológicos, que permita entender melhor suas respostas a diferentes condições climáticas, poderia conciliar esses resultados aparentemente contraditórios, e contribuir a explicar o porquê de certas florestas de terra-firme na Amazônia respondem com um declínio da produtividade (parcelas permanentes), enquanto outras mostram aumento na capacidade fotossintética (sensoriamento remoto).

Grande parte dos estudos avaliando o impacto do clima na Amazônia focam nos efeitos das condições de seca. No entanto, períodos muito úmidos também estão sendo mais frequentes e intensos ao longo da bacia (Barichivich *et al*., 2018; Gloor *et al*., 2013). P. ex., no norte da Amazônia tem havido um aumento na precipitação e na frequência de dias muito úmidos (Espinoza *et al*., 2019), enquanto na região central é observada uma tendência crescente da precipitação anual desde 1965 (Costa *et al*., 2020). Contudo, os efeitos dessas condições de alta umidade, assim como suas possíveis interações no nível do solo com períodos mais secos, na modulação da dinâmica e produtividade arbórea das florestas maduras de terra firme da Amazônia, ainda foram pouco explorados (Esteban *et al*., 2021).

A disponibilidade de água no solo, que define condições de déficit ou excesso de água para as plantas, é principalmente controlada por condições topográficas e edáficas, determinando amplamente as condições hidrológicas locais (Daws *et al.,* 2002; Horton e Hart, 1998; Tromp-van Meerveld e McDonnell, 2006). Assim, sob uma mesma condição climática, árvores de florestas de terra-firme podem estar em contato direto com a água, como em terras baixas e vales ("baixios"), onde o solo resulta ser mais úmido pela presença de um lençol freático superficial; ou suportando períodos com alto déficit hídrico e se tornando mais dependentes da precipitação, como em encostas e terras altas ("platôs"), onde o nível do lençol freático pode chegar a ser muito profundo (Fan *et al*., 2017; Hodnett *et al*., 1997; Jencso *et al*., 2009; Miguez-Macho e Fan, 2012). Esta variação espacial da umidade do solo ao longo de gradientes topográficos ("gradiente hidrológico no solo", variando de baixios a platôs), pode modular fortemente vários processos na floresta, como respiração no solo (Pacific *et al*., 2011), a evapotranspiração (Eberbach e Burrows, 2006), ou mesmo crescimento (Adams *et al*., 2014) e mortalidade (Itoh *et al*., 2012) das árvores em resposta aos efeitos do clima, podendo mitigar ou intensificar seus impactos (Broedel *et al*., 2017; Costa *et al*., 2022; Esteban *et al*., 2021; Hawthorne e Miniat, 2018; Sousa *et al*., 2020; Zuleta *et al*., 2017).

Uma função principal do solo é fornecer um meio para o estabelecimento e desenvolvimento das plantas, sendo determinante nos padrões de distribuição das espécies nas paisagens florestais (Clark *et al*., 1998, 1999; Itoh *et al*., 2003). Dado isso, espera-se que, além da variação de características físico-químicas (fertilidade e textura), a disponibilidade de água no solo possa ter influência em vários aspectos das florestas, como na composição, estrutura, e até desempenho fisiológico das árvores. De fato, variações nas condições hidrológicas locais têm atuado como filtros tanto da composição (Marca-Zevallos *et al*., 2022; Moulatlet *et al*. 2014; Schietti *et al*., 2014) como da estrutura funcional das plantas (Cosme *et al*., 2017; Garcia *et al*., 2022; Oliveira *et al*., 2019) em florestas de terra-firme na Amazônia.

E como essa variação hídrica no solo pode influenciar a produtividade das árvores nas florestas de terra-firme?

Nas florestas de terra-firme com lençol freático superficial, o encharcamento do solo durante períodos chuvosos têm filtrado a composição em direção a espécies adaptadas ao encharcamento e alta demanda de água, levando a um menor investimento em estruturas ligadas a segurança hidráulica (menor resistência a embolismo -P50 mais perto de zero- em espécies de baixio, Oliveira *et al*., 2019). Assim, a disponibilidade de água desses ambientes estaria levando as plantas a menor alocação estrutural em tecidos duros (i.e., menor parede celular), o que por sua vez *permitiria* uma maior alocação em enzimas e tecidos relacionados ao processo fotossintético, como células do mesófilo, protoplasma etc. (Sack *et al*., 2013; Wright *et al*., 2004). Dado que a estrutura interna das folhas é um fator determinante tanto da capacidade das plantas de interceptar luz como do seu potencial fotossintético (Niinemets e Sack 2006), e uma vez que fatores hidrológicos locais influenciam nessa estrutura, espera-se então que a "capacidade fotossintética" das árvores mude ao longo de gradientes hidrológicos no solo, como resultado das variações hídricas entre os ambientes.

Diversas características estruturais das folhas, operando em diferentes escalas hierárquicas, influenciam a capacidade de assimilação de CO_2 das plantas. Na escala dos tecidos, mudanças estruturais alteram a quantidade de luz interceptada por unidade de clorofila, enquanto na escala das folhas, variações estruturais mudam a exposição de cada folha. Assim, maior *capacidade fotossintética* nos ambientes com alta disponibilidade hídrica no solo (baixios) teria que estar relacionada a características estruturais das árvores (no nível foliar) que reflitam tais capacidades, como uma maior área foliar específica (SLA) (Niinemets e Sack 2006), e/ou uma menor densidade de venação foliar (LVD) (Sack *et al*., 2013). Além disso, e como consequência dessas relações, alocações estruturais no nível da planta inteira também serão influenciadas, como no caule, onde variações nas condições hidrológicas têm sido reportadas como moduladores da densidade da madeira de plantas em ecossistemas ripários (Lawson *et al*., 2015).

Com uma maior capacidade de assimilação, é possível esperar um maior crescimento da planta. Entretanto, taxas de crescimento em biomassa dependem não só das potencialidades dos indivíduos, mas também do *intervalo de tempo* em que as condições ambientais resultem favoráveis para crescer. Esse período, ou *janela temporal de crescimento*, é determinada por

fatores climáticos, como sazonalidade da precipitação, temperatura e radiação, e por fatores locais, como as condições hidrológicas e estruturais do solo.

O crescimento arbóreo em madeira -geralmente medido pelo incremento diamétrico do tronco-, embora não seja a única fonte de alocação de biomassa da produtividade total realizada pela planta (i.e., alocação também acontecendo em raízes, folhas, flores e frutos), ele representa até 50% da produção primária líquida das florestas tropicais (Malhi *et al*., 2011, 2015). Essa produtividade arbórea em madeira, avaliada neste trabalho, é fortemente influenciada pela sazonalidade climática nas florestas tropicais (Rowland *et al*., 2014; Wagner *et al*., 2014), sendo observada uma redução do incremento em diâmetro das árvores em condições de altas temperaturas (Clark *et al*., 2003, 2010) e de déficit hídrico (Brando *et al*., 2008; Worbes, 1999).

A disponibilidade de água no solo é relacionada à sazonalidade da chuva (p. ex. Stahl *et al.,* 2013). No entanto, a relação entre esses fatores não é direta e pode ser modulada pelas condições do solo e da topografia local. Nos "períodos secos" (menor quantidade de chuva), as árvores estabelecidas em áreas com lençol freático profundo podem experimentar estresse hídrico, pelo menor ingresso/recarga de água ao solo e a maior distância vertical do lençol freático, que impede as raízes captarem água diretamente dessa fonte, o que não aconteceria nas árvores estabelecidas em ambientes com lençol freático superficial, se tornando *menos dependentes da chuva*. Na estação chuvosa, por outro lado, os *platôs* apresentariam boas condições para o crescimento das arvores, dada a disponibilidade de água e a boa aeração no solo (não encharcado). Nos *baixios*, no entanto, as árvores podem estar mais vulneráveis a condições hipóxicas no solo (pouco oxigênio), devido à alta saturação de água (encharcamento) ao longo do período chuvoso (Hodnett *et al*., 1997).

Nas florestas alagáveis, p. ex., as árvores estão expostas a flutuações no nível da água que causam inundações anuais a longo prazo, conhecidas como pulsos de inundação (Junk *et al.*, 1989). Nos períodos em que o nível da água sobe, o alagamento do solo determina condições desfavoráveis para o crescimento das árvores, por conta de escassa disponibilidade de oxigênio no solo (condições hipóxicas ou anóxicas) para as raízes (Worbes 1986), reduzindo a atividade radicular (Meyer 1991), levando a um déficit hídrico nas copas (Worbes 1997), e finalmente a dormência cambial e supressão do crescimento (Schongart *et al*., 2002). Aliás, uma vez que as raízes precisam

de bom suprimento tanto de oxigênio como de água para satisfazer a necessidade hídrica e de nutrientes no nível da planta inteira (Pierret *et al*., 2007), uma desproporção no conteúdo de água e ar no solo pode gerar limitação para o enraizamento, afetando seu desempenho fisiológico (Piedade *et al*., 2010) e, com isso, o crescimento. Assim, além dos efeitos sobre a estruturação dos tecidos e capacidade de assimilação de CO_2 nas folhas, e do crescimento em diâmetro do tronco, espera-se que variações nas condições hidrológicas do solo (*baixio vs platô*) também modulem a biomassa arbórea abaixo do solo, especialmente das raízes finas, que são fundamentais para a absorção de água e nutrientes (Jackson *et al*., 1996; Smithwick *et al*., 2014). Estudos mostram que solos saturados de água podem restringir o desenvolvimento radicular a camadas superficiais do solo, alterando o particionamento -*alocação*- entre biomassa acima e abaixo do solo (Nepstad *et al*., 1994; Oliveira *et al*., 2019), com tais mudanças impactando diretamente a estruturação e produtividade da floresta, e consequentemente o balanço de carbono.

Por tanto, é esperado que as interações entre fatores do clima (sazonalidade da chuva, radiação, temperatura), as características intrínsecas das árvores (estrutura interna dos tecidos e sua fisiologia), e as condições locais dos ambientes onde elas estão estabelecidas (nutrientes, textura, e disponibilidade de água no solo), sejam fatores determinantes: (i) da capacidade fotossintética e assimilação do CO_2 no nível da folha, (ii) do crescimento em termos de incremento diamétrico no nível do tronco, e (iii) na quantidade e estruturação da biomassa de raízes, com consequências na repartição da biomassa (alocação para acima e abaixo do solo) e na estruturação das florestas. Contudo, nosso entendimento sobre como o funcionamento das arvores nesses três níveis (folha – madeira – raiz) muda entre ambientes hidrológicos contrastantes (*baixio vs platô*) ao longo de gradientes topográficos locais nas florestas maduras de terra-firme da Amazônia, ainda é bastante limitado.

Nesse contexto, meu objetivo nesta tese foi analisar como a variação nas condições hidrológicas locais (*ambientes hidrológicos contrastantes pela profundidade do lençol freático*) afeta, nos níveis folha-madeira-raiz, a produtividade das árvores em florestas maduras de terra-firme na Amazônia central. Para isso, a minha tese consta de três capítulos:

No primeiro capítulo, analisei como a associação das espécies a diferentes níveis de disponibilidade de agua (por meio da profundidade do lençol freático) e de nutrientes (P e N) no

solo, ao longo de um gradiente topográfico, modula a estruturação dos tecidos no nível da folha e madeira (características funcionais), a capacidade fotossintética (V_{cmax}), e qual a interação desses fatores na determinação das taxas de assimilação de carbono (A_{sat}) e de crescimento diamétrico do tronco, em 23 espécies arbóreas abundantes numa floresta madura de terra-firme na Amazonia central;

Pergunta cientifica 1: *Como as variações nas condições hidrológicas do solo e disponibilidade de nutrientes modulam a capacidade fotossintética, assimilação de CO_2 e crescimento diamétrico do tronco de espécies arbóreas abundantes numa floresta de terra-firme na Amazônia central?*

No segundo capítulo, usando medições diretas de biomassa acima e abaixo do solo (tronco e raiz), e do monitoramento da flutuação temporal do lençol freático, avaliei como o regime local do lençol freático, e a sua interação com o clima e disponibilidade de nutrientes no solo, modula a biomassa e a distribuição vertical das raízes finas na profundidade do solo, o particionamento da biomassa para acima e abaixo do solo (alocação BGB:AGB), e como isso associa-se a diferenças na estrutura horizontal das florestas (abundancia e tamanho dos indivíduos).

Pergunta cientifica 2: *Qual é o efeito do regime hidrológico no solo, clima e disponibilidade de nutrientes na biomassa de raízes, distribuição vertical de raízes finas e na alocação da biomassa acima e abaixo do solo, em florestas com lençol freático superficial?*

No terceiro e último capítulo, com dados de monitoramento mensal de incremento diamétrico do tronco, flutuação do lençol freático, e variáveis climáticas durante os últimos três anos (2022-2024), explorei a variação espaço-temporal do crescimento do tronco de mais de 1000 arvores estabelecidas em ambientes hidrológicos contrastantes (*platô vs baixio*), visando entender a importância (efeito causal) do lençol freático e do clima, quais são os principais moduladores do crescimento em cada ambiente, e como o efeito das secas mais recentes difere entre ambientes.

Pergunta cientifica 3: *Variações na profundidade do lençol freático modulam o impacto da sazonalidade climática e dos eventos de seca na fenologia de crescimento diamétrico do tronco das arvores na Amazonia central?*

Capítulo 1

Erick J. L. Esteban, Loren P. Albert, Maquelle N. Garcia, Marciel J. Ferreira, Flavia R. C. Costa

Water table and nutrient availability drive contrasting functional strategies but convergent performance in dominant Amazonian tree species

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Water table and nutrient availability drive contrasting functional strategies but convergent performance in dominant Amazonian tree species

Erick J. L. Esteban[1], Loren P. Albert[2], Maquelle N. Garcia[2], Marciel J. Ferreira[3] & Flávia R. C. Costa[4]

[1]Programa de Pós-Graduação em Ciências de Florestas Tropicais, Instituto Nacional de Pesquisas da Amazônia, Av. Ephigênio Sales 2239, 69060-20 Manaus, AM, Brazil; [2]Oregon State University, Department of Forest Ecosystems & Society, Corvallis, OR 97333, USA; [3]Universidade Federal do Amazonas, Departamento de Ciências Florestais, Manaus - AM, Brazil; [4]Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Av. Ephigênio Sales 2239, 69060-20 Manaus, AM, Brazil;

Abstract

Background and aims: Amazonian forests with shallow water tables (WT) are proposed as plant hydrological refuges, where greater soil moisture combined with plant acquisitive strategies maintains or even increases tree CO_2 assimilation and growth during droughts. Yet, the comparative photosynthetic and growth performance of trees along hydrological gradients (shallow to deep WT) remain unknown, limiting our ability to predict forest resilience to climate change. We explore the association between species affiliation to soil resources and traits and how their combined effects modulate tree photosynthetic and growth performance.

Methods: We collected an extensive dataset of structural traits, photosynthetic data, stem growth, and tree distribution for 23 dominant tree species across local gradients of soil moisture (WT variation) and nutrients -phosphorus (P) and nitrogen (N)- in a central Amazonian forest. We used structural equation modeling to unveil the direct and indirect pathways connecting resources affiliation and functional traits to photosynthetic and growth performance.

Results: Photosynthetic capacity is higher in trees established in deep WT areas, characterized by lower soil moisture and higher N availability, whereas in shallow WT areas, trees exhibit greater stomatal conductance. These trait–environment relationships were consistent at both inter- and intra-specific levels. Both stomatal conductance and photosynthetic capacity enhanced light-saturated CO_2 assimilation, which is positively related to stem growth. Yet, P availability, rather than N or soil moisture, emerges as the strongest driver of growth.

Synthesis: Our results reveal a local-scale physiological compensation driven by divergent resource limitations: while species in deep WT areas leverage higher soil N to enhance biochemical capacity, their potential gains are offset by higher maintenance respiration costs. Conversely, species in shallow WT areas exhibit greater stomatal conductance, rising carbon assimilation and ultimately positively affecting growth. This coordination of alternative trait-environment combinations leads to a functional convergence in tree performance across the soil hydrological gradient. Our findings underscore that Amazonian resilience is underpinned by fine-scale hydro-edaphic heterogeneity and the ability of dominant species to adaptively shift their strategies.

Keywords: Amazon forest; environmental filtering; hydrological gradient; nutrient availability; tree photosynthesis; soil moisture; stem growth; water table depth.

Introduction

Tropical forests play a central role in the global carbon cycle, yet their resilience under intensifying drought remains uncertain. In the Amazon, rising temperatures and shifting rainfall patterns are increasing the frequency and severity of drought events (Marengo et al., 2016; Papastefanou et al., 2022; Science Panel for the Amazon, 2024), threatening the resilience and capacity of trees to assimilate and allocate carbon (Boulton et al., 2022; Van Passel et al., 2024). Reduced photosynthetic carbon uptake and slower stem growth are commonly reported in response to drought (Brienen et al., 2015; Rifai et al., 2018). However, most of these findings come from forest areas with deep water tables (WT), leaving the physiological responses and growth responses of trees in areas with shallower WT — where groundwater may remain accessible during drought — relatively unexplored.

Approximately half of the Amazon forest comprises environments with shallow WT (depth <5m), where groundwater proximity can sustain soil moisture and potentially buffer drought impacts (Costa et al., 2023). Based on interannual census data, these environments have been proposed as potential hydrological refugia, maintaining tree productivity and precluding high mortality during droughts (Esteban et al., 2021; Sousa et al., 2020). Nonetheless, the mechanisms determining these effects are so far unknown. The resilience of the proposed hydrological refugia may stem from the effects of soil moisture itself, plant traits, or their combination on the performance of trees.

In Amazonian *terra-firme* forests, topographic variation – from upland plateaus with deep WT to lowland valleys with shallow WT – play a significant role in shaping local availability in both soil water and nutrients (Figueiredo et al., 2018; Quesada et al., 2010). Areas with shallow WT have greater soil moisture and may often be richer in phosphorus (P), due to the release from ferric phosphates during the seasonal waterlogging and the increased effective diffusion coefficient of P in water (Patrick & Mahapatra, 1968). Deep WT areas, on the other side, are more water-limited and tend to have higher soil nitrogen (N) availability due to increased organic matter turnover and higher water retention capacity given their clayey texture (Fyllas et al., 2009; Luizão et al., 2004). Consequently, water and nutrient availability often co-vary along local topography (hydro-edaphic gradients), challenging efforts to isolate their independent effects.

Plant responses to such hydro-edaphic gradients are mediated through both structural and physiological traits that ultimately determine carbon assimilation and allocation. Key structural traits such as leaf mass per area (LMA), vein length per area (VLA, also known as leaf vein density) and wood density (WD), influence photosynthetic performance and/or growth (Blonder et al., 2011; Fajardo et al., 2023; Sack &

Frole, 2006). For instance, higher LMA and WD are often associated with resource-conservative strategies, which may increase drought resistance but limit photosynthetic capacity and growth rates (Galbraith et al., 2013; Poorter et al., 2009). Conversely, traits associated with acquisitive strategies, such as low tissue density and high VLA, may promote faster resource use but increase vulnerability to stress (Blonder et al., 2013; Sack et al., 2013). Furthermore, the maximum rate of Rubisco carboxylation (V_{cmax}) and light-saturated photosynthesis (A_{sat}), which reflect the biochemical and diffusional capacities of leaves for CO_2 assimilation (photosynthetic performance), are both sensitive to the combination of environmental conditions and physiological traits. For instance, water limitation typically reduces stomatal conductance, lowering A_{sat}, while N availability enhances V_{cmax} via its role in protein synthesis and Rubisco activity (Rogers, 2014; Smith et al., 2019).

While many studies have examined the effect of soil resources availability on plant functional traits and biomass growth in the Amazon (Powell et al., 2017; Quesada et al., 2012; Ribeiro-Junior et al., 2023), they have often overlooked the spatial complexity of hydro-edaphic gradients and the possibility of environmental compensation. For instance, shallow WT forests may offer high soil moisture but low nutrient availability (N, and eventually P), raising the question of whether soil moisture is sufficient to sustain photosynthetic rates during stressful conditions such as droughts, or whether nutrient limitation offsets these potential benefits. Even the long-held understanding that soil N does not limit production in tropical forests needs to be re-examined, given its large regional (Nardoto et al., 2008) and landscape scale variation (Luizão et al., 2004). Thus, the novelty of this study lies in exploring how local variation in soil moisture and nutrient availability (hydro-edaphic gradient) relates to inter- and intra-specific variation in leaf and wood structural traits, photosynthetic performance, and stem growth rates of abundant tree species in a central Amazonian forest. This approach also allows us to evaluate whether patterns of trait selection and growth modulation are phylogenetically consistent or plastic within species. By integrating inter- and intra-specific analyses along fine-scale environmental gradients, our study provides novel insights into how trait–environment interactions influence forest functioning and resilience in a changing climate.

Using extensive field data on soil properties, species distribution, leaf and wood structural traits, leaf-level gas exchange measurements, and stem growth rates for 23 dominant species of a central-Amazonian forest, we address the following research question: How does species' affiliation to soil moisture and nutrient availability relate to differences in structural and physiological traits, and how these factors jointly modulate photosynthetic and growth performance? (Figure 1). We hypothesize that affiliation to environments with greater soil moisture (no water limitation) establishes plants with more acquisitive traits, and the combination of these factors promotes higher photosynthetic and growth performance.

Thus, we expect that in shallow WT forests, trees will show a reduced investment in dense tissues to conserve and transport water (lower VLA, LMA, WD), linked to an increased investment in photosynthetic tissues, finally enhancing CO_2 assimilation and growth. Alternatively, photosynthetic performance is mainly driven by soil N levels, through increased capacity for producing Rubisco, increasing V_{cmax} and then growth, especially in deep WT forests where soil N tend to be more abundant.

2. Materials and Methods

Study site

All the data used for this study were collected at the Reserva Florestal Ducke (RFD), a 10,000 ha (10 km x 10 km) terra-firme tropical rainforest located 26 km northwest of Manaus (02º55′S, 59º58′W) in the central Amazon basin. The vegetation is old-growth dense lowland evergreen forest, with high diversity of tree species (> 1200 sp, Ribeiro et al., 1999) and a closed canopy ranging from 30–37 m, with emergent trees reaching 40-45 m (Guillaumet, 1987). This forest experiences an 'Am' tropical climate according to Köppen–Geiger classification, with dry (typically from July to September) and rainy seasons governed by monsoons (Peel et al., 2007). Over the past 58 years (1966–2023), the mean (± SD) annual rainfall at the RFD was 2,568 ± 363 mm, with a positive trend of 4.3 mm yr^{-1} (Fig. S1).

The Brazilian Long-Term Ecological Program maintain at RFD a set of 72 permanent plots systematically distributed over a 64-km^2 grid formed by 8 km long trails (Costa & Magnusson, 2010). Each plot is at least 1 km away from any other. Plots are 250 m × 40 m (1 ha) and are positioned to follow the topographic isoclines and thus minimize altitude and soil variation within each plot.

Environmental properties

The RFD has a dense drainage network (Ribeiro et al., 1999) along with an undulating topography, with elevation varying from 40 to 140 m above sea level and highly correlated with soil texture (Chauvel et al., 1987). Local variation in soil hydrological conditions along the topography is strongly driven by the WT depth. Here we use the metric HAND (Height Above the Nearest Drainage, in meters) as a proxy for the vertical distance from any point on the terrain to the WT (Nobre et al., 2011). Higher HAND values correspond to deeper WT levels, i.e., less access to deep soil moisture (plateau environments). HAND values for each RFD plot were calculated by Schietti et al. (2013), using the HAND algorithm (Renno et

al., 2008) based on SRTM digital elevation model (90 m of spatial resolution) with a minimum drainage contribution area of 30 pixels (0.41 km^2).

Soils in the RFD are typically acidic, low in phosphorus, calcium and potassium, and often high in aluminum (Chauvel et al., 1987). We used total soil nitrogen (soil N) and soil available phosphorus (soil P) as proxies for soil nutrient availability. Soil N and soil P were obtained for each of the 72 plots following Donagema et al. (2011), based on a composite sample made from six topsoil cores (0-5cm) taken every 50 m along the centerline of each plot (Castilho et al., 2006; Mertens, 2004). Soil N was determined by wet oxidation (Kjeldahl method), converting organic N to ammonium (NH_4^+), expressed as percentage by mass (mass %). Soil P was obtained by the ammonium molybdate–ascorbic acid method (Murphy & Riley, 1962), expressed by mg per kg of soil (mg kg^{-1}).

Across the 72 plots, HAND varies from 1.4 to 52.5 m, with a mean ± SD of 21.8 ± 14.4 m, soil N (mass %) from 0.03 to 0.36, with a mean ± SD of 0.18 ± 0.08, and soil P (mg kg^{-1}) from 0.7 to 10.8, with a mean ± SD of 3.2 ± 2.2. Variation in soil WT depth and soil N, along with soil texture, stablishes a fine-scale hydro-edaphic gradient, from clayey latosols with deeper WT and greater soil N on the uplands (plateaus), to sandy podzols with shallow WT, some with seasonally waterlogging and patches permanently waterlogged, in the lowest parts (valleys). Soil P is not coupled with any other soil variable across the plots (Fig. S2), although soil P levels can increase in shallow WT areas during seasonal waterlogging (Checa-Cordoba et al., 2024; Patrick & Mahapatra, 1968). Overall, the RFD is representative of climate, soil type and WT depth of *c*. 30% of Amazonian forests, based on maps from Fan & Miguez-Macho (2010); Malhi et al., (2015); Miguez-Macho & Fan (2012a, b); Quesada et al., (2011), and Restrepo-Coupe et al., (2013).

Species selection

We selected 23 dominant tree species from 20 genera and 13 families (Table S1), based on DBH and taxonomic data from previous censuses in all 72 plots. We selected the most representative species in terms of abundance (number of individuals) and basal area, based on all trees with DBH ≥ 10cm. Our selection included species strongly affiliated to each extreme of the hydro-edaphic gradient ("specialists") and species widely distributed along the gradient ("generalists") (Fig. S3). Individuals of generalist species were sampled on each extreme of the hydro-edaphic gradient, providing data for the intra-specific analysis. Collectively, these 23 species represent 18% of the individuals and 20% of total basal area across >1000 species at the RFD plots, with 14 of them belonging to the 227 hyper dominant Amazonian tree species (ter Steege et al., 2013).

Species affiliation to soil moisture and nutrient availability

To characterize the affiliation of tree species to soil moisture and nutrient availability, we calculated weighted mean values at the species level in terms of HAND, soil P and soil N. Using data of tree population distribution (DBH ≥ 10cm) across the 72 plots, we weighed the values of HAND, soil P and soil N of each plot ($plot_i$) by the species abundance in each plot (a_i) and then divided by the total species abundance across all plots (a_t), as shown in the following example equation for HAND:

$$\text{Species HAND affiliation} = \frac{\sum_{i=1}^{n} \cdot ((plot\ HAND)_i * a_i)}{a_t}$$

Species with higher HAND affiliation values are mostly concentrated on areas with deeper WT ("plateau specialists"), while lower values denote species mostly concentrated in shallow WT areas ("valley specialists"). Due to their broad spatial distribution, generalist species tend to have intermediate HAND values. The same logic was applied to soil nutrients: species mostly distributed on soils with greater P or N availability are those with higher Species soil P and Species soil N values, respectively.

Photosynthetic data

Photosynthetic data were collected in campaigns conducted between 2021-2023, during the dry season (August-September) or in the dry-to-wet transition (October-November). Using an open gas exchange system (LI-6400XT, LI-COR, Lincoln, NE, USA). We initially measured 366 individuals representing 28 dominant species. After excluding 102 individuals due to chamber fan malfunction or low stomatal conductance (g_{sw} < 0.05 mol m^{-2} s^{-1}), the final dataset included 264 individuals from 23 species (Table S1). On average, 11 individuals per species were measured (range 5-24, Table S1). For generalist species, sampling was balanced across valleys and plateaus; for specialists, individuals were sampled only in their preferred environment. Due to logistical constraints related to the measurements of canopy leaves of tall trees, we focused the gas exchange measurements on understory trees ranging from 1.5 m to 4.5 m of height. Measurements were made in situ on attached branches, using a tripod. This avoided conductance loss associated with cut branches.

Gas exchange was measured on two fully developed, visibly healthy and mature leaves per tree, from a branch in the upper part of each individual tree canopy. Leaves were measured in a 6 cm^2 chamber at 31°C leaf temperature, 400 ppm sample CO_2 concentration, light intensity (photosynthetic photon flux

density, PPFD) of 1000 µmol m^{-2} s^{-1}, and maintaining 50-60% relative humidity, flow of 400 µmol s^{-1}, and leaf VPD below 2 kPa.

We used the parameters V_{cmax} (the maximum carboxylation capacity of Rubisco, in µmol m^{-2} s^{-1}) and A_{sat} (the rate of CO_2 assimilation at light saturation, in µmol m^{-2} s^{-1}) to represent the species photosynthetic capacity and performance, respectively. A_{sat} was collected at least five minutes after setting the leaf into the LI-6400XT chamber to ensure leaf gas exchange stabilization, i.e., when stable levels of internal CO_2 concentration, assimilation, stomatal conductance, transpiration, leaf temperature and relative humidity were reached. To test if 1000 µmol m^{-2} s^{-1} PPFD of light intensity indeed represents light saturation for the leaves of these species, for a subset of 97 individuals (4 to 5 trees per species) we collected an A_{sat} point using 2000 µmol m^{-2} s^{-1} PPFD after the measurement with 1000 µmol m^{-2} s^{-1} PPFD. A_{sat} values were not significantly different between light intensities (Fig. S4), indicating that 1000 µmol m^{-2} s^{-1} PPFD achieves light saturation for the 23 species studied here.

Aiming to increase our sampling representativity of V_{cmax}, we first assessed the performance of the one-point method, a more rapid measurement than traditional A-C_i curves (De Kauwe et al., 2016). While the A-C_i curve method is considered the gold standard for estimating V_{cmax} due to its comprehensive nature, it is also time-consuming. The one-point method models V_{cmax} from a single-point measurement of photosynthesis (A_{sat}) based on well-defined key parameters (Bernacchi et al., 2001; Long & Bernacchi, 2003). We compared V_{cmax} values obtained through the adjustment of a subset of 48 complete A-C_i curves (26 in valleys and 22 in plateaus), based on the Farquhar model, using the R package *plantecophys* (Duursma, 2015), with V_{cmax} estimates using the one-point method from the same sampled leaves (following the equation 3 in De Kauwe et al., 2016). We found strong correlations (R = 0.97) among the 48 individuals and for both plateau and valley environments (Fig. S5); thus, our test confirmed the appropriate use of the one-point method to estimate V_{cmax} values for these 23 abundant species along the hydro-edaphic gradient in the RFD. Both the A_{sat} and V_{cmax} values for each individual tree were the average of the two measured leaves. For each species, both parameters were calculated as the mean value of all their measured individuals.

To consider the potential influence of physiological traits on photosynthetic and stem growth performance, mean values of stomatal conductance (g_{sw}, mol m^{-2} s^{-1}), transpiration (E, mmol H_2O m^{-2} s^{-1}), and intrinsic water use efficiency ($WUE_i = A_{sat}/g_{sw}$, µmol CO_2 / mol H_2O) for each species, from the final dataset of 264 individual trees, were also calculated.

Leaf and wood structural traits

Following gas exchange measurements, the same two leaves per individual tree were processed to obtain leaf structural traits in 160 out of the 264 individuals. On average, seven individuals were measured per species (range 5-17, Table S1). The averages over the two leaves (or all the repetitions within these two leaves) per tree were used in all subsequent analyses. Leaf thickness (LT, mm) was measured with a micrometer of 0.001 mm precision at three leaf positions (base, middle, and upper), avoiding main and secondary veins. Leaf area (LA, cm^2) was measured without petiole using a leaf area meter (CI-202 Portable Leaf Area Meter, CID-BioScience). After drying the leaves at 60°C for 24 hours, the dry mass was obtained. The leaf mass per unit area (LMA, g m^{-2}) was obtained by dividing the dry mass by fresh leaf area. The same process was performed for a 4 cm^2 piece of each leaf excluding the midrib, to obtain a LMA with a leaf mass not influenced by the large veins (LMA_o). Vein length per leaf area (VLA, mm cm^{-2}), also known as vein density, was calculated dividing the sum of vein lengths by the leaf area. VLA was measured in squares of 1 cm cut in the middle region of the lamina of fresh leaves, also excluding the midrib. Leaf pieces were diaphanized and colored in 1% safranin, following a protocol adapted from Gardner (1975), and then, using a digital camera coupled to a magnifying glass, 2 to 4 images per sample were taken at a magnification of 40x, to be analyzed in the Leaf Extraction and Analysis Framework Graphical User Interface (LEAF GUI software tool, Price et al., 2011).

Moreover, we estimated branch wood density (WD, g cm^{-3}) for each tree, using a 5-cm-long wood sample taken from the base of the same branch used for leaf measurements. After bark removal, wood samples were immersed in water for 24 hours for saturation. The fresh volume was obtained using the water displacement method, by measuring the mass of the displaced water using a precision balance (0.001 g). The wood dry mass was determined after drying the samples in an oven at 105°C for 72 hours, utilizing the same balance. Then, the WD for each tree was calculated as the dry mass divided by the fresh volume of its wood sample. Finally, the average values of LT, LA, LMA, LMA_0, VLA, and WD for all individuals belonging to each species were used to represent the species' leaf and wood structural traits.

Growth performance

We used annual stem diameter growth rates (GR_{stem}) to represent growth performance across species. GR_{stem} were obtained using tree diameter data collected in four censuses along 21 plots of the RFD, in 2002, 2004, 2007 and 2014, with 12 plots being areas with shallow WT (valleys) and 9 plots with deep WT (plateaus). Within plots, tree DBH were measured with a fabric diameter tape (Forestry Suppliers, model 283D) following the RAINFOR protocol (Phillips et al., 2010). GR_{stem} was first calculated at the

individual level, for all trees belonging to the 23 species along the plots. GR_{stem} were calculated as annual inherent growth rates (in cm cm^{-1} yr^{-1}), following Lamont et al. (2023). To align with the size of individual trees measured for gas exchange, GR_{stem} values were calculated on individuals with a DBH < 10 cm (small, mostly understory trees). GR_{stem} values with ±2 standard deviations from the mean were considered extreme values and excluded from the analysis. Then, GR_{stem} of a species was the average of the GR_{stem} values of all its individuals. To assess potential differences of GR_{stem} values due to tree size, we calculated GR_{stem} also for big trees (DBH ≥ 10 cm) and for the whole population (all DBH). GR_{stem} values among different tree sizes were significantly correlated (Fig. S6).

To assess potential biases on our results due to tree size, statistical analyses (described below) were conducted using GR_{stem} calculated from small trees, big trees and the whole population. Although effect sizes (slopes) varied depending on the GR_{stem} used, the significance and main effects remained consistent, thus supporting the interpretation of our results based on GR_{stem} from small, understory trees.

Statistical analysis

Data analyses and visualization were performed in the R statistical software package (R Core Team, 2025), version 4.5.2. Regression analyses were conducted to evaluate the effect of resources affiliation on structural and physiological traits, with species HAND, soil N and soil P as predictor variables, and values of LT, LMA, LMA_0, VLA, WD, g_{sw}, E and WUE_i as response variables. To assess how the resources affiliation relates to the photosynthetic and growth performance across species, regression analyses were also conducted, with species HAND, soil N and soil P as predictors, and V_{cmax}, A_{sat} and GR_{stem} as response variables.

To analyze the interplay of factors as stated in our conceptual model (Fig. 1), we used piecewise structural equation modeling (pSEM). This method allows us to test diverse model structures, including different distributions and assumptions on the response variables (Liefcheck, 2016). We started the pSEM with the structure of our conceptual model, considering all variables, and then iteratively removed paths with non-significant effects until obtaining the model structure of effects that best fits our data, based on the P-value, AIC criteria and the variance explained by predictors. To indicate if any missing path should be incorporated, confirmatory path analyses were conducted based on the directional separation test (*d*-separation test, Shipley, 2013). This test assesses whether two variables that are predicted to be independent (separated) in the model are, in fact, statistically independent in the observed data, thereby checking the model's structural validity. pSEM was constructed using linear regression models using the

piecewiseSEM package (Liefcheck, 2016), reporting the variance explained by predictors (R^2) for each response variable, and the relative contribution (standard estimate) of significant predictors for the final model that exhibited the best fit to our data.

To assess intra-specific variation in functional traits and performance across contrasting hydro-edaphic conditions, we performed paired t-tests for the 14 generalist species (Table S1). For each species, mean values of structural and physiological traits, and parameters of photosynthetic and growth performance, were compared between individuals growing in shallow versus deep WT environments.

Results

Relationship between soil resources affiliation and plant functional traits

Across the 23 dominant tree species, values of species affiliation to soil moisture (HAND values, in m) varies from 4.2 to 33.2, with a mean ± SD of 19 ± 7.4, affiliation to N_{soil} (mass %) from 0.08 to 0.22, with a mean ± SD of 0.17 ± 0.03, and affiliation to P_{soil} (mg kg^{-1}) from 2.9 to 4.5, with a mean ± SD of 3.7 ± 0.2. The species affiliation to soil moisture is strongly positively correlated with the affiliation to N_{soil}. The affiliation to P_{soil} is not related to soil moisture nor to N_{soil} (Fig. S7). The affiliation to soil moisture - and thus, to N_{soil} - relates to some structural and physiological traits, with species affiliated to lower soil moisture and higher soil N (i.e., growing in deeper WT areas) exhibiting denser leaf venation (higher VLA), denser woods (higher WD), greater leaf mass per unit area (LMA_o) and lower stomatal conductance (g_{sw}) (Fig. 2). By contrast, the species affiliation to P_{soil} is not significantly related to any structural or physiological trait.

Differential effects of soil resources on photosynthetic and growth performance

Species affiliation to soil resources relates to photosynthetic and growth performance. The maximum carboxylation rate (V_{cmax}) is significantly related to soil moisture and soil N, with species affiliated to lower soil moisture and higher N_{soil} exhibiting higher V_{cmax}. Affiliation to soil moisture and N is not a significant predictor of species growth performance (GR_{stem}), but rather GR_{stem} significantly increases along the P_{soil} affiliation gradient (Fig. 3). Yet, the CO_2 assimilation rate at light saturation (A_{sat}) do not show significant relationship with any species-resource affiliation (Fig. S8).

Integrated effects of resources affiliation and traits on photosynthetic and growth performance

Our p-SEM results (Fig. 4 and Table S2) show the direct effects of species resource affiliation on trait selection (first tier) and species performance (arrows from first to last tier), the direct consequences of trait selection to the performance (second tier) and the indirect consequences (pathways through the tiers). The affiliation to deeper WT (lower soil moisture and higher N availability) positively affects leaf vein density (VLA) and LMA_o, with both structural traits positively affecting V_{cmax}. Thus, there is an indirect positive effect of HAND and soil N affiliation on V_{cmax}. The species affiliation to higher soil moisture (lower HAND) and richer-P soil both positively affect stomatal conductance (g_{sw}), while greater g_{sw} and V_{cmax} both increase A_{sat}. Therefore, there is an indirect positive effect of the species affiliation to soil P on A_{sat}. Moreover, higher A_{sat} and the species affiliation to richer-P soil led to higher GR_{stem}. The affiliation to deeper WT positively affects WD, which in turn negatively relates to GR_{stem}. Finally, parameters of photosynthetic performance and stem growth are significantly related across species, with V_{cmax} positively affecting A_{sat} and higher A_{sat} leading to higher GR_{stem}. No significant relationship between V_{cmax} and GR_{stem} was observed, species with the lowest and the highest V_{cmax} values exhibiting similar GR_{stem} (Fig. S9).

Intra-specific variation in traits and performance among hydro-edaphic environments

Across the 14 generalist species, structural and physiological traits, as well as parameters of photosynthetic and growth performance, exhibit intra-specific variation among contrasting hydro-edaphic environments (Fig. 5). LMA_o, VLA, WD and V_{cmax} are significantly higher for trees located in soils with lower moisture and higher N (i.e., deep WT areas). By contrast, g_{sw} is significantly higher in individuals established in shallow WT areas. Furthermore, there is no significant overall difference in A_{sat} among contrasting hydro-edaphic conditions across the 14 generalist species, as nine species exhibit higher A_{sat} values for individuals located on deep WT, while five species show greater A_{sat} on individuals growing in shallow WT areas. Similarly, GR_{stem} do not exhibit a consistent intra-specific response among environments, with six species having higher growth rates for individuals located on deeper WT, while eight species showing greater GR_{stem} on individuals growing in shallow WT.

Discussion

Our study reveals that fine-scale variation in soil moisture (WT depth) and nutrient availability strongly shapes the structural and physiological strategies and the photosynthetic and growth performance of

dominant Amazonian tree species. Species affiliated to deep WT areas (i.e., soils of lower moisture and higher N) exhibit denser leaves and woods and greater photosynthetic capacity (V_{cmax}), while species in shallow WT (higher moisture and lower N) show higher stomatal conductance but lower biochemical capacity. Surprisingly, phosphorus availability—not nitrogen or soil moisture—is the strongest predictor of growth performance (GR_{stem}), exerting a direct effect on stomatal conductance (g_{sw}) and indirectly enhancing leaf-level carbon assimilation (A_{sat}). The structural equation modeling shows that species' growth performance is not directly linked to biochemical capacity. Instead, it emerges from the coordinated interplay between species-specific functional traits and their environmental resource niches. Despite marked inter- and intra-specific variation in structural and physiological traits, species maintained consistent photosynthetic and growth performance across contrasting environments, suggesting that diverse trait coordination strategies enable functional convergence along soil hydrological gradients (Fig. 6).

Hydro-edaphic niche filtering plays a central role in shaping functional strategies and the photosynthetic and growth performance of dominant Amazonian tree species. Across a hydro-edaphic gradient in a central Amazonian forest, we found that species' affiliation to WT depth and soil nutrient availability modulates their structural and physiological traits, photosynthetic performance, and ultimately, growth. These results demonstrate that functional diversity and forest productivity are underpinned by fine-scale environmental heterogeneity and differential trait responses across resource gradients (Engelbrecht et al., 2007; Fine et al., 2004; Fortunel et al., 2012; Fyllas et al., 2009).

Species affiliated to areas with lower soil moisture and higher N exhibit combinations of higher leaf mass per area, greater leaf vein density and denser woods, considered conservative traits in the functional literature, allowing increased tissue longevity and hydraulic safety (Poorter et al., 2008; Sterck et al., 2011; Wright et al., 2004). Conservative traits would not be expected under high soil nutrient availability, which is typically associated with lower tissue density and more acquisitive plant strategies (Reich, 2014). Yet, leaves of trees growing on deep WT areas with N-richer soils (plateaus) were shown to have higher N concentrations than leaves of trees on valleys (da Silva et al., 2025), irrespective of their LMA (Luizão et al., 2004). This pattern likely reflects the combination of contrasting pressures: seasonal dry conditions forcing the selection of denser, structurally conservative, more hydraulically resistant tissues on plateaus, and the competition of young trees for light leading to biochemically active strategies, forcing the incorporation of nitrogen to grow taller as fast as possible, thus establishing a trade-off between longevity and enzyme investment.

We found trees in deep WT areas having higher photosynthetic capacity (V_{cmax}) than those in shallow WT areas. The elevated V_{cmax} in these N-enriched environments suggest enhanced investment in

photosynthetic enzymes such as Rubisco, consistent with the role of N in biochemical photosynthetic efficiency (Evans, 1989; Reich et al., 2009; Wright et al., 2004). In contrast, species affiliated to shallow WT areas, characterized by higher soil moisture, exhibit higher stomatal conductance that increases light-saturated photosynthesis (A_{sat}), despite lower V_{cmax}. Greater g_{sw} promoting CO_2 uptake even when biochemical capacity is constrained may be reflecting an adaptation of trees to nutrient-poor but hydrologically stable conditions (Goldsmith et al., 2012; Santiago et al., 2004). These findings further imply physiological compensation both across hydro-edaphic gradients, and between diffusional and biochemical limitations to CO_2 assimilation (Flexas et al., 2008; Medlyn et al., 2002).

Our structural equation modeling reveals distinct but complementary roles of soil moisture and nutrients in shaping tree photosynthetic and growth performance. Affiliation to N-richer soils is related with higher LMA_o and, indirectly, with higher V_{cmax}. Soil P affiliation has no effect on structural traits but emerges as a key predictor of GR_{stem}, with species affiliated to P-richer soils having higher growth performance. Soil P also exerts a direct positive effect on $g_{sw,}$ which may be linked to ATP generation for the K^+ pump activity that facilitates potassium influx into guard cells (Kayoumu et al., 2023; Sirichandra et al., 2009), and an indirect effect on A_{sat}, highlighting its critical role in metabolic energy supply and carbon assimilation (Reich & Schoettle, 1988; Vitousek, 1984; Walker et al., 2014).

No direct relationship between V_{cmax} and GR_{stem} is observed, indicating that leaf photosynthetic capacity alone is insufficient to predict tree growth performance. This decoupling may be explained by the multiple fates of the carbon fixed by Rubisco, which V_{cmax} represents: a considerable portion of carbon may be allocated to organs other than the stem—such as roots or leaves— thus, aboveground growth can become unlinked from carbon assimilation (Cabon et al., 2025; Körner, 2015). In addition, despite clear structural and physiological differentiation across hydrological environments, neither A_{sat} nor GR_{stem} varies significantly among species or individuals, which may reflect functional convergence and compensation in photosynthetic and growth performance along the hydro-edaphic gradient (Díaz et al., 2004; Marks & Lechowicz, 2006; Wright et al. 2003). Yet, the respiratory costs associated with higher photosynthetic capacity must also be considered. High V_{cmax} typically coincides with increased leaf N content and protein turnover, both increasing respiratory demand (Atkin et al., 2015; Heskel et al., 2016). In fact, trees in deep WT areas exhibit higher V_{cmax} but also significantly higher maintenance respiration rates (Fig. S10), which may offset potential carbon gain and lead to the observed similar performance across environments (Wright et al., 2003). These findings suggest that trees in deep WT areas allocate a greater fraction of carbon to maintenance metabolism, while those in shallow WT exhibit higher g_{sw} and potentially greater carbon gain per unit of respiratory cost.

Many generalist species exhibit intraspecific trait adjustments that mirror interspecific trends: individuals established in deep WT areas have higher LMA_o, VLA, WD, and V_{cmax}, while those in shallow WT areas exhibit higher g_{sw}. Yet, A_{sat} and GR_{stem} do not vary consistently with environment, underscoring the ability of these dominant species to maintain similar photosynthetic and growth performance via alternative trait–environment combinations (Worthy et al., 2020). This trait plasticity reveals a key mechanism of ecosystem resilience: by adjusting structural and physiological attributes to local conditions, generalist species can buffer productivity against spatial heterogeneity in soil moisture and nutrient availability (Anderegg et al., 2018; Fyllas et al., 2020; Valladares et al., 2007).

Our results suggest that limited soil N availability may be a more widespread constraint on tree productivity than previously recognized (Laurance et al., 1999), particularly in shallow WT forests with old-leached sandy soils (Hedin et al., 2009; Townsend et al., 2007). While greater soil P enhances g_{sw} and CO_2 assimilation, higher soil N at drier sites is associated with higher photosynthetic capacities. We show that soil N availability -strongly associated with deep WT areas in the geologically old Guiana shield- is a key factor shaping leaf traits and physiology, despite soil P availability remaining a central driver of tree growth. This contrasts to the long-held view that Amazon forest productivity is predominantly P-limited, and we suggest that the resilience of Amazonian forests to climate change may depend not only on soil P availability but also on local moisture and soil N dynamics, together with the ability of species to adjust their traits to fine-scale environmental gradients.

Broader implications

These findings have important implications for modeling forest productivity and responses to climate change. First, we highlight the need to incorporate hydro-edaphic heterogeneity and local trait–environment interactions into Earth system models (Cabon et al., 2025; Fisher et al., 2019; Sakschewski et al., 2016). Amazonian forests comprise a great variety of tree species and strategies shaped by local water and nutrient availability. Accounting for the effect of fine-scale variations, such as the observed local soil moisture and N modulation on tree performance, may further improve our knowledge of how Amazonian forests respond to ongoing climate change and future hypertropical climate (Chambers et al., 2025). Second, the observed V_{cmax}-GR_{stem} decoupling challenges the common assumption that photosynthetic capacity scales directly with tree productivity, suggesting the need of considering individual-level structural and physiological constraints, particularly those related to hydraulic safety and carbon allocation (Christoffersen et al., 2016; Falster et al., 2011).

Based on young trees confined to the understory stratum (1.5–3 m tall), our study highlights the importance of considering vertical stratification and microenvironmental variability when interpreting photosynthetic capacity across soil hydrological gradients. Higher V_{cmax} in trees growing in deep WT areas, despite lower soil moisture and higher LMA, was unexpected and suggests a complex interplay between light availability, leaf construction costs, and physiological investment in carbon assimilation. Even though understory trees contribute a relative small fraction to total forest GPP — typically around 5–25% depending on forest structure and disturbance history (Bonal et al., 2000; Clark & Clark, 2000; Meir et al., 2002) — their role cannot be neglected, particularly in Amazonian forests along the Guiana shield, where dense and physiologically active understories may represent the upper end of this spectrum (Nascimento & Laurance, 2004; Oliveira et al., 2017). Thus, ecosystem and carbon models should explicitly account for trait differences across hydro-edaphic gradients and forest strata (understory vs. canopy) when upscaling photosynthetic function and vegetation productivity (Bonan et al., 2012; Fisher et al., 2018; Rogers et al., 2017).

Conclusion

This study highlights the central role of environmental filtering in shaping tree functional strategies, as well as the interplay between species resource affiliations and functional traits in modulating photosynthetic and growth performance. Overall, our findings show that dominant Amazonian tree species, which form the ecological backbone of the forest, exhibit high functional plasticity and strong trait integration, allowing them to maintain comparable photosynthetic and growth performance across heterogeneous hydro-edaphic conditions. Accounting for such resource–performance relationships and functional heterogeneity is critical for improving predictions of Amazon forest responses to climate change.

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Author contributions.

EJLE and FRCC conceived the study. EJLE conducted field work and collected data with MNG supervision. EJLE, LPA, MNG and FRCC designed the analysis. EJLE analyzed the data and drafted the manuscript with critical contributions from LPA, MNG and FRCC. All authors contributed to the article and gave final approval for publication.

Competing interests.

The authors declare that they have no conflict of interest.

References

- Anderegg, W.R.L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A.F.A., Choat, B., & Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences*, 113(18), 5024–5029. https://doi.org/10.1073/pnas.1525678113
- Atkin, O. K., Bloomfield, K. J., Reich, P. B., Tjoelker, M. G., Asner, G. P., Bonal, D., Bönisch, G., Bradford, M. G., Cernusak, L. A., Cosio, E. G., Creek, D., Crous, K. Y., Domingues, T. F., Dukes, J. S., Egerton, J. J. G., Evans, J. R., Farquhar, G. D., Gauthier, P. P. G., Gentine, P., ... & Zaragoza-Castells, J. (2015). Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. *New Phytologist*, 206(2), 614–636. https://doi.org/10.1111/nph.13253
- Baraloto, C., Paine, C.E.T., Patino, S., Bonal, D., Hérault, B., & Chave, J. (2010). Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology*, 24(1), 208–216. https://doi.org/10.1111/j.1365-2435.2009.01600.x
- Blonder, B., Violle, C., Bentley, L. P., & Enquist, B. J. (2013). Venation networks and the origin of the leaf economics spectrum. Ecology Letters, 16(2), 203–211.

- Blonder, B., Violle, C., Patrick, L., & Enquist, B. J. (2011). The leaf-height-seed plant strategy spectrum. Ecology Letters, 14(2), 127–136.
- Bloom, A.J., Chapin, F.S., & Mooney, H.A. (1985). Resource limitation in plants—an economic analogy. *Annual Review of Ecology and Systematics*, 16, 363–392. https://doi.org/10.1146/annurev.es.16.110185.002051
- Bonal, D., Sabatier, D., Montpied, P., Tremeaux, D., & Guehl, J. M. (2000). Interspecific variability of δ13C among trees in rainforests of French Guiana: Functional groups and canopy integration. *Oecologia*, 124(3), 454–468. https://doi.org/10.1007/s004420000399
- Bonan, G. B., Williams, M., Fisher, R. A., & Oleson, K. W. (2012). Modeling stomatal conductance in the earth system: Linking leaf water-use efficiency and water transport along the soil–plant–atmosphere continuum. *Geoscientific Model Development*, 7(6), 2193–2222. https://doi.org/10.5194/gmd-7-2193-2014
- Boulton, C. A., Lenton, T. M., & Boers, N. (2022). Pronounced loss of Amazon rainforest resilience since the early 2000s. *Nature Climate Change.*
- Briant, G., Gond, V., & Laurance, W.F. (2010). Habitat fragmentation and the desiccation of forest canopies: A case study from eastern Amazonia. *Biological Conservation*, 143(11), 2763–2769. https://doi.org/10.1016/j.biocon.2010.07.024
- Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., et al. (2015). Long-term decline of the Amazon carbon sink. Nature, 519(7543), 344–348.
- Caleño-Ruiz BL, Garzón F, López-Camacho R, Pizano C, Salinas V, González-MR. 2023. Soil resources and functional trait trade-offs determine species biomass stocks and productivity in a tropical dry forest. Frontiers in Forests and Global Change 6: 1028359. https://doi.org/10.3389/ffgc.2023.1028359
- Castilho et al. (2006) - Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography.
- Clark, D. A., & Clark, D. B. (2000). Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management*, 137(1–3), 185–198. https://doi.org/10.1016/S0378-1127(99)00327-8
- Costa, F. R. C., Leite, M. F. A., Schietti, J., et al. (2024). Topography, hydrology, and forest function in the Amazon. Trends in Ecology & Evolution. [In press or preprint].
- Costa, F. R. C., Magnusson, W. E., & Luizão, R. C. C. (2005). Mesoscale distribution patterns of Amazonian understory herbs in relation to topography, soil and watersheds. Journal of Ecology, 93(5), 863–878.

- Craine, J.M. (2009). *Resource strategies of wild plants*. Princeton University Press. https://doi.org/10.1515/9781400831522
- Donagema GK, de Campos DVB, Calderano SB, Teixeira WG, Viana JHM (2011) Manual de Métodos De Análises De Solo. Empresa Brasileira De Pesquisa Agropecuária. Embrapa Solos, Rio de Janeiro
- Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447: 80–82.
- Esteban, E. J. L., Castilho, C. V., Melgaço, K. L., & Costa, F. R. C. (2021). The other side of droughts: Wet extremes and topography as buffers of negative drought effects in an Amazonian forest. New Phytologist, 229(4), 1995–2006.
- Evans, J. R., & Poorter, H. (2001). Photosynthetic acclimation of plants to growth irradiance: The relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant, Cell & Environment*, 24(8), 755–767. https://doi.org/10.1046/j.1365-3040.2001.00724.x
- Fajardo, A., Martínez-Vilalta, J., Lutz, J. A., et al. (2023). Conservatism of plant structural traits across elevation, climate, and phylogeny in temperate and tropical forests. Functional Ecology, 37(1), 157–169.
- Fernanda V. Costa et al. (2015) - Synthesis of the first 10 years of long-term ecological research in Amazonian Forest ecosystem – implications for conservation and management:
- Figueiredo, F. O. G., Zuquim, G., Tuomisto, H., et al. (2018). Beyond climate control on species range: The importance of soil data to predict distribution of Amazonian plant species. Journal of Biogeography, 45(1), 190–200.
- Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C., Farrior, C. E., Holm, J. A., Hurtt, G. C., Knox, R. G., Lawrence, P. J., Lichstein, J. W., Longo, M., Matheny, A. M., Medvigy, D., Muller-Landau, H. C., Powell, T. L., Serbin, S. P., Sato, H., Shuman, J. K., ... & Moorcroft, P. R. (2018). Vegetation demographics in Earth System Models: A review of progress and priorities. *Global Change Biology*, 24(1), 35–54. https://doi.org/10.1111/gcb.13910
- Fyllas, N. M., Quesada, C. A., Labrière, N., et al. (2009). Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. Biogeosciences, 6(11), 2677–2708.
- Fyllas, N.M., Patino, S., Baker, T.R., Bielefeld Nardoto, G., Martinelli, L.A., Quesada, C.A., Paiva, R., Schwarz, M., Mercardo, L.M., Santos, A., Arroyo, L., Jimenez, E.M., Luizão, F.J., Neill, D.A., Prieto, A., Silvério, D., Vieira, I.C.G., Terborgh, J., Lloyd, J., & Phillips, O.L. (2009). Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences*, 6(11), 2677–2708. https://doi.org/10.5194/bg-6-2677-2009

- Galbraith DR, Malhi Y, Affum-Baffoe K, Castilho CV, Doughty CE, Fisher RA, Johnson MO, Meir P, Moorcroft PR, Xu X. 2013. The influence of ecosystem composition and soil nutrients on tropical forest productivity. Environmental Research Letters 8: 044043. https://doi.org/10.1088/1748-9326/8/4/044043
- Galbraith, D. R., Malhi, Y., Affum-Baffoe, K., et al. (2013). Residence times of woody biomass in tropical forests. Plant Ecology & Diversity, 6(1), 139–157.
- Heskel, M. A., Atkin, O. K., Turnbull, M. H., Griffin, K. L., & Whitehead, D. (2016). Seasonality of foliar respiration in two dominant species in a temperate rainforest. *Functional Plant Biology*, 43(5), 468–476. https://doi.org/10.1071/FP15265
- Kitajima, K., Mulkey, S. S., & Wright, S. J. (2005). Variation in crown light utilization characteristics among tropical canopy trees. *Annals of Botany*, 95(3), 535–547. https://doi.org/10.1093/aob/mci052
- Lloyd, J., & Farquhar, G.D. (2008). Effects of rising temperatures and [CO_2] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1498), 1811–1817. https://doi.org/10.1098/rstb.2007.0032
- Luizão, F. J., Luizão, R. C. C., Paiva, R. Q., et al. (2004). Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. Global Change Biology, 10(5), 592–600.
- Malhi, Y., Doughty, C.E., Goldsmith, G.R., Metcalfe, D.B., Girardin, C.A.J., Marthews, T.R., del Aguila-Pasquel, J., Aragão, L.E.O.C., Araujo-Murakami, A., Brando, P., da Costa, A.C.L., Silva-Espejo, J.E., Farfan-Amezquita, F., Galbraith, D.R., Quesada, C.A., Salinas-Revilla, N., Silvério, D., Meir, P., & Phillips, O.L. (2015). The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology*, 21(6), 2283–2295. https://doi.org/10.1111/gcb.12859
- Malhi, Y., Gardner, T. A., Goldsmith, G. R., et al. (2014). Tropical forests in the Anthropocene. Annual Review of Environment and Resources, 39, 125–159.
- Malhi, Y., Roberts, J. T., Betts, R. A., et al. (2008). Climate change, deforestation, and the fate of the Amazon. Science, 319(5860), 169–172.
- Marengo JA, Espinoza JC. Extreme seasonal droughts and floods in Amazonia: causes, trends and impacts. International Journal of Climatology. 2016;36(3):1033-1050. doi:10.1002/joc.4420
- Markesteijn, L., Poorter, L., Paz, H., Sack, L., & Bongers, F. (2011). Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell & Environment*, 34(1), 137–148. https://doi.org/10.1111/j.1365-3040.2010.02231.x

- Meir, P., Grace, J., & Miranda, A. C. (2002). Photographic and micrometeorological methods for estimating leaf area index in a central Amazonian tropical rain forest. *Agricultural and Forest Meteorology*, 112(2), 79–83. https://doi.org/10.1016/S0168-1923(02)00041-5
- Mercado LM, Lloyd J, Dolman AJ, Sitch S, Patino S, Los SO, Malhi Y, Meir P, Phillips OL, Grace J. 2011. Variations in Amazon forest productivity correlated with seasonal changes in climate and soil moisture. Global Change Biology 17: 2283–2293. https://doi.org/10.1111/j.1365-2486.2011.02441.x
- Mercado, L. M., Huntingford, C., Gash, J. H. C., et al. (2009). Impact of changes in diffuse radiation on the global land carbon sink. Nature, 458(7241), 1014–1017.
- Mertens, J., 2004. The characterization of selected physical and chemical soil properties of the surface soil layer in the ‘‘Reserva Ducke’’, Manaus, Brazil, with emphasis on their spatial distribution. Bachelor Thesis. Humboldt-Universität Zu Berlin. Berlin.
- Moeslund JE, Arge L, Bøcher PK, Dalgaard T, Ejrnæs R, Odgaard MV, Svenning JC. 2013. Topographically controlled soil moisture drives plant diversity patterns within grasslands. Biodiversity and Conservation 22: 2151–2166.
- Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27, 31–36.
- Nascimento, H. E. M., & Laurance, W. F. (2004). Biomass dynamics in Amazonian forest fragments. *Ecological Applications*, 14(sp4), 127–138. https://doi.org/10.1890/01-6013
- Niinemets, Ü. (2001). Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, 82(2), 453–469. https://doi.org/10.1890/0012-9658(2001)082[0453:GSCCOL]2.0.CO;2
- Oliveira, A. A., Mori, S. A., Richter, W., & Smith, N. (2017). Tree diversity in central Amazonian terra firme forests. *Biodiversity and Conservation*, 26, 323–336. https://doi.org/10.1007/s10531-016-1236-3
- Onoda, Y., Wright, I. J., Evans, J. R., Hikosaka, K., Kitajima, K., Niinemets, Ü., Poorter, H., Tosens, T., & Westoby, M. (2017). Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytologist*, 214(4), 1447–1463. https://doi.org/10.1111/nph.14496
- Papastefanou P, Zang CS, Angelov Z, de Castro AA, Jimenez JC, De Rezende LFC, Ruscica RC, Sakschewski B, Sörensson AA, Thonicke K, Vera C, Viovy N, Von Randow C, Rammig A. Recent extreme drought events in the Amazon rainforest: assessment of different precipitation and evapotranspiration datasets and drought indicators. Biogeosciences. 2022;19(16):3843- 3861. doi:10.5194/bg-19-3843-2022.

- Phillips, O. L., Aragão, L. E. O. C., Lewis, S. L., et al. (2009). Drought sensitivity of the Amazon rainforest. Science, 323(5919), 1344–1347.
- Poorter, L., Bongers, F., Sterck, F. J., & Wöll, H. (2006). Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology*, 87(5), 1289–1301. https://doi.org/10.1890/0012-9658(2006)87[1289:AORFTS]2.0.CO;2
- Poorter, L., Wright, S. J., Paz, H., et al. (2009). Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. Ecology, 89(7), 1908–1920.
- Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G., Harms, K.E., Licona, J.C., Martínez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Peña-Claros, M., Webb, C.O., & Wright, I.J. (2010). Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology*, 91(7), 1908–1920. https://doi.org/10.1890/09-1537.1
- Powell, T. L., Wheeler, J. K., de Oliveira, A., et al. (2017). Differences in xylem and leaf hydraulic traits explain differences in drought tolerance among mature Amazon rainforest trees. Global Change Biology, 23(10), 4280–4293.
- Quesada, C. A., Phillips, O. L., Schwarz, M., et al. (2012). Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences, 9(6), 2203–2246.
- Quesada, C.A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T.R., Czimczik, C.I., Fyllas, N.M., Martinelli, L., Nardoto, G.B., Schmerler, J., Santos, A.J.B., Hodnett, M.G., Herrera, R., Luizão, F.J., Arneth, A., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., ... Phillips, O.L. (2010). Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences*, 7(5), 1515–1541. https://doi.org/10.5194/bg-7-1515-2010
- Reich (2014). The world-wide "fast–slow" plant economics spectrum: A traits manifesto. https://doi.org/10.1111/1365-2745.12211
- Reich, P.B., Ellsworth, D.S., & Walters, M.B. (1998). Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology*, 12(6), 948–958. https://doi.org/10.1046/j.1365-2435.1998.00274.x
- Reich, P.B., Walters, M.B., & Ellsworth, D.S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences*, 94(25), 13730–13734. https://doi.org/10.1073/pnas.94.25.13730
- Ribeiro-Júnior NG, Marimon BH Jr, Marimon BS, Cruz WJA, Silva IV, Galbraith DR, Gloor E, Phillips OL. 2023. Anatomical functional traits and hydraulic vulnerability of trees in different water conditions in southern Amazonia. American Journal of Botany e16146. https://doi.org/10.1002/ajb2.16146

- Ribeiro-Junior, M. A., de Oliveira, R. S., & Quesada, C. A. (2023). Soil resource gradients shape the hydraulic strategies of Amazonian trees. Functional Ecology, 37(2), 330–343.
- Rifai, S. W., Girardin, C. A. J., Malhi, Y., et al. (2018). ENSO drives interannual variation of forest woody growth across the Amazon basin. Proceedings of the National Academy of Sciences, 115(33), 8281–8286.
- Rogers A. 2014. The influence of environmental variables on leaf-level photosynthesis: Implications for predicting vegetation responses to climate change. New Phytologist 204: 318–324. https://doi.org/10.1111/nph.12852
- Rogers, A. (2014). The use and misuse of Vcmax in Earth System Models. Photosynthesis Research, 119(1–2), 15–29.
- Rogers, A., Serbin, S. P., Ely, K. S., & Wolfe, B. T. (2017). Terrestrial biosphere models underestimate photosynthetic capacity and productivity of tropical forests. *Nature Plants*, 3(8), 17063. https://doi.org/10.1038/nplants.2017.63
- Rozendaal, D. M. A., Hurtado, V. H., & Poorter, L. (2006). Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology*, 20(2), 207–216. https://doi.org/10.1111/j.1365-2435.2006.01105.x
- Sack, L., & Frole, K. (2006). Leaf structural diversity is related to hydraulic capacity in tropical rain forest trees. Ecology, 87(2), 483–491.
- Sack, L., Scoffoni, C., McKown, A. D., et al. (2013). How do leaf veins influence the worldwide leaf economic spectrum? Review and synthesis. Journal of Experimental Botany, 64(13), 4053–4080.
- Santiago, L.S., Wright, S.J., Harms, K.E., Yavitt, J.B., & Korine, C. (2004). Leaf functional traits of tropical forest plants in relation to soil and light availability. *Functional Ecology*, 18(6), 787–795. https://doi.org/10.1111/j.0269-8463.2004.00904.x
- Schietti, J., Emilio, T., Rennó, C. D., et al. (2014). Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. Plant Ecology & Diversity, 7(1–2), 241–253.
- Science Panel for the Amazon. Policy Brief: Droughts in the Amazon. Science Panel for the Amazon; 2024 Sep. Available from: https://www.theamazonwewant.org/spa_publication/pb-droughts/. Accessed June 22, 2025.
- Smith P, Soussana JF, Angers D, Schipper L, Chenu C, Rasse DP, Batjes NH, van Egmond F, McNeill S, Kuhnert M, et al. 2019. How to measure, report, and verify soil carbon change to realize the potential of soil carbon sequestration for atmospheric greenhouse gas removal. Global Change Biology 25: 3–18. https://doi.org/10.1111/gcb.14466

- Smith, N. G., Keenan, T. F., Colin Prentice, I., et al. (2019). Global photosynthetic capacity is optimized to the environment. Ecology Letters, 22(3), 506–517.
- Sousa, T. R., Schietti, J., Drucker, D. P., et al. (2020). Topographic constraints on water table depth shape the structural and functional composition of Amazonian forests. Plant and Soil, 449(1–2), 103–119.
- Valladares, F., Wright, S. J., Lasso, E., Kitajima, K., & Pearcy, R. W. (2000). Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology*, 81(7), 1925–1936. https://doi.org/10.1890/0012-9658(2000)081[1925:PPRTLO]2.0.CO;2
- Van Passel, J., Bernardino, P. N., Lhermitte, S., Rius, B. F., Hirota, M., Conradi, T., de Keersmaecker, W., Van Meerbeek, K., & Somers, B. (2024). Critical slowing down of the Amazon forest after increased drought occurrence. *Proceedings of the National Academy of Sciences of the United States of America, 121*(22), e2316924121. https://doi.org/10.1073/pnas.2316924121
- Wright, I.J., Reich, P.B., & Westoby, M. (2001). Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, 15(4), 423–434. https://doi.org/10.1046/j.0269-8463.2001.00542.x
- Wright, I.J., Reich, P.B., & Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. https://doi.org/10.1038/nature02403

Figures

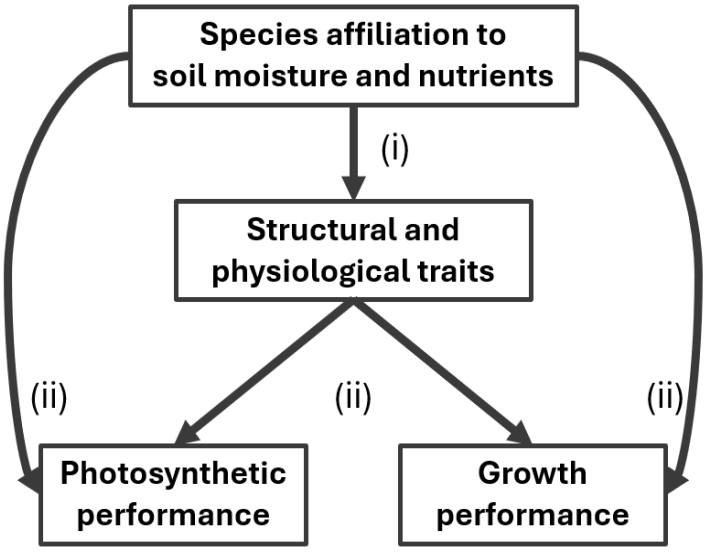

Figure 1. Conceptual model for testing: (i) the influence of species affiliation to soil moisture and nutrients on leaf- and wood- traits; and (ii) the interplay of resources affiliation and plant traits on photosynthetic (leaf-level) and growth (stem-level) performance of 23 dominant tree species along a fine-scale hydro-edaphic gradient in a central Amazon forest. Single-headed arrows represent direct effects.

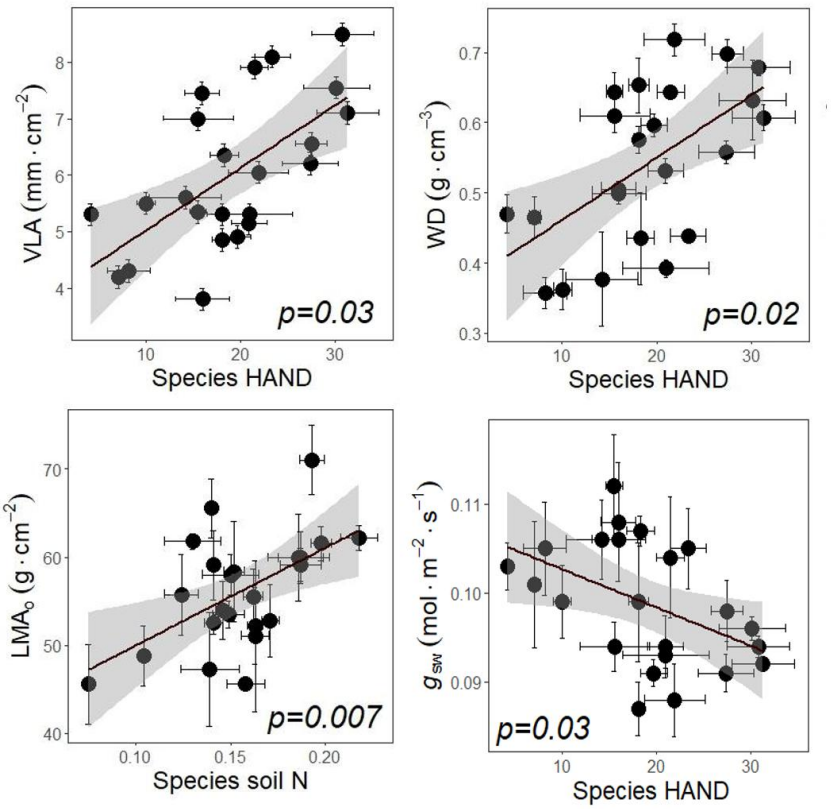

Figure 2. Relationship between soil resources affiliation and leaf- and wood-structural traits across species. Graphs show the relationship between the weighted mean values ± SE (standard error bars) of species affiliation to soil moisture (HAND, m) and soil N (%), with the species mean values ± SD (standard deviation bars) of leaf vein density (VLA), wood density (WD) and leaf mass per area (LMA_o) across 23 locally dominant tree species in a Central Amazonian forest. Higher HAND values indicate species more affiliated to deeper WT areas (lower soil moisture and higher soil N). Regression lines with 95% confidence intervals and P-values of linear regression model analysis are shown.

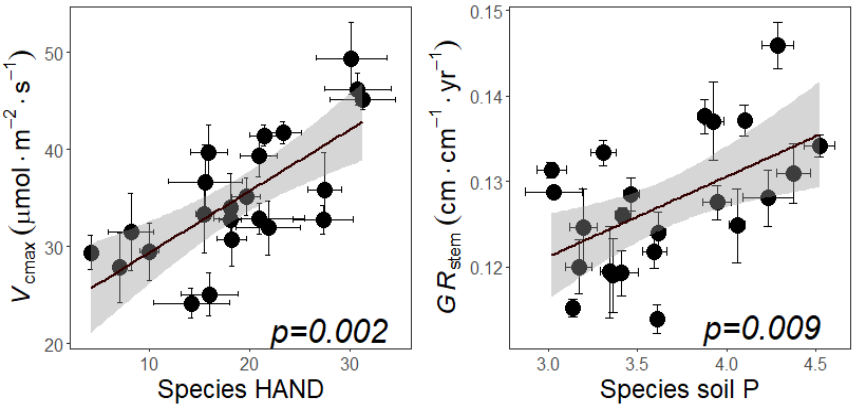

Figure 3. Relationship between soil resources affiliation and photosynthetic traits and stem growth across species. Graphs show the relationship between the weighted mean values ± SE (standard error

bars) of species affiliation to soil moisture (HAND, in m) and soil P (in mg kg^{-1}) with the species mean values ± SD (standard deviation bars) of the parameters g_{sw} (mol m^{-2} s^{-1}), V_{cmax} (µmol m^{-2} s^{-1}), and GR_{stem} (cm cm^{-1} yr^{-1}), across 23 locally dominant tree species in a central Amazonian forest. Regression lines with 95% confidence intervals and P-values of linear regression model analysis are shown.

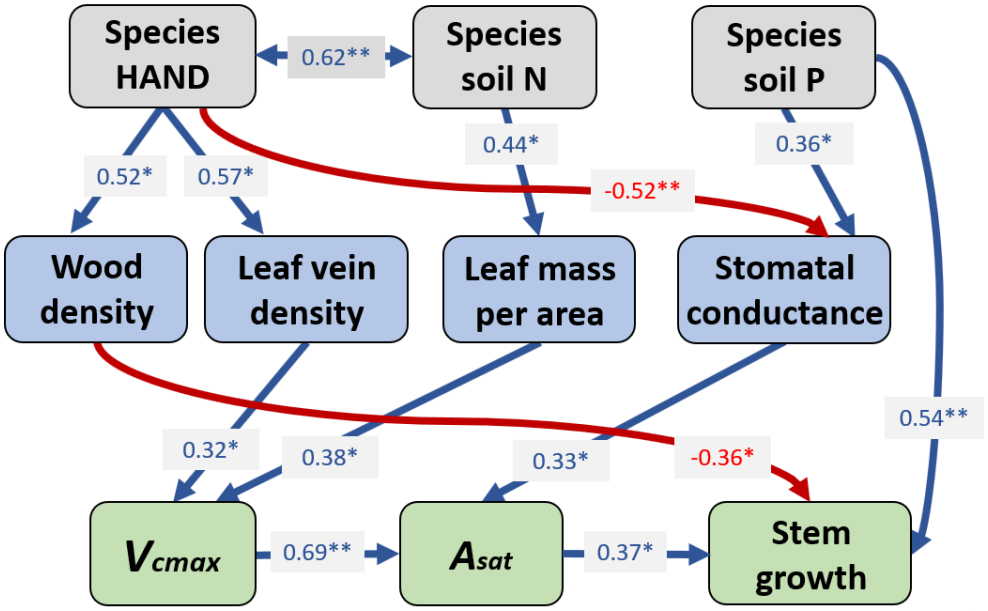

Figure 4. Results of the pSEM model structure that best fit our data. The model was fit to test: (i) the effect of soil resources affiliation on structural and physiological traits; and (ii) the interplay of resources affiliation and plant traits on modulating leaf-to-stem productivity across 23 locally dominant tree species in a central Amazonian forest. Gray boxes indicate the first tier, blue boxes the second tier, and green boxes the third tier. The pSEM also evaluated the correlation between species HAND, soil N and soil P, and between structural and photosynthetic traits. Single-headed arrows represent direct effects, double-headed arrows represent correlations. Blue and red denote significant positive and negative relationships, respectively. Numbers are the standardized coefficients of determination for each predictor. (*) $p<0.01$, (**) $p<0.005$.

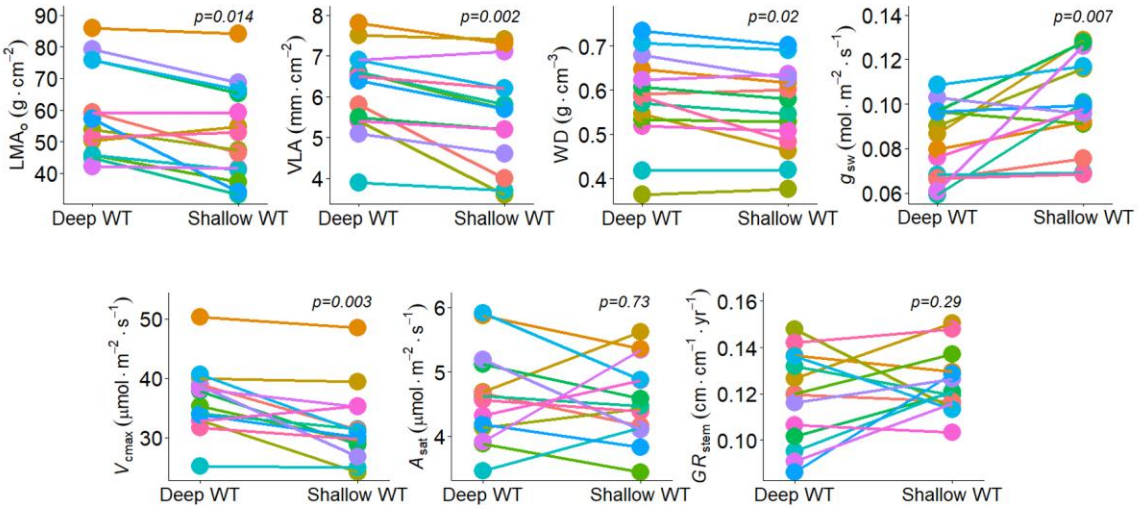

Figure 5. Intra-specific variation of structural traits and parameters of leaf-to-stem productivity along a local hydro-edaphic gradient. Graphs show the result of paired t-tests comparing the mean values of LMA_o, VLA, WD, g_{sw}, V_{cmax}, A_{sat} and GR_{stem} of individual trees located on deep and shallow WT areas, across 14 generalist locally dominant tree species in a central Amazonian forest. Different colors represent different species, with lines connecting the mean values of individuals belonging to the same species but located in contrasting environments.

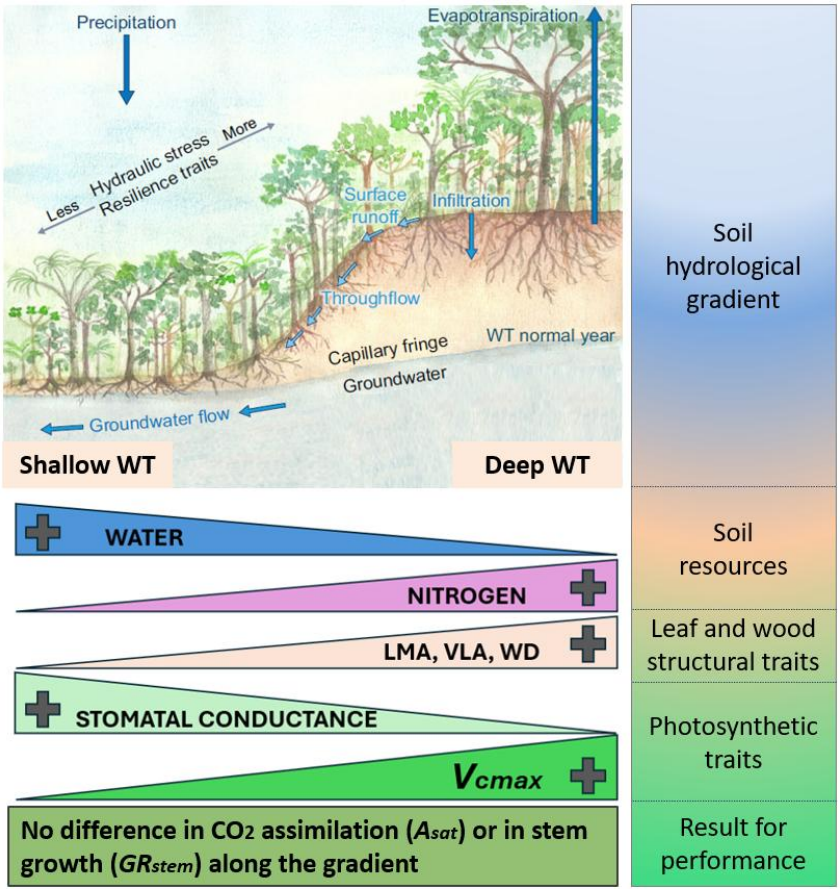

Figure 6. Conceptual synthesis illustrating how variation in soil moisture and nitrogen availability influences leaf and wood structure and photosynthetic traits, and their interplay on CO_2 assimilation and stem growth. Across 23 locally dominant Amazonian tree species, affiliation to soil moisture (through WT depth) and soil nitrogen modulate structural traits (LMA_o, VLA and WD) and photosynthetic traits (g_{sw} and V_{cmax}), with the combined effects of these factors resulting in similar performance -CO_2 assimilation (A_{sat}) and stem growth rates (GR_{stem})- along the hydrological gradient.

Supplemental material

Fig. S1. Temporal trend in annual rainfall at the RFD (1966-2023)

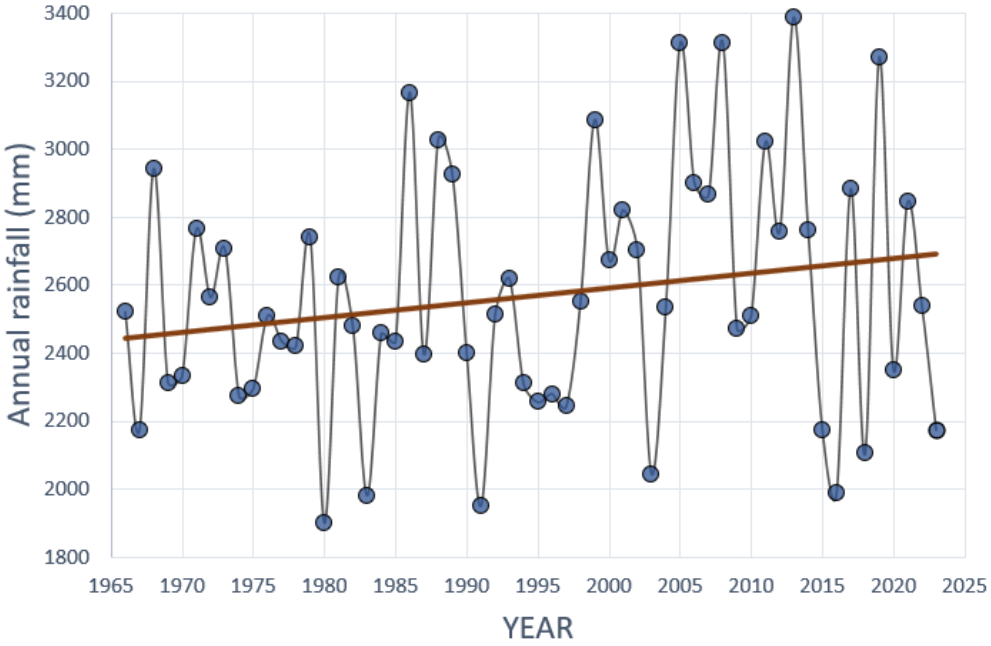

Fig. S2. Correlation between soil variables across the 72 1-ha plots in the RFD.

	HAND	Elevation	Clay (%)	Sand (%)	Soil Phosphorus
Soil Nitrogen	**0.58**	**0.66**	**0.67**	**-0.66**	**0.04**
HAND		**0.82**	**0.88**	**-0.88**	**-0.07**
Elevation			**0.94**	**-0.94**	**-0.07**
Clay (%)				**-1.00**	**-0.11**
Sand (%)					**0.11**

Fig. S3. Tree abundance distribution of 23 dominant Amazonian tree species along the topographic gradient in the RFD.

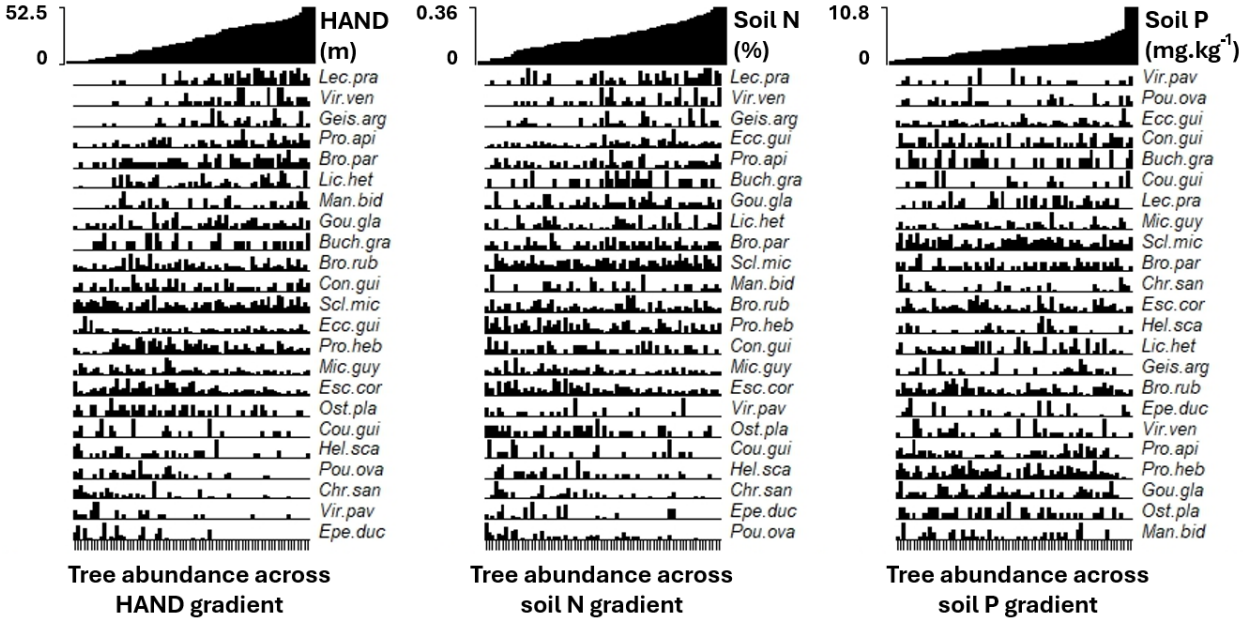

Fig. S4.- Comparison of values of CO2 assimilation at light saturation using light intensities of 1000 and 2000 µmol m^{-2} s^{-1} PFD, to test light saturation along 97 individuals of the 23 locally dominant Amazonian tree species.

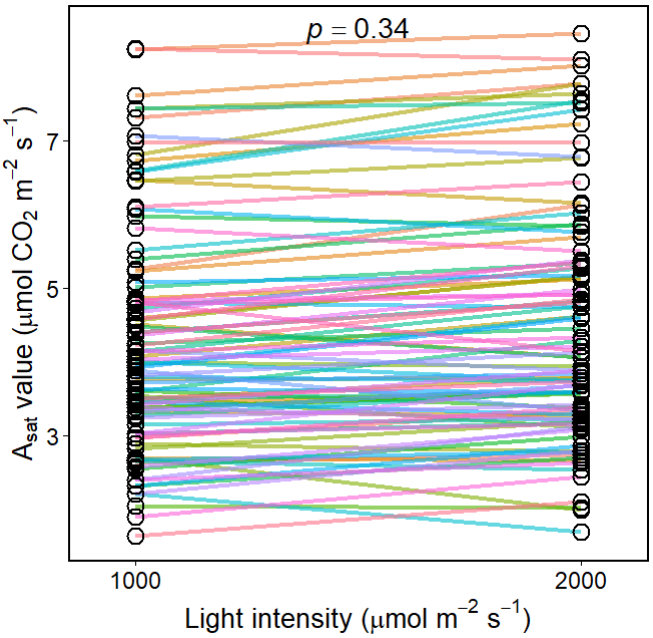

Fig. S5. Correlation between V_{cmax} values estimated by adjusting whole A-Ci curves and those estimated by the One Point method

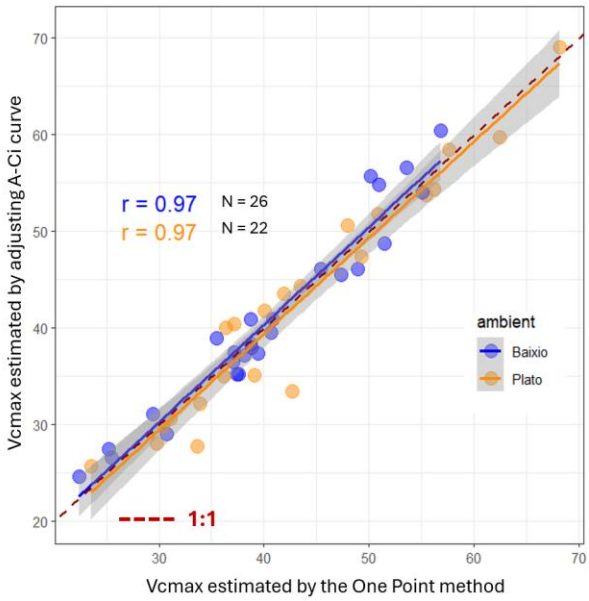

Figure S6. The relationship between species-mean (± SE) stem growth rates for small trees (DBH 1-10cm) and for big trees (DBH >= 10cm) across 23 dominant tree-species in a Central Amazonian forest. Stem growth rates of small trees (saplings) are significantly correlated with stem growth rates of big trees (adults)

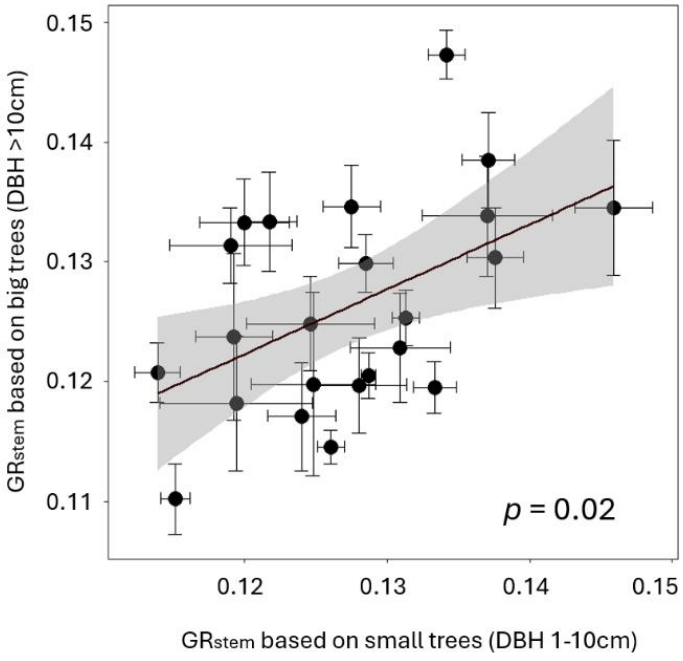

Figure S7. The relationship between the association with HAND and soil nutrients across species. Graphs show the correlation between the weighted mean values ± SE (standard error) representing the species association with soil moisture (through HAND, in m), soil N (%) and soil P ($mg.kg^{-1}$) across 23 dominant tree species in a Central Amazonian forest. Higher HAND values represent species more associated with deeper WT areas (lower soil moisture). Correlation lines with confidence intervals and p-values of Pearson correlation analysis are also shown.

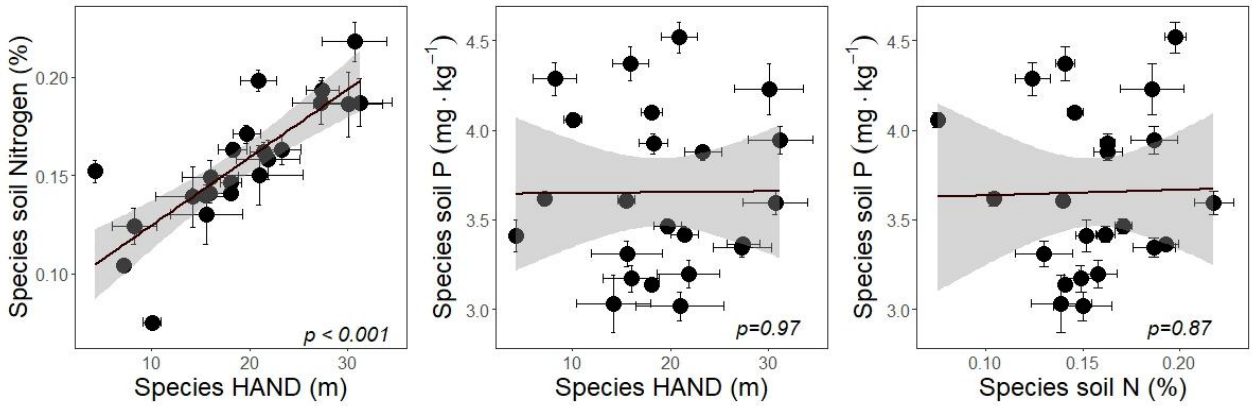

Fig. S8. The relationship between the association with soil resources and the CO_2 assimilation rates at light saturation (A_{sat}). Graphs show the correlation between the weighted mean values ± SE (standard error) representing the species association with soil moisture (through HAND, in m), soil N (%) and soil P ($mg.kg^{-1}$) and the A_{sat} values across 23 dominant tree species in a Central Amazonian forest. Higher HAND values represent species more associated with deeper WT areas (lower soil moisture). Correlation lines with confidence intervals and p-values of Pearson correlation analysis are also shown.

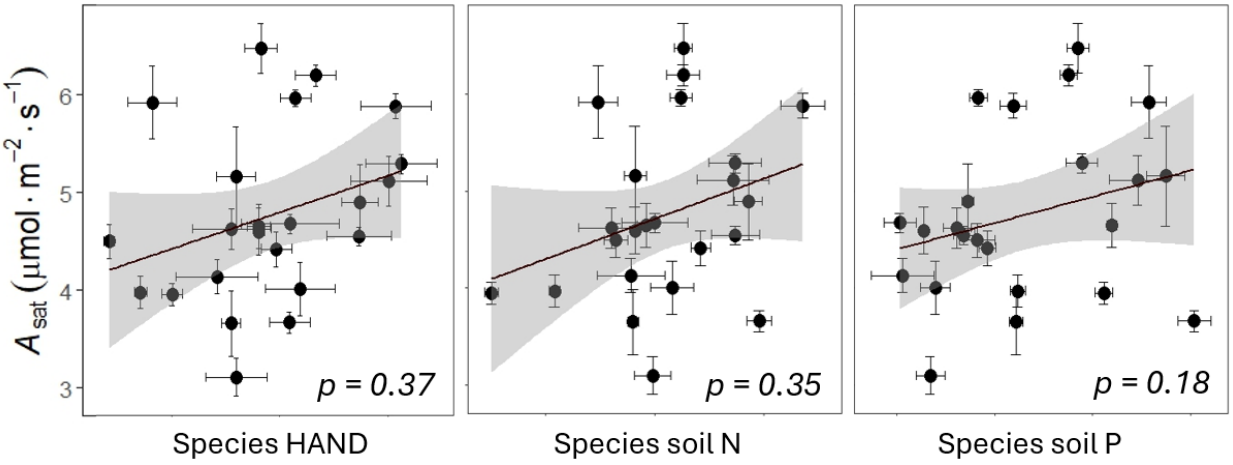

Figure S9. Relationship between parameters of photosynthetic performance and stem growth across species. Graphs show the relationship between the mean values ± SD (standard deviation) of parameters reflecting photosynthetic performance: V_{cmax} (µmol.m^{-2}.s^{-1}) and A_{sat} (µmol CO_2.m^{-2}.s^{-1}), and stem productivity: GR_{stem} (cm.cm^{-1}.yr^{-1}), across 23 dominant tree species in a central Amazonian forest. Correlation lines with confidence intervals, correlation coefficients (r) and p-values of Pearson correlation analysis are also shown.

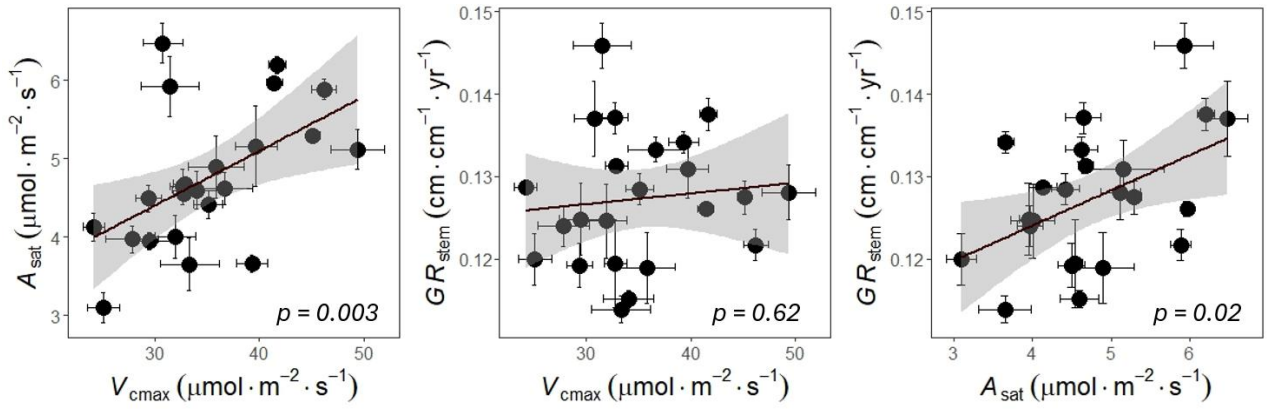

Figure S10. Leaf respiration rates of trees under shallow and deep water table (WT) conditions. Trees growing in deep WT areas exhibit significantly higher respiration rates than those in shallow WT areas (p = 0.00091).

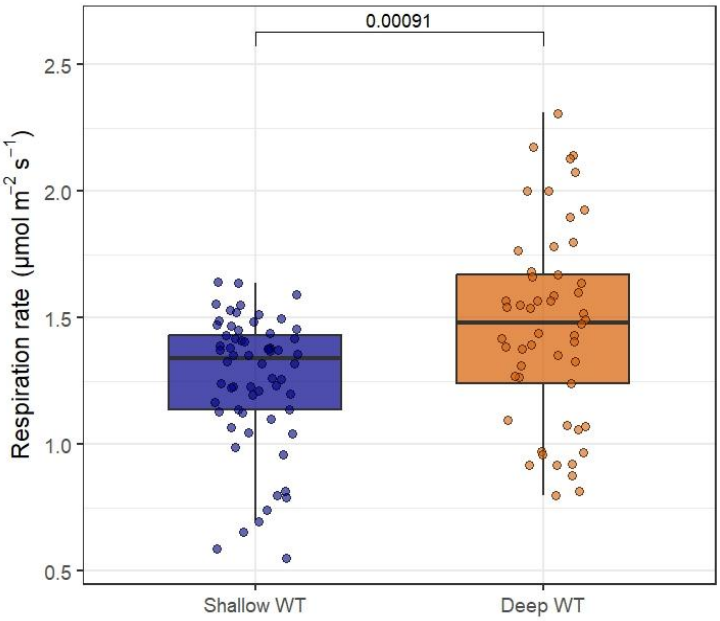

Table S1. List of 23 dominant Amazonian tree species selected for this study. Species were selected according to their representativeness in terms of abundance (number of individuals) and basal area (m^2) in the RFD. All individuals have diameter at breast height (DBH) of at least 10 cm.

Family	Species	Total of trees	HAND	soil P	soil N	Trees for gas exchange	Trees for structural traits
MORACEAE	*Brosimum parinarioides*[p]	85	27.3	3.28	0.19	10	6
MORACEAE	*Brosimum rubescens*[g]	245	22	3.06	0.17	11	8
COMBRETACEAE	*Buchenavia grandis*[g]	37	22.7	3.22	0.24	13	6
SAPOTACEAE	*Chrysophyllum sanguinolentum*[v]	195	7.1	3.15	0.17	8	6
EUPHORBIACEAE	*Conceveiba guianensis*[g]	75	22	3.25	0.16	8	6
APOCYNACEAE	*Couma guianensis*[g]	28	14.8	3.11	0.14	10	6
SAPOTACEAE	*Ecclinusa guianensis*[g]	173	22	3.47	0.16	24	12
FABACEAE	*Eperua duckeana*[v]	114	4.2	3.04	0.13	12	5
LECYTHIDACEAE	*Eschweilera coriacea*[g]	589	17.6	3.23	0.16	14	8
APOCYNACEAE	*Geissospermum argenteum*[p]	70	30.5	3.1	0.22	5	5
GOUPIACEAE	*Goupia glabra*[g]	119	23.7	2.97	0.19	10	6
MORACEAE	*Helicostylis scabra*[g]	50	14.6	3.21	0.14	8	7
LECYTHIDACEAE	*Lecythis prancei*[p]	92	33.2	3.41	0.23	7	6
CHRYSOBALANACEAE	*Licania heteromorpha*[g]	139	25.5	3.13	0.19	14	8
SAPOTACEAE	*Manilkara bidentata*[g]	60	24.1	2.98	0.19	15	7
SAPOTACEAE	*Micropholis guyanensis*[g]	215	17.9	3.19	0.14	11	9
MYRISTICACEAE	*Osteophloeum platyspermum*[g]	58	16.8	2.89	0.18	11	6
URTICACEAE	*Pourouma ovata*[v]	99	10.5	3.5	0.11	14	6
BURSERACEAE	*Protium apiculatum*[p]	118	28.7	3.11	0.14	5	5
BURSERACEAE	*Protium hebetatum*[g]	393	21.4	2.97	0.17	23	13
MALVACEAE	*Scleronema micranthum*[g]	310	22	3.29	0.19	10	9
MYRISTICACEAE	*Virola pavonis*[v]	29	8.9	3.23	0.15	13	5
MYRISTICACEAE	*Virola venosa*[p]	56	31.5	3.19	0.22	8	5

[g]: generalist species; [p]: plateau-specialist; [v]: valley-specialist

Table S2. Summary of the pSEM model that best fits our data. *Std. est* is the standard estimate, showing the relative contribution of significant predictors. For each response variable, R^2 is the variance explained by predictors. The model fit statistics Akaike's information criterion (AIC), Fisher's *C* statistic, and associated *p* value (P > 0.05 indicating reasonable fit of model to data; Shipley, 2009) are also shown.

Path	Response	Std. est	p value	R^2
Predictor				
Species HAND	Leaf venation density	0.57	0.043	0.25
Species soil N	Leaf mass per area	0.44	0.035	0.19
Species soil P	Stomatal conductance	0.36	0.020	
Species HAND	Stomatal conductance	-0.52	0.002	0.41
Species HAND	V_{cmax}	0.51	0.002	
Leaf mass per area	V_{cmax}	0.38	0.014	
Leaf venation density	V_{cmax}	0.32	0.036	0.67
Stomatal conductance	A_{sat}	0.33	0.016	
V_{cmax}	A_{sat}	0.69	0.003	0.65
Species HAND	Wood density	0.52	0.048	0.24
Species soil P	Stem growth	0.54	0.002	
A_{sat}	Stem growth	0.37	0.023	
Wood density	Stem growth	-0.36	0.037	0.59
Correlation				
Species HAND	Species soil N	0.62	0.003	
Fisher's *C*		71.4		
AIC		179.9		
p value		0.111		

Capítulo 2

Erick J. L. Esteban, Sean McMahon, Scott Stark, Edher Checa-Cordoba, Manuel Marca-Zevallos, Kelves C. A. da Silva, Gabriela Ushida, Flavia R. C. Costa

Water table depth modulates rainfall effect and drought impact on stem growth of Amazonian trees

Manuscrito em preparação

Water table depth modulates rainfall effect and drought impact on stem growth of Amazonian trees

Erick J. L. Esteban, Sean McMahon, Scott Stark, Edher Checa-Cordoba, Manuel Marca-Zevallos, Kelves C. A. da Silva, Gabriela Ushida & Flavia R. C. Costa

Abstract

- Drought sensitivity of Amazonian forests is tightly associated with soil water availability and thus linked to the water-table depth (WT). Yet, the importance of WT variation over forest functioning is rarely considered into drought impact assessments. While extensive research reports declining forest productivity and increased drought vulnerability in deep WT areas (>20m depth), recent studies show shallow WT (<5m depth) acting as hydrological refugia during drought.
- Using three years of monthly records of local climate, WT fluctuation and stem diameter increment for 1054 trees established on shallow and deep WT areas, spanning the 2023–2024 droughts, we asked: (i) do shallow WT areas protect tree functioning (stem growth) during dry periods and drought events? and, (ii) what are the main drivers of stem growth among each hydrological environment?
- During normal dry conditions (2022), stem growth exhibited similar patterns in both hydrological environments. While in deep WT areas a significant reduction of stem growth was observed, trees in shallow WT areas sustained growth during droughts, not differing from pre-drought baselines. Recent rainfall (2-month lag) enhances growth on deep WT areas but suppresses it on shallow WT areas, consistent with waterlogging stress. Elevated vapor-pressure deficit (VPD) reduced growth everywhere, with stronger effect on deep WT soils. Moreover, transient WT declines strongly promoted growth on shallow WT areas, underscoring benefits of temporary soil aeration.
- Approximately 40% of the Amazon have shallow WT, and our findings reinforce these areas as hydrological refugia, maintaining tree growth rates under moderate-to-severe drought. Yet, the opposing responses to rainfall across environments imply that intensifying droughts, coupled with heavier rain events -*hydrological cycle intensification*- could amplify spatial heterogeneity in Amazon forest functioning. Integrating WT depth and its fine-scale temporal variability into Earth-system and vegetation models is therefore critical for realistic forecasts of Amazon forest resilience to ongoing climate change.

Introduction

The intensification of drought events under ongoing climate change poses significant threats to tropical forests, particularly in the Amazon Basin, where hydrological conditions play a pivotal role in modulating tree growth and mortality (Costa *et al*., 2022). Recent decades have been scenario of more frequent and intense droughts, with severe impacts on Amazonian tree growth, mortality, and carbon dynamics (Phillips *et al*., 2009; Brienen *et al*., 2015). These events have significantly altered forest composition and structure, raising concerns about the resilience and future carbon balance of these ecosystems (Esquivel-Muelbert *et al*., 2019; Hubau *et al*., 2020). Nonetheless, not all Amazonian forests respond uniformly to drought, as hydrological conditions, mainly those driven by water table depth (WT), significantly modulate drought impacts (Esteban *et al*., 2021; Sousa *et al*., 2022).

Forest areas with shallow WT (< 5 m depth) have recently been proposed as potential hydrological refugia, mitigating drought impacts through sustained water availability despite prolonged dry conditions (Costa *et al*., 2022). These regions, typically underrepresented in ecological studies, may buffer trees against drought stress via continued groundwater accessibility, allowing for sustained physiological functioning and reduced mortality compared to areas where WT is deeper, which are more drought sensitive due to limited soil water (Esteban *et al*., 2021; Spanner *et al*., 2022).

The contrasting impacts of drought between shallow and deep WT forests may also be driven by variations in tree functional traits, such as species-specific wood density (WD). Species in shallow WT forests typically exhibit lower WD and higher growth rates, traits traditionally associated with more drought vulnerability (Aleixo *et al*., 2019). Nonetheless, the proximity to the WT provides a hydrological buffer, substantially reducing drought-induced mortality (Sousa *et al*., 2020; Costa *et al*., 2022). This interaction highlights the complexity in predicting drought impacts solely based on functional traits, emphasizing the necessity of integrating hydrological conditions into vegetation models. Moreover, extreme wet periods preceding drought events may significantly mitigate drought negative impacts, through a *soil hydrological memory effect* that replenishes soil moisture and groundwater resources, buffering subsequent drought stress (Esteban *et al*., 2021). This wet-dry interaction underscores the importance of temporal sequencing in climate anomalies, with implications for forest resilience assessments under future climate scenarios characterized by increasing variability in precipitation extremes (intensification of the hydrological cycle, Gloor *et al*., 2013; Barichivich *et al*., 2018).

The diameter growth of tropical trees is strongly influenced by climatic and soil variables (Clark *et al*., 2003; Brienen et al., 2015), but responses can be modulated by local hydrological conditions, especially in forests with high variability in WT depth (Fan *et al*., 2017; Oliveira *et al.*, 2019). Thus, understanding how stem growth varies temporally as a function of seasonality and water stress across different hydrological environments is fundamental to predicting the impacts of climate change on forest productivity and the resilience of the Amazon ecosystem (Bennett *et al*., 2023; Costa *et al*., 2023). Moreover, improving our knowledge of how varying hydrological conditions modulate tree responses to drought is vital, given the critical role of Amazonian forests in global carbon and water cycles. This study aims to elucidate the contrasting impacts of drought across hydrologically distinct Amazonian environments, exploring the mechanisms underpinning temporal and spatial heterogeneity in forest responses, specifically in tree stem growth. Our findings are relevant to refining predictive models and inform conservation and management strategies, particularly due to increasingly frequent and severe drought events projected under climate change scenarios.

Materials and methods

Study site

All the data used for this study were collected at the Reserva Florestal Ducke (RFD), a reserve that covers 10 000 ha (10 km x 10 km) of terra-firme tropical rainforest, located 26 km northwest of Manaus (02º55′S, 59º58′W) in the central region of the Amazon basin. The vegetation of the RFD is old-growth dense lowland evergreen forest, with high diversity of tree species (> 1200 sp, Ribeiro et al. 1999) and a closed canopy of 30–37 m, with emergent trees reaching 40-45 m (Guillaumet, 1987). This forest experiences an 'Am' tropical climate according to Köppen–Geiger classification, with dry and rainy seasons governed by monsoons (Peel et al., 2007). Over the past 58 years (1966–2023), the mean (± SD) annual rainfall at the RFD was 2568 ± 363 mm, with an increasing trend of 4.3 $mm.yr^{-1}$. The RFD has 72 permanent plots systematically distributed over a 64-km^2 grid formed by 8 km long trails. Each plot is at least 1 km away from any other. Plots are 250 m × 40 m (1 ha) and are positioned to follow the topographic isoclines and thus minimize altitude and soil variation within each plot.

Environmental properties

The RFD has a dense drainage network (Ribeiro et al., 1999) along with an undulating topography, with elevation varying from 40 to 140 m above sea level and highly correlated with soil texture (Chauvel et al., 1987). Local variation in soil hydrological conditions along the topographic gradient is driven by the WT depth. Soils in the RFD are typically acidic and poor in nutrients such as phosphorus, calcium and potassium, while often high in aluminum (Chauvel et al., 1987).

Variation in soil WT depth, along with soil texture, stablishes fine-scale hydro-edaphic gradients, from clayey latosols with deeper WT on the uplands (plateaus), to sandy podzols with shallow WT, some with seasonally waterlogging and patches permanently waterlogged, in the lowest parts (valleys). Overall, the RFD is representative of climate, soil and WT depth of c. 30% of Amazonian forests, based on maps from Fan & Miguez-Macho, 2010; Quesada et al., 2011; Míguez-Macho & Fan, 2012a, b; Restrepo-Coupe et al., 2013; Malhi et al., 2015; and Esquivel-Muelbert et al., 2019.

Monitoring of stem diameter increment and environmental variables

A total of 1,057 trees were monitored monthly in 10 permanent 1-hectare plots (5 on plateaus and 5 on valleys) between February 2022 and December 2024. Increment of stem diameter was measured using dendrometric bands and analyzed using the Rdendrom package. Climatic (rainfall, radiation, VPD, air temperature) and hydrological (water table depth fluctuation) variables were continuously monitored, also at monthly periods and duing the same interval.

Statistical analysis

Data analyses and visualization were performed in the R statistical software package (R Development Core Team, 2022). Generalized additive models (GAMs) were used to describe the temporal dynamics of growth. For causal assessment, a directed acyclic graph (DAG) approach was adopted to model the direct and indirect effects of climatic variables and WT fluctuation on growth (Fig. 1). Statistical modeling was performed in the R environment, supported by Bayesian models using the brms package (Bayesian multivariate multilevel models using the Stan software) to estimate effects with uncertainty.

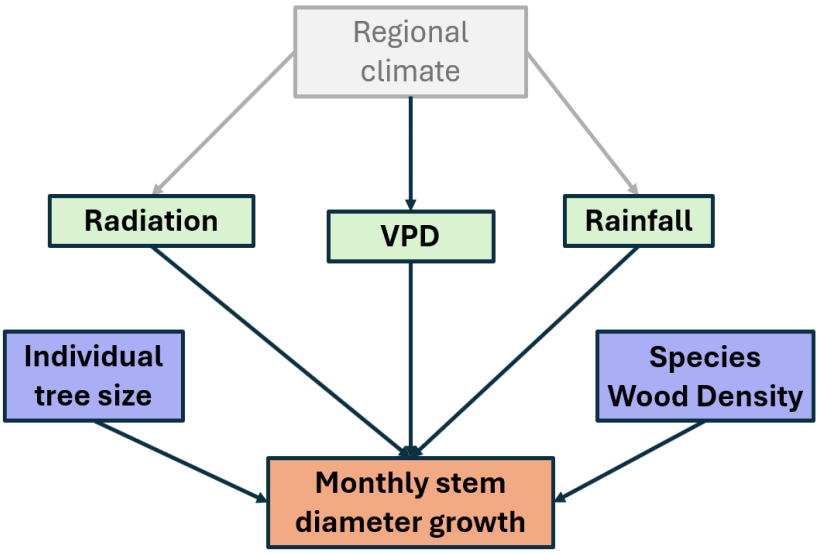

Fig. 1. Directed acyclic graph (DAG) proposed to test the causal effect of environmental variability, tree size and species-specific wood density on stem growth phenology of trees established along contrasting hydrological environments in a central Amazonian forest. Water table depth is not included in this DAG but was tested together with the other variables during the Bayesian modelling for trees in shallow water table areas.

Results

Spatio-temporal variation of stem diameter growth

In a typical year (2022), i.e., normal dry conditions, tree diameter growth was similar between environments. However, during drought years (2023 and 2024), a significant reduction in stem growth was observed in plateau areas, while in valley plots trees maintained or even increased their growth rates (Fig. 2).

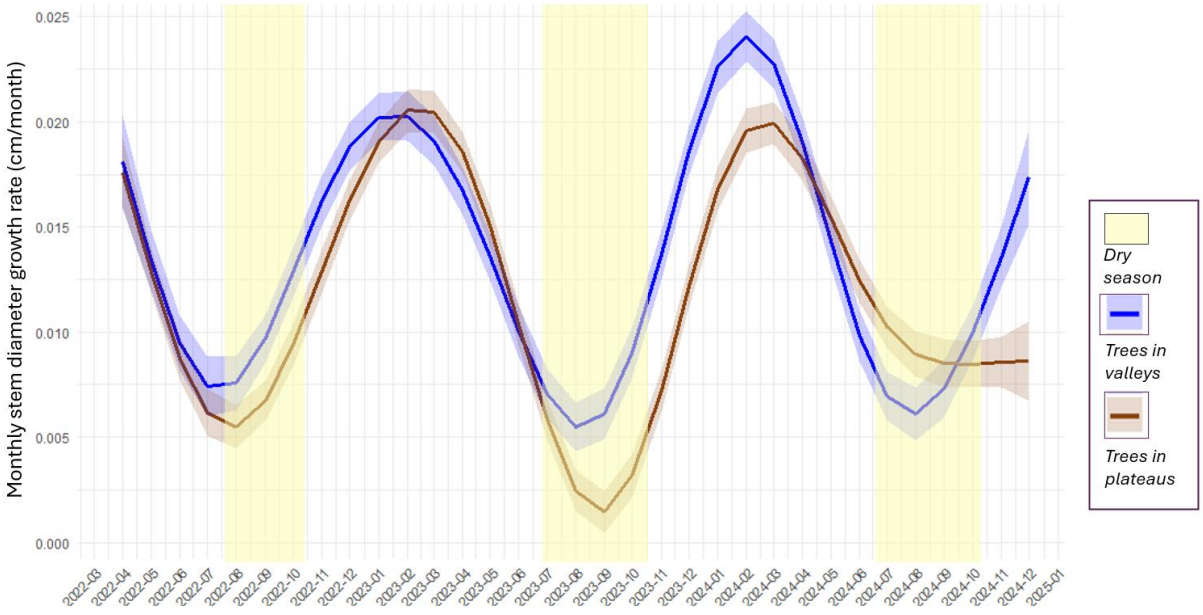

Figure 2. The spatio-temporal variation of monthly stem diameter growth rates of 1054 trees distributed in shallow and deep-water table areas, with the monitoring period (2022-2024) covering the last two severe droughts in 2023 and 2024.

Drivers of stem growth across hydrological environments

Causal inference using Directed Acyclic Graphs (DAGs) revealed distinct tree responses to climatic variables and WT fluctuation (Fig. 3 and Fig. S1 and S2). Radiation had a stronger positive effect on stem growth, while VPD consistently exerted negative effects in both environments. Tree-level traits such as wood density and stem diameter (tree size) also influenced growth, with negative effects observed in both environments but particularly in shallow WT forests.

In plateau areas, stem growth showed a strong dependence on rainfall, particularly with a two-month lag. Higher amount of previous rainfall led to greater stem growth rates in these areas. In contrast, growth in valley areas was negatively affected by greater rainfall but positively associated with a deepening of the WT occurring four months prior. Moreover, across both contrasting hydrological environments, higher solar radiation increased stem growth while higher vapor pressure deficit (VPD) reduced it.

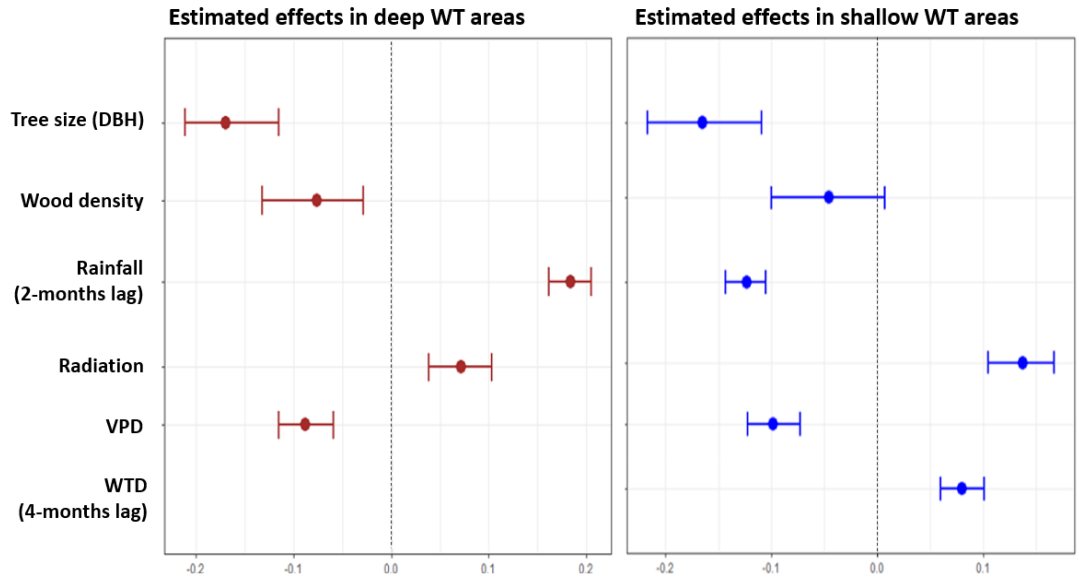

Figure 3. Estimated effects of tree size, wood density, climatic variables and water table fluctuations on stem growth rates across contrasting hydrological environments.

Discussion

This study assessed how monthly tree diameter growth is influenced by climatic variability and water table fluctuation in contrasting Amazonian hydrological environments—plateaus with deep water tables and valleys with shallow water tables. Our results demonstrate that hydrological conditions fundamentally shape how tree growth responds to seasonal climate variability. In plateau environments, where water is limited during the dry season, stem growth is directly dependent on rainfall availability. In contrast, forest with shallow WT—where groundwater is accessible and rainfall variability is less limiting—exhibit increased growth during dry periods. This counter-cyclical response suggests -and reinforce- that shallow WT forests may act as hydrological refugia during droughts, maintaining higher stem growth rates when deeper WT forests are under severe water stress.

These findings are consistent with prior studies indicating that shallow WT systems can buffer drought negative impacts (Fan *et al*., 2017), while also being vulnerable to waterlogging (Costa *et al*., 2023). The observed positive effects of increased WT depth (lagged by four months) on stem growth in valleys reinforce the role of soil hydrology and soil aeration in modulating forest functioning (Esteban et al., 2021; Sousa et al., 2022; Checa-Cordoba et al., 2024). Furthermore, the divergent impacts of rainfall in shallow and deep WT environments underscore the importance of WT depth as a key predictor of drought vulnerability (Costa et al., 2022). In shallow WT areas,

excess rainfall may reduce soil oxygenation, limiting root function and carbon uptake, while in plateaus, growth is strongly rainfall-dependent due to lack of groundwater access.

VPD emerged as a consistent negative driver of growth across environments, in line with its well-documented role in inducing stomatal closure and limiting photosynthesis under high atmospheric drought (Davidson et al., 2011; Spanner et al., 2022). Conversely, radiation enhanced growth, especially in valleys, likely by improving photosynthetic performance -increased carbon assimilation- during drier, non-saturated and less cloudy periods.

Overall, our findings highlight the importance of considering lag effects of environmental conditions and the soil hydrological memory effect: the delayed impacts of soil water conditions, particularly water table fluctuations, on tree growth. This lagged response indicates that short-term climatic events can have prolonged consequences on forest dynamics, requiring time-aware modeling approaches (Esteban et al., 2021; Costa et al., 2022).

Conclusion

This study highlights how contrasting hydrological environments shape tree growth responses to climate in Central Amazonia. Shallow WT forests display greater resistance to atmospheric drought but are more sensitive to rainfall-induced waterlogging. In contrast, plateau forests are highly vulnerable to rainfall deficits but benefit directly from precipitation events (more rainfall-dependent). Altogether, these results highlight that the interplay between rainfall, VPD, radiation, and WT depth modulates forest functioning, with environment-specific effects. Given the high spatial heterogeneity of Amazonian soils and water regimes, predictive models must incorporate local hydrological conditions and tree functional strategies to assess more comprehensive forest vulnerability under climate change. Finally, our results stress the need for continued monitoring of soil water dynamics, especially in areas with shallow WT, to better inform and improve conservation and management strategies for Amazonian forests facing more frequent droughts and changing rainfall patterns.

Supplemental material

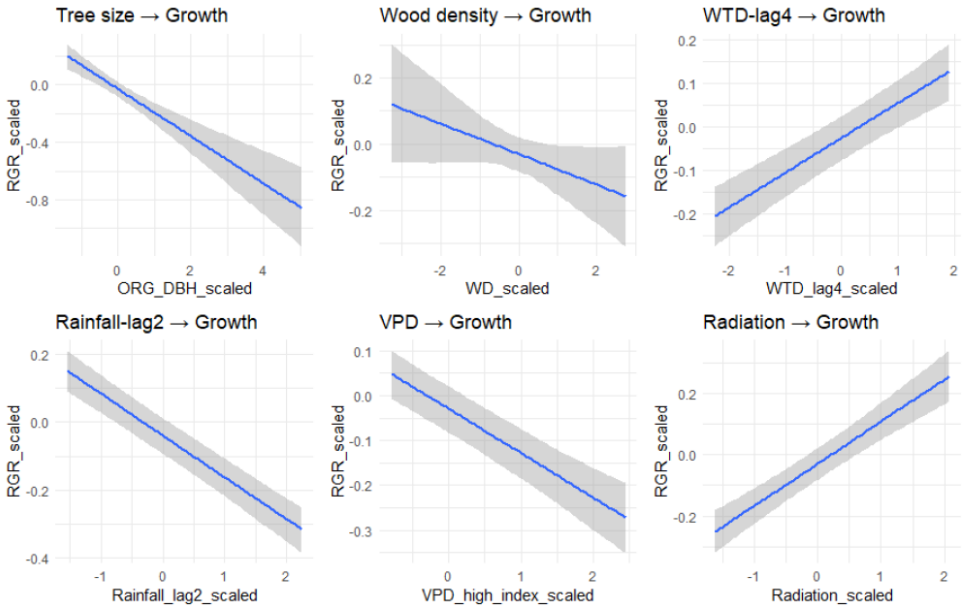

Figure S1. Predicted marginal effects of each variable over stem growth rates along shallow water table areas (valleys), as a result of Bayesian model with the best power prediction based on the proposed directed acyclic graph (DAG).

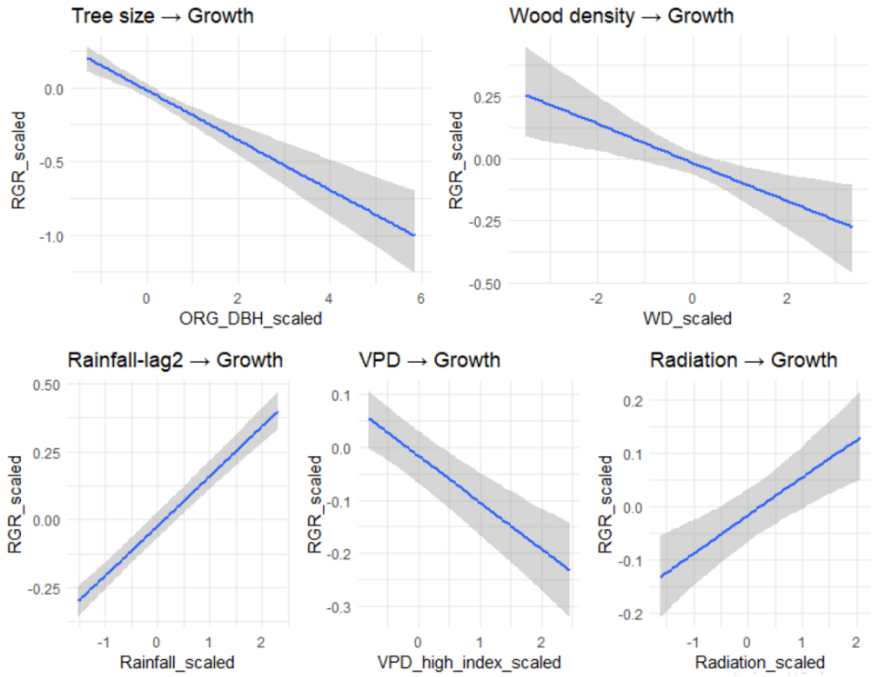

Figure S2. Predicted marginal effects of each variable over stem growth rates along deep water table areas (plateaus), as a result of Bayesian model with the best power prediction based on the proposed directed acyclic graph (DAG).

Capítulo 3

Edher Checa-Cordoba, Erick J. L. Esteban, Thaise Emilio, Demétrius Lira-Martins, Juliana Schietti, José P. V. Pinto, Javier Tomasella and Flávia R. C. Costa

Soil water regime and nutrient availability modulate fine root distribution and biomass allocation in Amazon forests with shallow water tables

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Soil water regime and nutrient availability modulate fine root distribution and biomass allocation in Amazon forests with shallow water tables

Edher Checa-Cordoba[1]*, Erick J. L. Esteban[2]*, Thaise Emilio[3], Demétrius Lira-Martins[4], Juliana Schietti[5], José P. V. Pinto[6], Javier Tomasella[7] and Flávia R. C. Costa[8]

[1] Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. Ephigênio Sales 2239, Manaus, AM 69060-20, Brazil;

[2] Programa de Pós-Graduação em Ciências de Florestas Tropicais, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. Ephigênio Sales 2239, Manaus, AM 69060-20, Brazil;

[3] Departamento de Biodiversidade, Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil;

[4] Departamento de Biologia Vegetal, Universidade Estadual de Campinas (UNICAMP), Campinas, Brazil;

[5] Departamento de Biologia, Universidade Federal do Amazonas, Av. General Rodrigo Octávio Jordão Ramos, 1200 CEP: 69067-005, Manaus-Amazonas, Brazil;

[6] Independent researcher;

[7] Centro Nacional de Monitoramento e Alertas de Desastres Naturais (Cemaden/MCTI), Rodovia Presidente Dutra, Km 40, 12630-000 Cachoeira Paulista, SP, Brazil;

[8] Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. Ephigênio Sales 2239, Manaus, AM 69060-20, Brazil

* These authors were equal co-leaders of this work.

Abstract

Background and Aims

Shallow water table (WT) forests (representing ~50% of Amazonian land areas) exhibit different characteristics and functioning compared to the more widely studied deep WT forests. However, less is understood about the determinants of biomass allocation to aerial and belowground components in shallow WT forests. Here we investigate how limitations imposed by soil water and nutrient availability influence the distribution of fine root biomass and the partitioning of biomass (BGB:AGB ratio) in shallow WT forests, and the relationships with their stand structure.

Methods

We used extensive ground-based data on soil properties, soil nutrients, WT monitoring, and direct biomass measurements along a 600 km transect of shallow WT forests in the central Amazon region.

Results

Soil water excess, due to a wetter climate or a consistently shallow WT, restricts fine-root distribution to the upper soil layers. This restriction, alone or combined with phosphorus limitation, leads to a higher biomass allocation belowground, associated with stand structures characterized by a higher density of smaller trees. Opposite patterns are found where the soil experiences no excess water or does so infrequently. Soil nutrient availability contributes to biomass partitioning, but with WT regimes strongly modulating its effects.

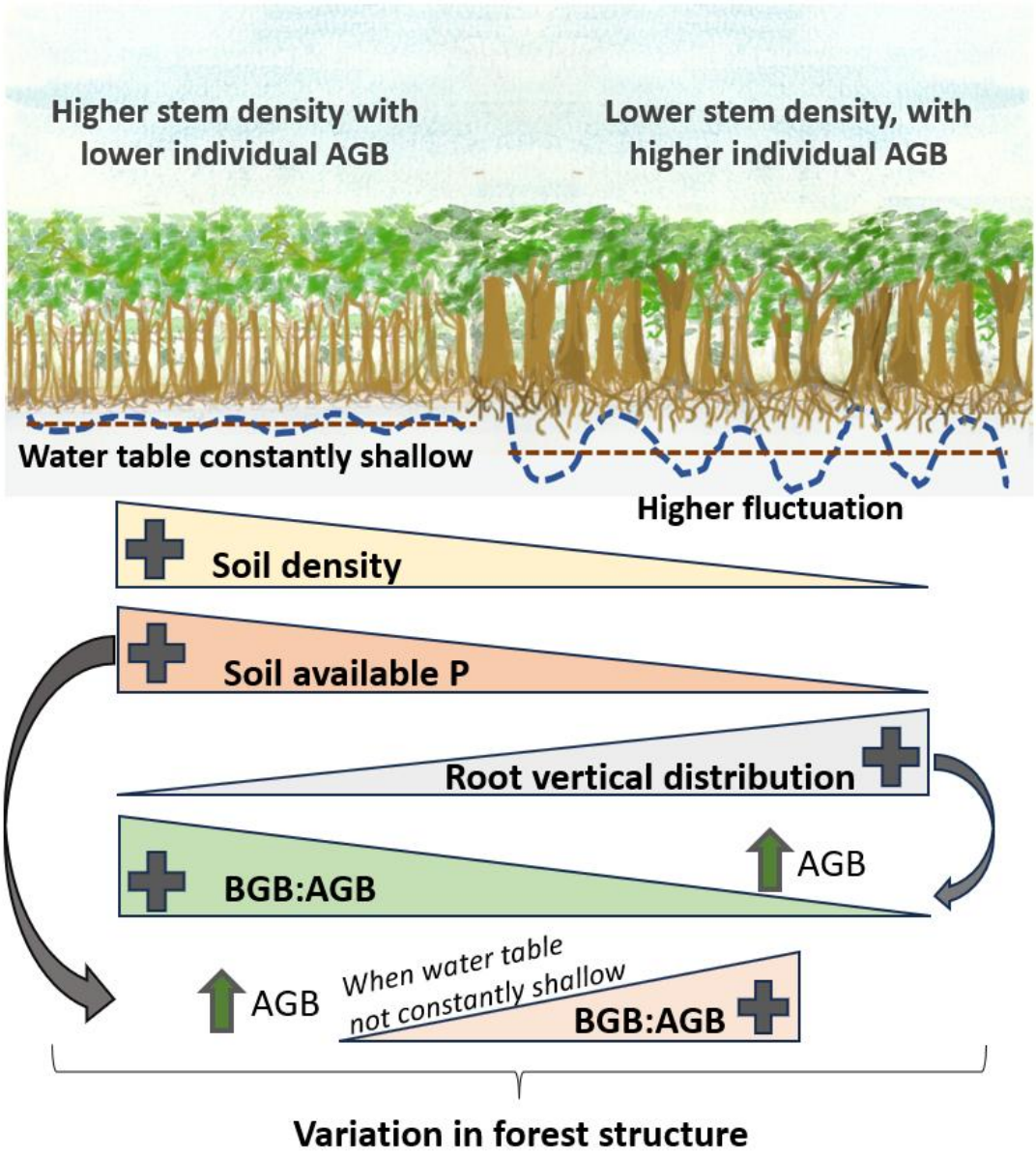
Conclusion

Finding that soil water regime have an overarching control on fine-root distribution and biomass partitioning in shallow WT forests challenges the dominant perspective of allocation being mostly affected by soil nutrients and climate. These findings improve our understanding of a large fraction of the Amazon rainforest, with important implications for modeling and predicting its functioning as a carbon store and the regulation of biogeochemical cycles.

Keywords:

Amazonia, BGB:AGB ratio, fine-root biomass, forest stand structure, water table.

Graphical abstract



Variation of root vertical distribution, biomass allocation and forest structure along a gradient of hydrological regime and soil properties in forest areas with shallow water tables. We summarize how the variation of water table regime, along with soil physical restrictions and nutrient availability, modulate root vertical distribution, biomass allocation to below- and above-ground components (BGB:AGB ratio), and their consequences on forest structure, in areas with shallow water tables.

Introduction

Amazonian forests are of global significance due to their contribution to the balance of biogeochemical and water cycles (Malhi et al. 2021), capturing and storing a quarter of the planet's terrestrial carbon (Le Quéré et al. 2018). Much of the carbon processed by the vegetation is used in the construction and accumulation of biomass both above- (AGB) and below-ground (BGB) (Malhi et al. 2011). Most ecological research has focused on identifying drivers of the variation and distribution of AGB (Hofhansl et al. 2015, 2020). BGB can contribute up to 31.4 ± 3.5% (estimated fine-root production) of total vegetation carbon in Amazon forest (Aragão et al. 2009). Nonetheless, horizontal and vertical distributions of BGB in the tropics are much less known (Litton et al. 2007; Obersteiner and Klein 2022). Therefore, recent studies evaluate how edaphic and climatic conditions simultaneously modulate AGB and BGB allocation in different types of forests (Jimenez et al. 2014; Sun et al. 2018; Zhou et al. 2020), but these do not include forests over shallow water tables. This approach plays a crucial role in enhancing our comprehension of how tropical forests might adapt their functioning in response to the escalating effects of climate change.

The "optimal partition theory" (Gedroc et al. 1996) or "balanced growth hypothesis" (Shipley and Meneziane 2002), states that adjustments in BGB:AGB allocation are the result of resource availability constraints. The investment in biomass will be greater for the plant organ that allows mitigating the strongest restrictions imposed by limited resources either above- (CO_2, light) or below-ground (water, soil nutrients). Thus, if light is the most limiting resource, the investment would be directed to aerial structures, such as increasing the specific leaf area for a given unit of plant biomass (higher SLA), or stems that gain height rapidly, both adjustments linked to efficient light capture (Poorter et al. 2011). When soil water is limited, the biomass investment would then be greater for underground structures, such as the construction of deeper roots (Yaffar and Norby 2020), and the increase in specific root length (SRL, the ratio of root length to dry mass of fine roots) per unit of plant biomass, improving the efficiency in the search for and absorption of soil limited resources (Addo-Danso et al. 2020; Cordeiro et al. 2020).

Into the soil, the same principle of limitation by resources in lower supply can be expected (Gedroc et al. 1996, Poorter et al. 2011). Root growth can be limited by nutrient availability (Powers et al. 2004; Cordeiro et al. 2020) and the deficit or excess of water (Fujita et al. 2021; Gaxiola et al. 2010), but also soil physical restrictions (Unger and Kaspar 1994). Soil bulk density directly affects water retention (Assouline 2006; Zipper et al. 2015), which in shallow WT areas may lead to soil waterlogging influencing not only the proportion of biomass allocated belowground but also how

roots distribute along the soil profile (Cusack and Turner 2020; Noguchi et al. 2014). While an increase in rooting depth can improve water foraging in water deficit conditions, a more superficial root distribution can be expected to avoid anoxic conditions in waterlogged soils (Fujita et al. 2021). Moreover, water excess also interacts with soil chemical composition through redox reactions, modulating soil nutrient availability for plants (Ponnamperuma 1972). In P-poor soils , a substantial carbon investment is expected in strategies such as longer fine roots with lower tissue density, high activity of the enzyme phosphatase and the presence of arbuscular mycorrhizal associations, which facilitate the exploration and capture of soil P (Lugli et al. 2020; 2021). Thus, patterns of root vertical distribution and plant biomass allocation should be examined integrating the effects of both soil water and soil nutrient availability, especially in Amazonian soils, which tend to be limited in soil available P (Du et al. 2020; Cunha et al., 2022).

Most of our knowledge about BGB:AGB ratios in tropical forests come from contrasting conditions in terms of rainfall seasonality, soil nutrients, and light availability (Freschet et al. 2015; Paz 2003) but not yet from gradients of WT depth. However, it has been well established that the depth of the water table (WT) limits rooting depth (Fan et al. 2017), due to the oxygen limitation by water excess. At the same time, dry climates may induce an increase of fine-root biomass at deeper soil layers as a response to drought conditions (Engelbrecht and Kursar 2003). On the AGB side, the interaction of climate and WT depth have been shown to modulate the Amazonian AGB productivity (Sousa et al. 2022), potentially due to the temporal fluctuation of the WT levels. Therefore, WT depth seems to be critical to the regulation of BGB:AGB ratios but has not yet been evaluated. Moreover, forests with shallow WTs (depth <5 m) occupy ~50% of total Amazon upland (terra-firme) area, and recent studies have found that shallow WT can prevent these forests from experiencing the negative effects of water deficit during periods of low rainfall or even during drought events (Esteban et al. 2021; Sousa et al. 2020). The integration of above-and belowground water sources is thus critical to model above- and below-ground biomass distributions. We propose that plants can benefit from access to underground water (shallow WT) or experience some negative effects due to water excess (constantly shallow WT), which will affect biomass allocation to roots and BGB:AGB ratios in interaction with the local climate.

In this study, we aim to determine the interplay of precipitation-related water deficit (maximum cumulative water deficit, MCWD), WT regime, soil physical restrictions (soil bulk density),and soil nutrient availability (phosphorus -P, nitrogen -N and the concentration of exchangeable base cations -Base Cations) on the root biomass vertical distribution and on the forest biomass allocation to below- and aboveground components (BGB:AGB ratio) in shallow WT forests. We take advantage

of a large and diverse set of soil, WT, BGB and AGB data from a 600 km transect of shallow WT forests in the central Amazon region. We address the following research questions: (i) Do precipitation-related water deficit (MCWD) and soil density modulate WT regimes?, (ii) Do local variations in WT regime relate to differences in soil nutrient availability?, (iii) How do precipitation-related water deficit and hydro-edaphic conditions (soil density, WT regime and soil nutrient availability) modulate fine-root biomass distribution?, and finally, (iv) How do all these factors interact to modulate the BGB:AGB ratio in these forests? (Figure 1). In addition, we analyze how differences in biomass allocation relate to stem density and average individual AGB, which characterize the forest stand structure.

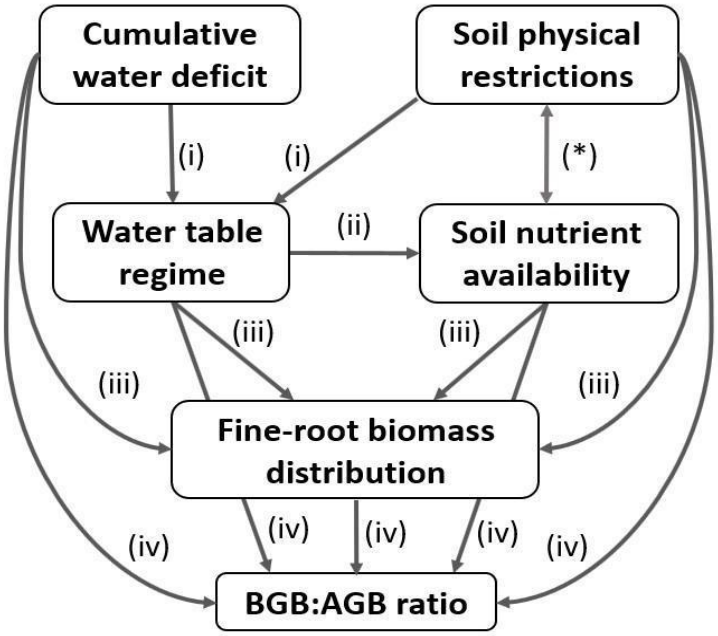


Fig. 1. Conceptual model for testing: (i) the effect of climate precipitation-related water deficit (MCWD) and soil physical restrictions (soil bulk density) on local water table regime; (ii) the influence of water table regime on soil nutrient availability; (iii) their combined effects on vertical fine-root biomass distribution and, (iv) the interplay of these factors in shaping biomass allocation to below- and aboveground components (BGB:AGB ratio) across an Amazon forest region characterized by predominantly shallow water table levels. Single-headed arrows show expected direct effects. (*) We also included an expected correlation between soil physical restriction and nutrient availability, here represented by a double- headed arrow.

Materials and Methods

Study site

The study area is the Purus–Madeira interfluvial region, south of the Amazon River in central Amazonia, Brazil, which has a relatively recent geological origin with unstable sediments from Late Pleistocene or Early Holocene and predominantly flat topography (Sombroek 2000). This region is part of the 'loamy plains' (Sombroek 2000), a landform covering around 11% of the Amazon basin. The mean annual precipitation varies from 2000 to 2400 mm, with two to four consecutive months with <100 mm rainfall ("dry months") per year (Sombroek 2001). The topography is generally flat, with elevation above sea level from 30 to 80 m over large distances (Shuttle Radar Topography Mission data; Rodríguez et al. 2006). The WT is mostly shallow, within 7 m of the surface throughout the year in most of the region (2.8 m ± 2 deep [$M \pm SD$], Sousa et al. 2020). Large areas are waterlogged during the rainy season, some exhibit a shallow flooding column of ~50 cm when the WT reaches its highest levels (Moulatlet et al. 2014). The predominant soil types are Gleysols and Plinthosols with poor drainage, predominant silt to fine-sand texture, and varying degrees of soil water saturation and anoxic conditions (Martins et al. 2014; Sombroek 2000). Soils are generally dense and restrictive to root growth, with varying degrees of hardness and effective soil depth (Martins et al. 2014). The vegetation is classified as lowland dense rainforest in the north and lowland open rainforest dominated by palms in the south (Doi et al. 1978).

Data used in this study was collected in 55 1-ha plots along a 600 km transect in the Purus–Madeira interfluvial region. These plots were systematically distributed in eight research sites along the BR-319 highway, which have been established by the Brazilian Program for Biodiversity Research (PPBio) and follow the RAPELD design (Costa and Magnusson 2010). Each site has five plots regularly distributed along a 5 km trail, 1 km apart from each other, and at least 1 km from the road to avoid sampling forests that may have been recently disturbed by human activity. Plots are 250 m long and follow the terrain altitudinal contour line to reduce within-plot edaphic and hydrological variation and to maximize among plots variation. Our analysis considered 37 plots with data on soil, WT, AGB, BGB and root distribution.

Vegetation data

AGB ($Mg.ha^{-1}$) was based on a census made in 2010-2011 where diameter at breast height (dbh) of all stems with dbh ≥ 30 cm was measured in the full 1 ha (250 m x 40 m) of each plot, stems with dbh ≥ 10 cm were measured in a subplot of 0.5 ha (250 m x 20 m) and stems with dbh ≥ 1 cm were

measured in subplot of 0.025 ha (250 m x 1 m) (Schietti et al. 2016). All palms and trees with above-ground stems measured were considered in the analyses. The AGB of individual trees was calculated based on dbh, height and wood specific gravity, using the pantropical allocation model developed by Chave et al. (2014), with tree height estimations based on diameter-height allometric equations adjusted for each research site along the transect (Schietti et al. 2016). Palm biomass was estimated using the family-level biomass allometric equation based on diameter only (Goodman et al. 2013). Individual biomass in the subplots was summed and extrapolated to a 1 ha basis to express the stand AGB per ha. The stem density and the average individual AGB (descriptors of AGB forest structure) were calculated by summing the number of stems in the subplots and dividing the stand AGB by the density of stems, respectively.

BGB ($Mg.ha^{-1}$) was obtained from roots collected on three soil monoliths per plot in 2012, in the same plots sampled for AGB. The monoliths were cylindrical with 30 cm of diameter and 50 cm in depth. The three monoliths were set 125 m apart from each other and they were used to collect six horizontal soil layers. The first layer was from soil surface to 10 cm above, to account for root biomass formation above the ground. The other five layers were belowground and 10 cm deep, the last being 40 to 50 cm deep. Root measurements across all six layers were considered for both BGB and fine-root distribution. Root material was separated from the soil through decluttering and manual picking on appropriate surfaces, identification of biomass was made by layer and by monolith. After washing, roots were measured using a caliper and separated into four classes according to their diameter (<2, 2-5, 5-20 and >20 mm). Root biomass in each soil layer was estimated as the mean of the total root biomass for that layer across the three soil monoliths per plot. Values of BGB per plot are the sum of the average root biomass in each root diameter class along all measured soil layers. We observed that BGB data in the >20 mm diameter class (coarse roots) exhibit great variability both between and within each plot. Since this variability may potentially bias the total BGB values across plots, we conducted our analyses considering BGB as the sum of all root diameter classes (total BGB) but also excluding the coarse roots biomass to check if, and how, our results may vary depending on the inclusion of coarse roots.

The BGB:AGB ratio - the proportion of forest biomass allocated to its components below and above ground - was calculated based on total (or excluding coarse roots) BGB and total AGB per plot.

Fine-root vertical distribution

To characterize the vertical fine-root (< 2mm diameter) biomass distribution along the soil depth, we adjusted an asymptotic nonlinear model following Gale and Grigal (1987):

$$Y = 1 - \beta^d$$

where d is the soil depth (cm), Y is the accumulated fine-root biomass up to that depth, and β is an index that represents the shape of the vertical distribution curve of this biomass along the soil profile. Based on field data of Y and d up to 50 cm, we fitted the model and obtained a β value for each of the 37 plots. Low values of this index are indicative of shallower distributions, i.e., with a higher concentration of root biomass in (or restricted to) the upper soil layers. By contrast, higher values of β characterize curves with a fine-root biomass distribution reaching deeper soil layers. In addition, based on this β index, we further estimated the total fine-root biomass per plot across the soil profile (i.e. for depths > 50 cm) and determined the depth (in cm) at which 90% of this total fine-root biomass is accumulated (i.e., d for $Y = 0.9$).

Soil and environmental data

Soil bulk density was measured by extracting soil samples in the same depths and locations along the plots where root biomass was estimated. Soil samples were collected using metal rings and each sample was dried in an oven at 105º C up to obtain constant weight after three successive measurements (dry mass). Soil bulk density was obtained dividing the soil dry mass by the volume of the ring used to extract the soil. Soil bulk density for each 10-cm layer was the average of the density value obtained in each of the three rings for that soil layer. Here we used soil bulk density per plot as the average density value over the five soil depth layers (0-50 cm).

As proxies of soil nutrient availability , we used the available P content, N content, and the concentration of exchangeable cations (Ca^{2+}, K^+, Mg^{2+}). Soil chemical properties were determined in a compound sample derived from six subsamples from the first 30 cm depth of soil extracted with an auger every 50 m along the central line in each of the 37 plots. Available Ca^{2+} and Mg^{2+} were extracted by KCl 1N method; available K^+ and P by Mehlich's I extraction solution and read by atomic spectrometry; and total N determined via Kjeldahl digestion using sulfuric acid digestion (Donagema et al. 2011). The analyses were conducted at the Plant and Soil Thematic Laboratory at INPA (Manaus, Brazil).

MCWD (maximum cumulative water deficit) is the maximum value of monthly accumulated precipitation-related water deficit, i.e., the sum of deficit values over consecutive months when

evapotranspiration (ET) is greater than rainfall within each hydrological year (Aragão et al., 2007; Esquivel-Muelbert et al., 2019). The hydrological year is defined as starting in the wettest month of each site, determined from its precipitation time series, thus adjusting for differences in seasonality among sites. Here, MCWD was based on the long-term average of annual MCWD values per plot, from 1958 to 2020, to represent historical mean climatic conditions at each site. Rainfall data were extracted from the Tropical Rainfall Measuring Mission satellite (3B43 7A; Huffman et al. 2007), at 0.25º spatial resolution. Monthly ET was assumed to be fixed at 100 mm per month, considering that Amazonian forest canopies have a nearly constant ET rate (Rocha et al. 2004; Shuttleworth 1988).

WT depth was monitored using piezometers from 2010 to 2013 in all plots. Each plot had one piezometer 7 m deep in the ground, monitored every 2-4 months. From these temporal data, we first classified each WT depth value into five categories, from shallow (depth 4-7 m) to very shallow WT levels (depth < 1 m). We then give weights to each category, from 4 (fluctuating shallow) to 0 (persistently shallow), calculated the weighted mean value per plot and used that as an index to represent not just the mean but also the temporal WT depth fluctuation (hereafter WT regime) (Figure S1), shown to be an important modulator factor in Amazon forests (Costa et al. 2023). Hence, lower values of WT regime index denote a persistently shallow WT, whereas higher values indicate a fluctuating shallow WT.

Statistical analysis

All data analyses and visualizations were performed in the R (version 4.2.3) statistical software package (R Core Team 2023). To analyze the interplay of factors as stated in our conceptual model (Figure 1), we used piecewise structural equation modeling (pSEM) since it incorporates a wide variety of model structures, distributions, and assumptions on the response variables (Liefcheck 2016). A total of six pSEMs were analyzed, one per proxy of soil nutrient availability (P, N and Base Cations), with each model being repeated for BGB with and without coarse roots to obtain BGB:AGB ratios. We started with our full hypothesized conceptual model, iteratively removing non-significant paths and considering other reasonable pathways and interaction effects, beyond those described on the conceptual model. Sites were included as random effects to account for the nested design (Zuur et al. 2009). We used linear mixed-effect regression models to construct the pSEM using the piecewiseSEM package (Lefcheck 2016), and to indicate if any missing path should be incorporated, confirmatory path analyses were conducted based on the directional separation test (*d*-separation test) (Shipley 2013). We report the variance explained by fixed predictors (R^2_m) and by both fixed and

random effects (R^2_c) for each response variable in the pSEM, the relative contribution (standard estimate) of each significant predictor, as well as the model fit statistics Akaike's information criterion (AIC), Fisher's *C* statistic, and associated *p*-value ($P > 0.05$ indicating reasonable fit of model to data; Shipley 2009). Finally, Pearson's correlation analyses were conducted to assess how BGB:AGB ratios are associated to the total number of stems and to mean individual AGB, both descriptors of AGB forest structure.

Results

BGB:AGB ratio and fine-root biomass distribution in shallow WT forests

AGB of trees and palms with dbh ≥ 1 cm ranged from 80.2 to 274.5 $Mg.ha^{-1}$ (mean ± SD = 156.7 ± 47.4 $Mg.ha^{-1}$), while BGB for roots with diameter up to 20 mm and within a soil depth of 50 cm varied from 7.7 to 36.3 $Mg.ha^{-1}$ (mean ± SD = 24.1 ± 7.2 $Mg.ha^{-1}$). This resulted in a BGB:AGB ratio ranging from 0.04 to 0.35 (mean ± SD = 0.17 ± 0.07) across 37 1-ha plots of shallow WT forests.

Estimated β values show the variability of the fine-root biomass vertical distribution across shallow WT forests. β values varied from 0.87, representing a fine-root biomass strongly restricted to the most superficial soil layers, where 90% of biomass is located into the first 17 cm of the soil, up to a value of 0.95, indicating deeper distributions, with 90% of fine-root biomass reaching 45 cm of soil depth (Figure 2). This distribution index is tightly correlated with the rooting depth, with more uniform distribution along soil depth (higher β values) being associated with greater rooting depth (Figure S2a). Moreover, the relationship observed between β index and the estimated total fine-root biomass suggest higher root biomass in shallower distributions. (Figure S2b).

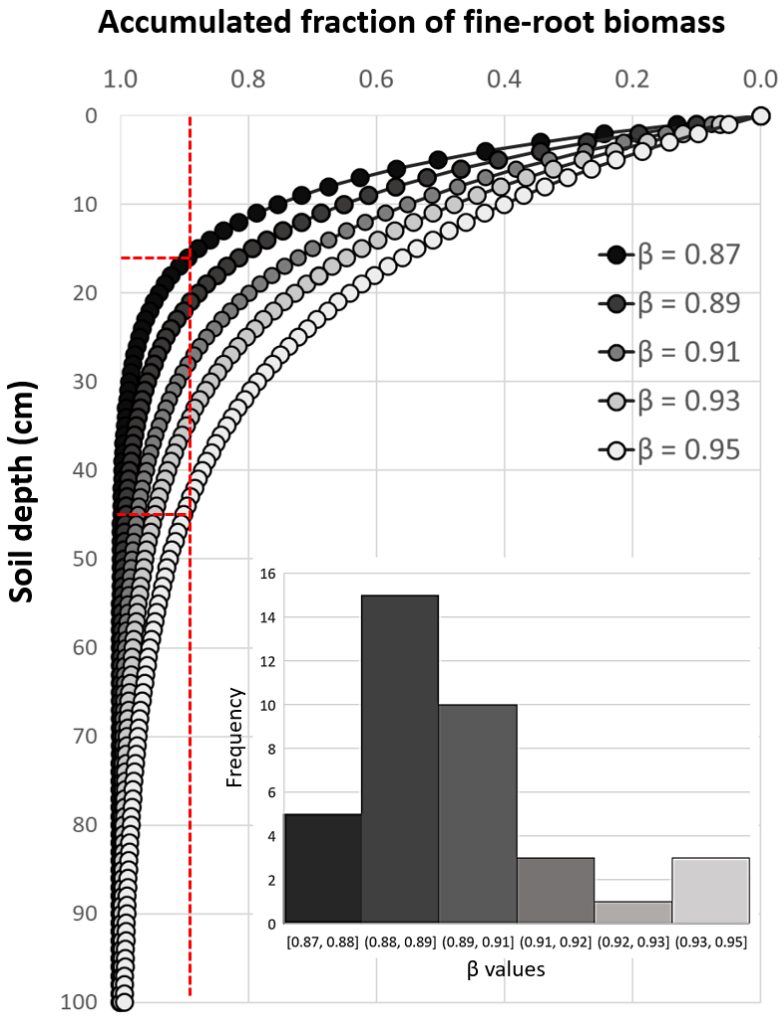


Fig. 2. Variation in the vertical distribution of fine-root biomass for Amazonian terra-firme forests with shallow water tables. Each curve represents the distribution of fine-root biomass (as the cumulative fraction of the total biomass, horizontal axis) along the soil depth (vertical axis, in cm) obtained across the 37 study plots. The vertical dashed red line indicates the point at which 90% of the total fine-root biomass is accumulated, and the horizontal red lines exemplify the depth at which this value is reached in the plot with the lowest (0.87) β values (17 cm of soil depth), and for the plot with the highest (0.95) β values (45 cm depth). A histogram depicting the frequency distribution of β values across the 37 plots is also shown.

Associations of fine-root biomass distribution and BGB:AGB ratio with soil water regime and nutrient availability

The pSEM model using soil-available P and BGB values without coarse roots, retained significant effects in some of the pathways stated in our general conceptual model (thick lines on Fig. 3). This

pSEM shows effects of: (i) soil density on the WT regime; (ii) WT regime on soil available P, (iii) MCWD and WT regime on fine-root biomass distribution; and (iv) fine-root biomass distribution and soil available P on BGB:AGB ratios (Figure 3, S3 and Table 1). When the model is run including coarse roots in the BGB values, most of the significant effects persisted, except for the effect of fine-root distribution on the BGB:AGB ratio (Fig. S4). Furthermore, models using soil N and Base Cations also show the effect of soil density on the WT regime and the effect of MCWD and WT regime on fine-root biomass distribution, but both models do not exhibit significant effects associated with nutrient availability (Figure S5 and Tables S1 and S2).

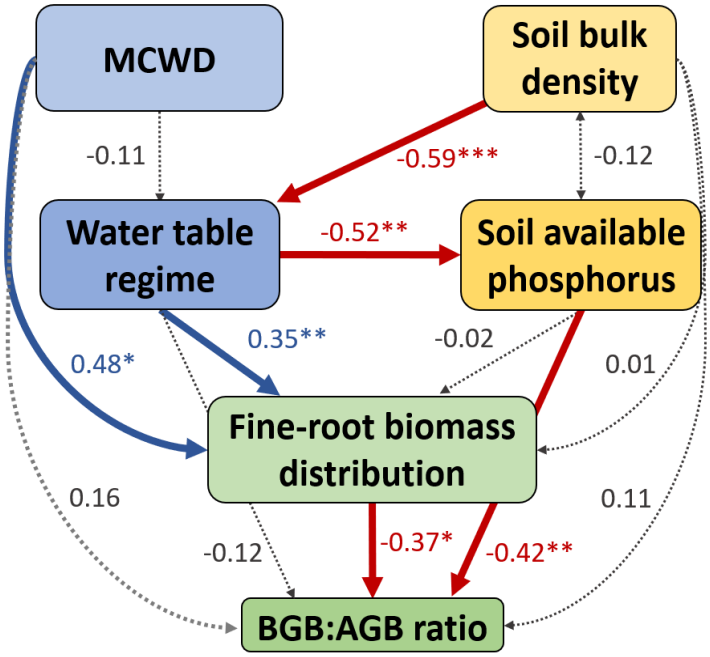


Fig. 3. Result of piecewise SEM model to understand the distribution of fine-roots and the BGB:AGB ratio of Amazonian terra-firme forests (37 plots) characterized by shallow WTs along the Purus-Madeira interfluve. Results shown here are for the model using soil available P as a proxy of soil nutrient availability and BGB values without coarse roots. The model was fitted to test: (i) the effect of cumulative water deficit and soil density on WT regime (lower values indicate consistently shallow WT levels year-round); (ii) the influence of WT regime on soil nutrient availability; (iii) their combined effects on vertical fine-root biomass distribution (lower values indicate a higher concentration of fine-root biomass in the upper soil layers) and, (iv) the interplay of these factors in shaping biomass allocation to below- and aboveground components (BGB:AGB ratio). Blue and red arrows denote significant positive and negative relationships, respectively. Dashed gray arrows represent paths included in our general conceptual model that were not retained

as significant effects in the final model. Numbers are the standardized coefficients of determination for each predictor. (*) p<0.05, (**) p<0.01, (***) p <0.001.

Table 1. Summary of piecewise structural equation model (pSEM) results when using soil available phosphorus as a proxy for soil nutrient availability. In the table, *Std. est* denotes the standardized estimation values for each predictor; *P* is the associated probability, with values in bold indicating significant effects; R^2_m is the fixed-effects coefficient of determination, representing the proportion of the variance for a response variable explained by all fixed effects included in the model; R^2_c is the conditional-effect coefficient of determination, representing the proportion of the variance explained by the random effects included in the model. Model fit statistics Fisher's C, AIC (Akaike information criteria) and P (p-value) are also shown.

Path	Response	Std. est	P	R2m	R2c
Predictor					
MCWD	WT regime	-0.11	0.616		
Soil bulk density	WT regime	-0.59	**<0.001**	0.35	0.54
WT regime	Soil available P	-0.52	**0.004**	0.23	0.46
MCWD	Fine-root distribution	0.48	**0.038**		
Soil bulk density	Fine-root distribution	0.01	0.961		
WT regime	Fine-root distribution	0.35	**0.003**		
Soil available P	Fine-root distribution	-0.02	0.859	0.41	0.75
MCWD	BGB:AGB ratio	0.16	0.368		
Soil bulk density	BGB:AGB ratio	0.11	0.552		
WT regime	BGB:AGB ratio	-0.12	0.234		
Soil available P	BGB:AGB ratio	-0.42	**0.006**		
Fine-root distribution	BGB:AGB ratio	-0.37	**0.025**	0.30	0.37
Correlation					
Soil bulk density	Soil available P	-0.12	0.234		
Fisher's *C*		10.64			
AIC		-115.02			
P		0.831			

Soil bulk density had no significant direct effect on the fine-root biomass distribution ($p=0.961$), but had a positive direct effect on the WT regime ($p<0.001$), with denser soils associated with more superficial WT levels year-round. MCWD had no significant effect on the WT regime ($p=0.616$). Differences in WT regimes were associated with variation in soil nutrient availability ($p=0.004$), with shallower WT regimes associated with P-richer soils. Moreover, both MCWD ($p=0.038$) and WT regime ($p=0.003$) had direct effects on fine-root biomass distribution, with regions with low cumulative water deficit or constantly shallow WT year- round exhibiting a fine-root biomass more restricted to upper soil layers. No significant direct effect of soil available P on fine-root biomass distribution was observed ($p=0.859$). Moreover, soil density indirectly affects the fine-root biomass distribution and soil phosphorus availability, via the WT regime. Finally, the BGB:AGB ratio was directly affected by the fine-root biomass distribution ($p=0.025$) and soil-available P ($p=0.006$), with indirect effects of MCWD and the WT regime. With more restricted root distributions to surface soil layers, or higher nutrient limitation, shallow WT forests allocate more biomass to their belowground components (higher BGB:AGB ratio). It is important to note that our results are partially influenced by the inclusion of coarse roots (>20 mm diameter) (Fig. S4). Through simulations, we found that the effect of soil-available P (Fig. S6) remains constant regardless of whether coarse root biomass is included or not. However, the effect weakens or is lost when biomass values exceed 40 mg/ha. By contrast, the distribution of fine root biomass loses its effect on the BGB:AGB ratio when coarse root biomass is considered.

During the pSEM modeling, a significant interaction effect was detected between soil available P and the WT regime on BGB:AGB ratio (Figure 4, Table S3). The interaction indicates that P levels affect the below to aboveground biomass allocation only in sites that are not constantly limited by water excess (seasonally shallow WT regime, black line on Fig. 4), with forests allocating less biomass for roots (lower BGB:AGB) in P- richer soils. Yet, in areas where the WT remains very close to the soil surface year-round (constantly shallow WT regimes), variation in soil P does not affect BGB:AGB ratios (dotted gray line, Fig. 4).

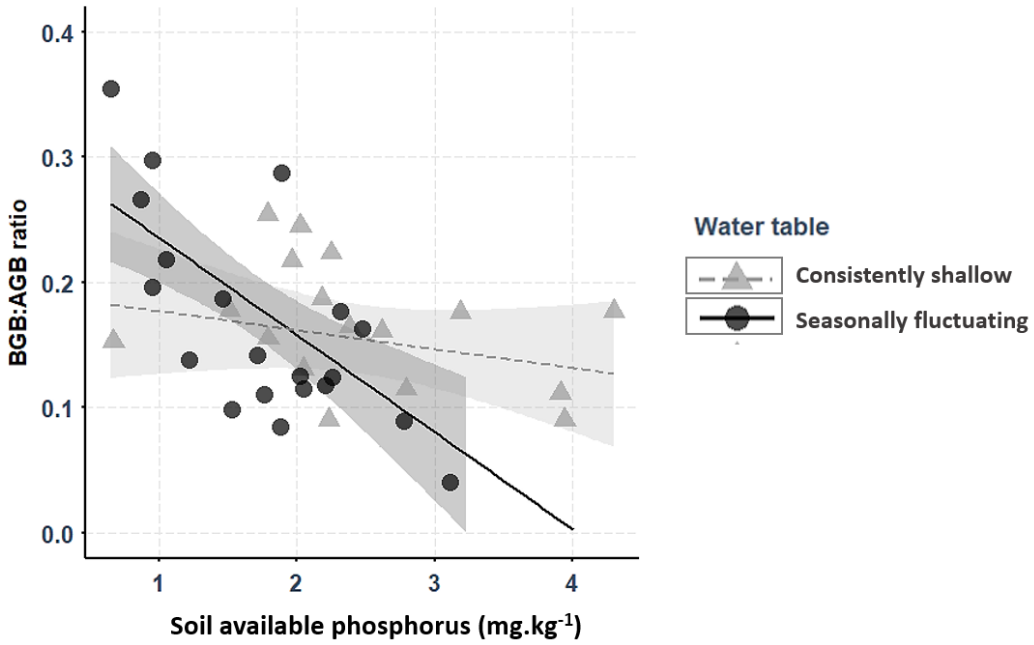


Fig. 4. Significant interaction effect between soil P availability and WT regime on BGB:AGB ratio of Amazonian forests (37 plots) characterized by shallow WTs along the Purus-Madeira interfluve, central Amazon. Forests were classified in two categories based on the WT regime: areas where the WT remains superficial year-round (consistently shallow WT), and areas where the WT fluctuates throughout the year (seasonally fluctuating WT).

BGB:AGB ratio relationship with stem density and mean individual AGB

The variation in BGB:AGB ratio correlates with both the stem density and the mean individual biomass. Forests that allocate more biomass to the aerial component (lower BGB:AGB) have AGB structures characterized by lower number of stems with greater individual biomass. In contrast, forests allocating more biomass to their belowground component (higher BGB:AGB) exhibit higher stem density, albeit with lower mean individual biomass (Figure 5).

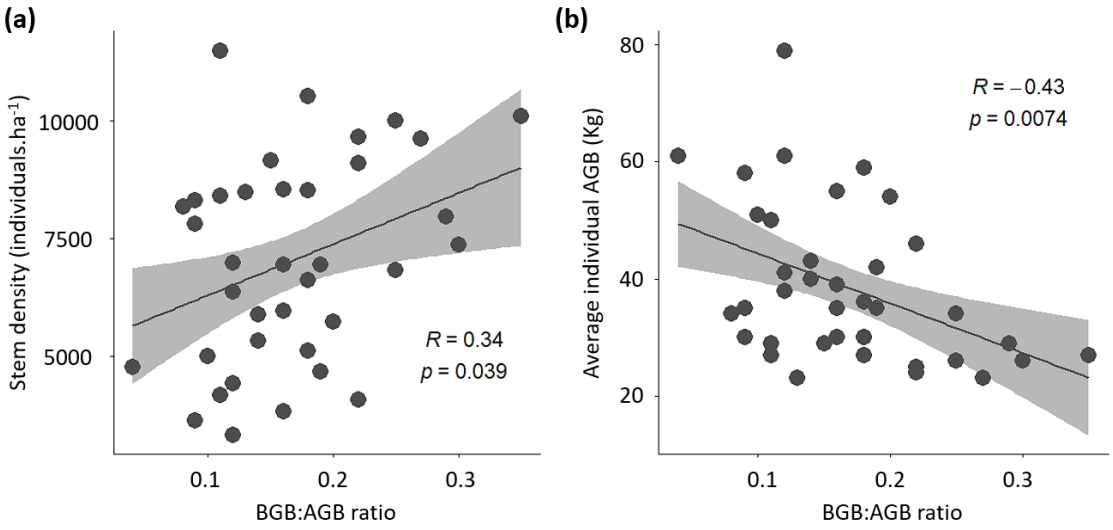


Fig. 5. Association between the distribution of forest biomass to below- and aboveground components (BGB:AGB ratio) with (a) the stem density (the number of stems per unit area) and (b) the average individual AGB (the result of dividing the total AGB of each plot by the number of stems in that plot), in 37 plots along the Purus-madeira interfluve, central Amazon.

Discussion

We aimed at investigating the interplay of water availability (represented by MCWD and WT regime), soil physical restrictions (represented by soil density) and soil nutrient availability (P, N and Base Cations) on fine-root biomass vertical distribution and below to aboveground biomass allocation on Amazon terra-firme forests with shallow WTs. The study reveals that (i) denser soils contribute to maintain a WT constantly superficial throughout the year (constantly shallow WT regime), (ii) soils with constantly shallower WT regimes have higher soil available P, (iii) shallower WT regimes and/or lower MCWD lead to fine-root biomass being more concentrated in upper soil layers, and (iv) fine-root biomass distribution and soil available P are then the direct predictors of forest biomass allocation, with higher allocation to belowground components (higher BGB:AGB ratio) where fine roots are more surface-constrained and/or in more P-limited soils (Figure 3). Such variation in biomass allocation is linked to the aboveground forest structure, as forests with higher BGB:AGB ratio have higher stem density with lower individual AGB (Figure 5). We further detected that low phosphorus levels only limit the allocation to AGB when it is not already limited by the water excess created by constantly shallow WT (Figure 4).

More constantly shallow WT regimes were associated with a higher soil bulk density, and contrary to our expectation, not significantly related to low MCWD. Soil density along the study region

varies from 1.2 to 1.65 $g.cm^{-3}$, with some areas having values higher than 1.40 $g.cm^{-3}$ (Figure S7). Denser soils are associated with finer texture and greater binding between soil particles, properties that increase soil water retention, limit infiltration, and reduce drainage (Quesada et al. 2010). Here, denser soils combined with shallow WTs and a flat topography may keep groundwater levels close to the surface for longer periods (i.e., constantly shallow WT regimes), leading to extended saturation of the pore spaces and potentially to soil waterlogging (Nobre et al. 2011). In the study sites, the WT fluctuates mostly within the first 7 m of soil depth, with just four plots recording deeper WT levels, and in 30% of plots WT fluctuates mostly within the first 3 m throughout the year (Figure S1). The simultaneous presence of denser soils and shallow WT regimes imply that a good portion of these areas may experience transient or even prolonged soil waterlogging conditions.

The higher soil P availability associated with constantly shallow WT regimes can be related to the waterlogging effect on soil chemical properties, mainly due to soil oxygen depletion (Blom and Voesenek 1996). In waterlogged soils, water and air movement is limited, with water filling the air spaces between the pores, leading to low (hypoxia) or no (anoxia) available oxygen and an accumulation of carbon dioxide (Kozlowski 1985). As oxygen decreases, microbial processes are affected, soil redox potential decreases, soil pH changes, N is reduced to non-assimilable forms and reduced metal ions, organic and volatile acids that can be toxic for plants are accumulated (Arslan 2012; Jackson and Colmer 2005; Lucassen et al. 2000). Yet, soil P may become more available in such conditions, mainly due to the solubilization of complexes with Fe and Al, and the increased P effective diffusion coefficient in water (Ponnamperuma 1972; Patrick and Mahapatra 1968). Nonetheless, since low oxygen levels and the presence of toxic compounds negatively affect root functioning (Fan et al. 2017; Schenk and Jackson 2005; Unger and Kaspar 1994), an expected positive impact of higher P availability on plant performance may occur only when soil water excess is not a limiting factor.

The higher proportion of fine-root biomass constrained to upper soil layers in areas with constantly shallow WT regimes and/or with lower MCWD may reflect plant adaptations to potential lack of oxygen due to soil waterlogging conditions. Prolonged anoxic conditions raise cellular acidity levels, due to a series of metabolic adjustments such as the activation of anaerobic fermentation (Kreuzwieser et al. 2009; Kreuzwieser and Rennenberg 2014). This greater acidity reduces the conductance of the roots, which induces the closure of the stomata, reducing CO_2 absorption and, consequently, limiting the photosynthetic process (Parent et al. 2008, Aroca et al. 2011). Thus, a higher proportion of fine-root biomass restricted to superficial soil layers may function to

counterbalance the physiological limitations occurring at deeper water-saturated layers, helping to recover or maintain hydraulic conductance at the whole plant level (Fujita et al. 2021).

The restriction of root biomass distribution with soil water excess can therefore be directly linked to a limitation in the AGB allocation, with forests allocating less biomass to the aboveground component (thus, increasing BGB:AGB ratio) when fine-roots are more restricted to upper soil layers. Higher BGB:AGB ratios are commonly reported for trees in seasonal forests, being related to plant responses for enhancing soil water uptake (Cusack et al. 2021; Hodge 2004; Mokany et al. 2006; Poorter et al. 2011). Conversely, higher BGB:AGB ratio in shallow WT forests is linked to more restricted root biomass distribution, associated with higher root biomass (Figure S2b) along with limitations on AGB allocation, in response to conditions of soil water excess, rather than to water deficit. Previous studies do not show a clear pattern of waterlogging effect on forest biomass allocation, with some showing an increase in root allocation, attributed to increased adventitious root production (Lenssen et al. 2003; Parolin 2001), while others show decreased root allocation (Rubio et al. 1997; Voesenek et al. 1989), no waterlogging effect (Rubio and Lavado 1999), or responses being dependent on the species (Gaxiola et al. 2010).

Contrary to our expectation, and to results observed in central Amazon forest areas with deeper WT (see Cordeiro et al., 2020), soil nutrient availability was not significantly related to fine-root biomass distribution. The more superficial fine-root distributions associated to shallow WT regimes but not to soil nutrient availability suggest that, among the studied plots, soil water conditions impose a stronger limitation than soil nutrient availability on this belowground forest component. The stronger effect of soil water excess than that of soil P limitation is also seen for the biomass allocation. We detected that forests had lower BGB:AGB ratios in richer-P soils when soil water excess was not common, i.e., when shallow WT levels were seasonal rather than constant year-round (Figure 4). This is in accordance with the optimal partition theory, with plants reducing root investment to capture and absorb soil nutrients in richer soils (Reich et al. 1998; Reynolds and Thornley 1982; Thornley 1972). Here we argue that the combination of shallow WT regimes less prone to soil waterlogging (seasonal) and with higher soil nutrient availability may establish favorable below ground conditions for plants, leading forests to reduce root investment and increase allocation to aboveground components (Cruz-Amo et al. 2020; Cusack and Turner 2020; Zhou et al. 2020). By contrast, with constantly shallow WT regimes leading to low soil oxygen, roots may face constraints to respiration and thus the production of ATP (adenosine triphosphate) to support physiological processes. Thus, the interaction between the WT regime and soil P implies that water regime affects plant nutrient uptake, preventing the expected positive effect of soil nutrient

availability on biomass allocation when the WT regime is too shallow. This also reinforces that, when multiple stress conditions interact, their effects on biomass allocation can be different than expected with isolated effects (Gaxiola et al. 2010).

Finally, we show that varying BGB:AGB ratios translate into variations of stem density and average individual mass among the studied shallow WT forests. As forests allocate more biomass to their belowground components (higher BGB:AGB ratios), their stand structures are characterized by a higher number of stems with lower mean individual AGB (high density of small trees). We argue that this allocation-size structure relationship develops from soil water constraints on BGB and its cascading effects on the dynamics of AGB. Shallow WT regimes limit roots to more superficial distributions and lower rooting depth (Figure S2a, Fan et al. 2017), leading to poor anchoring that may increase stem fall and uprooting (Ferry et al. 2010; Toledo et al. 2016), giving rise to more dynamic forests (Vilanova et al. 2018).

In the same region, Cintra et al. (2013) found that soils with higher bulk density, shallow effective depth and high water saturation harbor more dynamic forests, with higher biomass turnover rates and younger forest stands. They suggest that constraints to plant growth imposed by waterlogging limit the stands' development. Our results contribute to reveal how this limitation occurs. To compensate for waterlogging stress and improve resource uptake, forests allocate more biomass to roots (restricted to upper soil layers) and consequently, lower biomass is available to aerial components. The combination of higher root biomass and lower aerial biomass (smaller trees) is likely an appropriate strategy to deal with such environmental conditions. Small stem sizes can reflect younger forests (as shown in Cintra et al., 2013 for some plots analyzed here), where higher allocation to roots is expected to improve soil resources' uptake for fast growth and survival (Cairns et al. 1997; Niklas 2005; Poorter et al. 2011). Moreover, higher dynamism is linked to increased gap formation (Goulamoussène et al. 2017), favoring the establishment of new individuals, finally resulting in higher density of lower-AGB trees.

Conclusion

This study is pioneering in assessing the impact of soil water regime and nutrient availability on biomass distribution and allocation in forest areas dominated by shallow water tables. We show that the combined effect of soil water excess and nutrient limitation strongly shapes the distribution of fine-root biomass and BGB:AGB ratios, with consequences for the size structure of the aboveground component. Our findings of groundwater fluctuation being primarily conditioned by soil density, rather than climatic factors, highlights the main role of soil constraints in shaping forest

structure, suggesting soil density as a proxy for soil water regime in shallow WT regions. In addition, restrictions to fine-root distribution linked to soil water conditions, but not to soil nutrient availability, suggest that water regime imposes a stronger limitation than soil nutrients on the belowground component of shallow WT forests.

In a scenario of shifting rainfall patterns and drier conditions, a deepening of the WT can be expected. In regions characterized by deep WT, where rainfall is the main water source for plants, this drier scenario negatively affects forests, increasing tree mortality and limiting growth (Bennet et al. 2023). Yet, in areas with shallow WT, a deepening of WT regimes may alleviate plant waterlogging stress. A continuous water supply, coupled with the diverse P-acquisition strategies of plants in P-impoverished Amazonian soils (Lugli et al. 2020), may potentially lead to counterintuitive effects in shallow WT forests, such as increased growth. Representing over 50% of terra-firme forests in the Amazon region, what happens to shallow WT forests is of high relevance to the future of this region (Costa et al. 2023; Miguez-Macho and Fan 2012). Further efforts should focus on continuing and expanding the monitoring of soil water regimes in shallow WT forests, along with a comprehensive assessment of fine-root dynamics and plant strategies for resource acquisition in these environments. This broader approach will contribute to elucidating spatial and temporal soil water regime variations and its anticipated impact on Amazon forests' response and resilience to rapid climate change.

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Author contributions.

ECC and EJLE were equal co-leaders of this work. FRCC, JPVP, JS, JT and TE conceived the study. ECC, EJLE and FRCC designed the analysis. TE, DLM, JS and JPVP conducted field work and collected the data. ECC and EJLE carried out the analysis and wrote the first draft of the manuscript. FRCC, TE, DLM, JS and JT critically reviewed and commented on the article. FRCC helped with the writing of the article. All authors gave final approval for publication.

Competing interests.

The authors declare that they have no conflict of interest.

References

Addo-Danso SD, Defrenne CE, McCormack ML, Ostonen I, Addo-Danso, A, Foli, EG, Borden KA, Isaac ME, Prescott CE (2020) Fine-root morphological trait variation in tropical forest ecosystems: an evidence synthesis. Plant Ecol. https://doi.org/10.1007/s11258-019-00986-1

Aragão LEOC, Malhi Y, Roman-Cuesta RM, Saatchi S, Anderson LO, Shimabukuro YE (2007) Spatial patterns and fire response of recent Amazonian droughts. Geophys Res Lett. https://doi.org/10.1029/2006GL028946

Aragão LEOC, Malhi Y, Metcalfe DB, Silva-Espejo JE, Jiménez E, Navarrete D, Almeida S, Costa ACL, Salinas N, Phillips OL, Anderson LO, Alvarez E, Baker TR, Goncalvez PH, Huamán-Ovalle J, Mamani-Solórzano M, Meir P, Monteagudo A, Patiño S, Peñuela MC, Prieto A, Quesada CA, Rozas-Dávila A, Rudas A, Silva Jr JA, Vásquez R (2009) Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. Biogeosciences. https://doi.org/10.5194/bg-6-2759-2009

Aroca R, Porcel R, Ruis-Lozano JM (2011) Regulation of root water uptake under abiotic stress conditions. J Ex. Bot. https://doi.org/10.1093/jxb/err266

Arslan M (2012) Waterlogging stress in plants: A review. Afr J Agric Res 7(13):1976-1981. https://doi.org/10.5897/AJARX11.084

Assouline S (2006) Modeling the relationship between soil bulk density and water retention curve. Vadose Zone J 5:554–563. https://doi:10.2136/vzj2005.0083

Bennett AC, Sousa TR, Monteagudo-Mendoza A et al (2023) Sensitivity of South American tropical forests to an extreme climate anomaly. Nat Clim Change 13:967-974. https://doi.org/10.1038/s41558-023-01776-4

Blom CW, Voesenek LA (1996) Flooding: The survival strategies of plants. Trends Ecol Evol 11(7):290-295. https://doi.org/10.1016/0169-5347(96)10034-3

Cairns MA, Brown S, Helmer EH, Baumgardner GA (1997) Root biomass allocation in the world's upland forests. Oecologia 111:1-11.

Chave J, Réjou-Méchain M, Búrquez A et al (2014).: Improved allometric models to estimate the aboveground biomass of tropical trees. Glob Change Biol 20(10):3177-3190. https://doi.org/10.1111/gcb.12629

Cintra BBL, Schietti J, Emillio T, Martins D, Moulatlet G, Souza P, Levis C, Quesada CA, Schöngart J (2013) Soil physical restrictions and hydrology regulate stand age and wood biomass turnover rates of Purus-Madeira interfluvial wetlands in Amazonia. Biogeosciences 10:7759–7774. https//: doi:10.5194/bg-10-7759-2013.

Cordeiro AL, Norby RJ, Andersen KM, Valverde-Barrantes O, Fuchslueger L, Oblitas E, Hartley IP, Iversen CM, Gonçalves NB, Takeshi B, Lapola DM, Quesada CA (2020) Fine-root dynamics vary with soil depth and precipitation in a low-nutrient tropical forest in the Central Amazonia. Plant-Environment Interactions1:3-16. https://doi:10.1002/pei3.10010

Costa FRC, Magnusson WE (2010) The need for large-scale, integrated studies of biodiversity - the experience of the program for biodiversity research in Brazilian Amazonia. Nat Conserv 8:3–12. https://doi: 10.4322/natcon.0080 1001.

Costa FRC, Lang C, Sousa TR, Emilio T, Esquivel-Muelbert A, Schietti J (2023) Fine-grained water availability drives divergent trait selection in Amazonian trees. Front For Glob Change 6:1112560. https://doi: 10.3389/ffgc.2023.1112560

Cruz-Amo L, Bañares-de-Dios G, Cala V, Granzow-de la Cerda I, Espinosa CI, Ledo A, Salinas N, Macía MJ, Cayuela L (2020) Trade-offs among aboveground, belowground, and soil organic carbon stocks along altitudinal gradients in Andean Tropical Montane Forests. Front Plant Sci 11:1-11. https//doi: 10.3389/fpls.2020.00106

Cusack DF, Addo-Danso S, Agee EA et al (2021) Tradeoffs and Synergies in Tropical Forest Root Traits and Dynamics for Nutrient and Water Acquisition: Field and Modeling Advances. Front For Glob Change 4:704469. https://doi: 10.3389/ffgc.2021.704469

Cusack DF, Turner BL (2020) Fine root and soil organic carbon depth distributions are inversely related across fertility and rainfall gradients in lowland tropical forests. Ecosystems 24:075–1092. https://doi: 10.1007/s10021-020- 00569-6

Doi S, Guimarães JG, Sillman MS, Barros-Silva S, Ribeiro AG, Ferreira H, Araújo ATR, Junior OK, Almeida, EF, Furtado PP, Magnago H, Veloso HP, Góes-Filho L (1978) Vegetação: As regiões fitoecológicas, sua natureza e seus recursos econômicos, in: Folha SB. 20 Purus ; geologia, geomorfologia, pedologia, vegetação, uso potencial da terra / Projeto RADAMBRASIL, Projeto RADAMBRASIL, Rio de Janeiro, pp 365-490

Donagema GK., de Campos DVB, Calderano SB, Teixeira WG, Viana, JHM (2011) Manual de Métodos de Análises de Solo. Empresa Brasileira de Pesquisa Agropecuária: Embrapa Solos, Rio de Janeiro, Brasil

Engelbretch BMJ, Kursar TA (2003) Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. Oecologia 136:383-393. https://doi.org/10.1007/s00442-003-1290-8

Esquivel-Muelbert A, Baker TR, Dexter KG et al (2019) Compositional response of Amazon forests to climate change. Glob Change Biol 5:39–56. https://doi: 10.1111/gcb.14413

Esteban EJL, Castilho CV, Melgaço KL, Costa FRC (2021) The other side of droughts: wet extremes and topography as buffers of negative drought effects in an Amazonian forest. New Phytol 229(4):1995-2006. https://doi.org/10.1111/nph.17005

Fan Y, Miguez-Macho G, Jobbagy EG, Jackson RB, Otero-Casal C (2017) Hydrologic regulation of plant rooting depth. Proc Natl Acad Sci 114(40):10572-10577. https://doi.org/10.1073/pnas.1712381114

Ferry B, Morneau F, Bontemps JD, Blanc L, Freycon V (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rainforest. J Ecol 98(1):106-116. https://doi.org/10.1111/j.1365-2745.2009.01604.x

Freschet G, Swart EM, Cornelissen JHC (2015) Integrated plant phenotypic responses to contrasting above- and below-ground resources: key roles of specific leaf area and root mass fraction. New Phytol 206:1247-1260. https://doi: 10.1111/nph.13352

Fujita S, Noguchi K, Tange T (2021) Different waterlogging depths affect spatial distribution of fine root growth for *Pinus thunbergii* seedlings. Front Plant Sci, 12:614764. https://doi: 10.3389/fpls.2021.614764

Gaxiola A, McNeill SM, Coomes DA (2010) What drives retrogressive succession? Plant strategies to tolerate infertile and poorly drained soils. Funct Ecol 24:714–722. https://doi: 10.1111/j.1365-2435.2010.01688.x

Gale MR, Grigal DF (1987) Vertical root distributions of northern tree species in relation to successional status. Canadian Journal of Forest Research 17:829–834. https://doi.org/10.1139/x87-131

Gedroc JJ, Mcconnaughay KDM, Coleman JS (1996) Plasticity in root/shoot partitioning: optimal, ontogenetic, or both?. Functional Ecology 10(1):44-50. https://doi.org/10.2307/2390260

Goodman RC, Phillips OL, del Castillo Torres D, Freitas L, Cortese ST, Monteagudo A, Baker TR (2013) Amazon palm biomass and allometry. Forest Ecol Manag 310:994–1004. https://doi.org/10.1016/j.foreco.2013.09.045

Goulamoussène Y, Bedeau C, Descroix L, Linguet L, Hérault B (2017) Environmental control of natural gap size distribution in tropical forests. Biogeosciences 14:353-364. https://doi.org/10.5194/bg-14-353-2017

Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytol 162:9–24. https://doi: 10.1111/j.1469-8137.2004.01015.x

Hofhansl F, Chacón-Madrigal E, Fuchslueger L, Jenking D, Morera-Beita A, Plutzar C, Wanek W (2020) Climatic and edaphic controls over tropical forest diversity and vegetation carbon storage. Scientific Reports 10:5066. https://doi.org/10.1038/s41598-020-61868-5

Hofhansl F, Schnecker J, Singer G, Wanek W (2015) New insights into mechanisms driving carbon allocation in tropical forests. New Phytol 205:137-146. https://doi: 10.1111/nph.13007

Huffman GJ, Bolvin DT, Nelkin EJ, Wolff DB, Adler RF, Gu G, Hong Y, Bowman KP, Stocker EF (2007) The TRMM multisatellite precipitation analysis (TMPA): Quasi-global, multiyear, combined-sensor precipitation estimates at fine scales. J Hydrometeorol 8:38–55. https://doi.org/10.1175/JHM560.1

Jackson MB, Colmer TD (2005) Response and adaptation by plants to flooding stress. Annals of Botany 96(4):501–505. https://doi.org/10.1093/aob/mci205

Jiménez EM, Peñuela-Mora MC, Sierra CA, LLoyd J, Phillips OL, Moreno FH, Navarrete D, Prieto A, Rudas A, Álvarez E, Quesada CA, Grande-Ortiz MA., García-Abril A, Patiño S (2014) Edaphic controls on ecosystem-level carbon allocation in two contrasting Amazon forests. J Geophys Res Biogeosci 119:1820–1830. https://doi:10.1002/2014JG002653

Kozlowski TT (1985) Soil aeration, flooding and tree growth. Journal of Arboriculture 11:85-96

Kreuzwieser J, Hauberg J, Howell KA, Carroll A, Rennenberg H, Millar AH, Whelan J (2009) Differential response of Grey poplar leaves and roots underpins stress adaptation during hypoxia. Plant Physiol 149(1): 461–473. https://doi.org/10.1104/pp.108.125989

Kreuzwieser J, Rennenberg H (2014) Molecular and physiological responses of trees to waterlogging stress. Plant cell environ 37:2245-2259, https://doi.org/10.1111/pce.12310

Le Quéré C, Andrew RM, Friedlingstein P et al (2018) Global Carbon Budget 2018. Earth Syst Sci Data 10:2141–2194. https://doi.org/10.5194/essd-10-2141-2018

Lenssen JPM, Menting FBJ, Van der Putten WH (2003) Plant responses to simultaneous stress of waterlogging and shade: amplified or hierarchical effects? New Phytol 157(2): 281-290. https://doi.org/10.1046/j.1469-8137.2003.00666.x

Liefcheck JS (2016) piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol Evol 7:573–579. https://doi.org/10.1111/2041-210X.12512

Litton GM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. Glob Change Biol 13(10):2089-2109. https://doi.org/10.1111/j.1365-2486.2007.01420.x

Lucassen ECHET, Smolders AJP, Roelofs JGM (2000) Increased ground-water levels cause iron toxicity in *Glyceria fluitans* (L). Aquat Bot 66:321–327. https://doi.org/10.1016/S0304-3770(99)00083-2.

Lugli LF, Andersen KM, Aragao LEOC, Cordeiro AL, Cunha HFV, Fuchslueger L, Meir P, Mercado LM, Oblitas E, Quesada CA, Rosa JS, Schaap KJ, Valverde-Barrantes O, Hartley IP (2020) Multiple phosphorus acquisition strategies adopted by fine roots in low-fertility soils in Central Amazonia. Plant Soil 450: 49-63. https://doi.org/10.1007/s11104-019-03963-9

Lugli LF, Rosa JS, Andersen KM, Pires M, Cordeiro AL, Di Ponzio R, Moraes ACM, Souza ST, Aragão LEOC, Cunha HFV, Martins NP, Camargo JL, Almeida RV, Assis RL, Fuchslueger L, Schaap KJ, Valverde-Barrantes OJ, Meir P, Quesada CA, Mercado LM, Hartley IP (2021) Rapid responses of root traits and productivity to phosphorus and cation additions in a tropical lowland forest in Amazonia. New Phytol 230:116-128. https://doi:10.1111/nph.17154

Malhi Y, Doughty C, Galbraith D (2011) The allocation of ecosystem net primary productivity in tropical forests. P Roy Soc B-Biol Si 366(1582):3225–3245. https://doi.org/10.1098/rstb.2011.0062

Malhi Y, Melack J, Gatti, LV, Ometto J, Kesselmeier J, Wolff S, Aragão LEO, Costa M, Saleska S, Pangala SR, Basso LS, Rizzo L, Araùjo AC, Restrepo-Coupe N, Junior CHLS (2021) Biogeochemical cycles of the Amazon, in: Nobre C, Encalada A, Anderson E et al (eds) Amazon Assessment Report 2021 United Nations Sustainable Development Solutions Network, New York, USA, pp 3-40. https://doi.org/10.55161/TAKR3454

Martins DL, Schietti J, Feldpausch TR, Luizão FJ, Phillips OL, Andrade A, Castilho CV, Laurance SG, Oliveira A, Amaral IL, Toledo JJ, Lugli LF, Pinto JLPV, Oblitas EM, Quesada CA (2014) Soil-induced impacts on forest structure drive coarse woody debris stocks across central Amazonia. Plant Ecol Divers 8(2):229–2. https://doi.org/10.1080/17550874.2013.879942

Miguez-Macho G, Fan Y (2012) The role of groundwater in the Amazon water cycle: 2. Influence on seasonal soil moisture and evapotranspiration. Journal Geophysical Research Atmosphere 117:1-27. https://doi.org/10.1029/2012JD017540

Mokany K, Raison RJ, Prokushkin A (2006) Critical analysis of root: shoot ratios in terrestrial biomes. Glob Change Biol 12:84-96. https://doi.org/10.1111/j.1365-2486.2005.001043.x

Moulatlet GM, Costa FRC, Rennó CD, Emilio T, Schietti J (2014) Local hydrological conditions explain floristic composition in lowland Amazonian forests. Biotropica 46:395-403. https://doi.org/10.1111/btp.12117

Niklas KJ (2005) Modelling below- and above-ground biomass for nonwoody and woody plants. Ann. Bot.-London, 95:315–321. https://doi.org/10.1093/aob/mci028

Nobre AD, Cuartas LA, Hodnett M, Rennó CD, Rodrigues G, Silveira A, Waterloo M, Saleska S (2011) Height Above the Nearest Drainage – a hydrologically relevant new terrain model. J Hydrol 404(1-2):13-29. https://doi:10.1016/j.jhydrol.2011.03.051

Noguchi H, Suwa R, de Souza CAS, da Silva RP, dos Santos J, Higuchi N, Kajimoto T, Ishizuka M (2014) Examination of vertical distribution of fine root biomass in a tropical moist forest of the Central Amazon, Brazil. Japan Agricultural Research Quarterly 48(2):231-235. https://doi.org/10.6090/jarq.48.231, 2014.

Obersteiner S, Klein T (2022) Closing in on the last frontier: C allocation in the rhizosphere. Glob Change Biol 28(23):6835–6837. https://doi.org/10.1111/gcb.16432

Parent C, Capelli N, Berger A, Crèvecoeur M, Dat JF (2008) An overview of plant responses to soil waterlogging. Plant Stress 2(1):20-27

Parolin P (2001) Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. Oecologia 128:326-35. doi:10.1007/s004420100660, 2001.

Patrick Jr. WH, Mahapatra IC (1968) Transformation and availability to rice of nitrogen and phosphorus in waterlogged soils. Adv Agron 20:323–359. https://doi.org/10.1016/S0065-2113(08)60860-3

Paz H (2003) Root/Shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. Biotropica 35(3):318-332. https://doi.org/10.1111/j.1744-7429.2003.tb00586.x

Ponnamperuma FN (1972) The chemistry of submerged soils. Adv Agron 24(C):29–96. https://doi.org/10.1016/S0065-2113(08)60633-1

Poorter H, Nikklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2011) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193:30–50. https://doi: 10.1111/j.1469- 8137.2011.03952.x

Powers JS, Treseder KK, Lerdau MT (2004) Fine roots, arbuscular mycorrhizal hyphae and soil nutrients in four neotropical rain forests: patterns across large geographic distances. New Phytol 165(3):913-921. https://doi: 10.1111/j.1469-8137.2004.01279.x

Quesada CA, Lloyd J, Schwarz M, Patiño S, Baker TR, Czimczik C, Fyllas NM, Martinelli L, Nardoto GB, Schmerler J, Santos AJB. Hodnett MG, Herrera R, Luizão FJ, Arneth A, Lloyd G, Dezzeo N, Hilke I, Kuhlmann I, Raessler M, Brand WA, Geilmann H, Moraes-Filho JO, Carvalho FP, Araujo-Filho RN, Chaves JE, Cruz-Junior OF, Pimentel TP, Paiva R (2010) Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. Biogeosciences 7(5):1515–1541. https://doi: org/10.5194/bg-7-1515-2010

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, [WWW document] URL https://www.R-project.org/

Reich PB, Tjoelker MG, Walters MB, Vanderklein DW, Buschena C (1998) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. Funct Ecol 12:327–338. https://doi.org/10.1046/j.1365-2435.1998.00209.x

Reynolds JF, Thornley JHM (1982) A Shoot:Root Partitioning Model. Ann Bot 49(5): 585-597

Rocha HR, Goulden ML, Miller SD, Menton MC, Pinto LDVO, de Freitas HC, Figueira AM (2004) Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. Ecol Appl 14(4):22–32. https://doi: org/10.1890/02-6001

Rodríguez E, Morris CS, Belz JE (2006) A global assessment of the SRTM performance, Photogramm. Eng Rem S 72(3):249–260. https://doi.org/10.14358 /PERS.72.3.249

Rubio G, Lavado RS (1999) Acquisition and allocation of resources in two waterlogging-tolerant grasses. New Phytol 143:539–546. https://doi.org/10.1046/j.1469-8137.1999.00482.x

Rubio G, Oesterheld M, Alvarez CR, Lavado RS (1997) Mechanisms for the increase in phosphorus uptake of waterlogged plants: soil phosphorus availability, root morphology and uptake kinetics. Oecologia 112:150– 155

Schenk HJ, Jackson RB (2002) The global biogeography of roots. Ecol Monogr 72(3):311-328. https://doi:10.2307/3100092

Schietti J, Martins D, Emilio T, Souza PF, Levis C, Baccaro FB, Pinto JLPV, Moulatlet GM, Stark SC, Sarmento K, de Araújo RNO, Costa FRC, Schöngart J, Quesada CA, Saleska SR, Tomasella J, Magnusson WE (2016) Forest structure along a 600 km transect of natural disturbances and seasonality gradients in central-southern Amazonia. J Ecol 104(5):1335–1346. https://doi: org/10.1111/1365-2745.12596

Shipley B (2009) Confirmatory path analysis in a generalized multilevel context. Ecology 90(2):363-368. https://doi.org/10.1890/08-1034.1

Shipley B (2013) The AIC model selection method applied to path analytic models compared using a d-separation test. Ecology 94(3):560-564. https://doi.org/10.1890/12-0976.1

Shipley B, Meziane D (2002) The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. Funct Ecol 16:326–331. https://doi.org/10.1046/j.1365-2435.2002.00626.x

Shuttleworth WJ (1998) Evaporation from Amazonian rainforest. P Roy Soc B-Biol Si 233(1272):321–346. https://doi: org/10.1098/rspb.1988.0024

Sombroek W (2000) Amazon landforms and soils in relation to biological diversity. Acta Amaz 30(1):81–100. https://doi.org/10.1590/1809-43922000301100

Sombroek W (2001) Spatial and temporal patterns of amazon rainfall. AMBIO: A J. of the Human Environment 30(7):388–396. https://doi: org/10.1579/0044-7447-30.7.388

Sousa TR, Schietti J, Coelho de Souza F, Esquivel-Muelbert A, Ribeiro IO, Emílio T, Pequeno PACL, Costa FRC (2020) Palms and trees resist extreme drought in Amazon forests with shallow water tables. J Ecol 108:2070–2082. https://doi: 10.1111/1365-2745.13377

Sousa TR, Schietti J, Ribeiro IO et al (2022) Water table depth modulates productivity and biomass across Amazonian forests. Glob Ecol Biogeogr 32:1571–1588. https://doi: 10.1111/geb.13531, 2022.

Sun J, Niu S, Wang J (2018) Divergent biomass partitioning to aboveground and belowground across forests in China. J Plant Ecol 11(3):484-492. http//:doi:10.1093/jpe/rtx021

Thornley JHM (1972) A balanced quantitative model for Root: Shoot ratios in vegetative plants. Ann Bot 36(145):431-441

Toledo JJ, Castilho CV, Magnusson WE, Nascimento HEM (2017) Soil controls biomass and dynamics of an Amazonian forest through the shifting of species and traits. Braz J Bot 40(2):451-461. https//: doi:10.1007/s40415-016-0351-2

Unger PW, Kaspar TC (1994) Soil compaction and root growth: A review. Agron J 86:759-766. https://doi.org/10.2134/agronj1994.00021962008600050004x

Vilanova E, Ramírez-Angulo H, Torres-Lezama A, Aymard G, Gámez L, Durán C, Hernández L, Herrera R, van der Heijden G, Phillips O L, Ettl GJ (2018) Environmental drivers of forest structure and stem turnover across Venezuelan tropical forests. PLoS ONE 13(6):e0198489. https://doi.org/10.1371/journal.pone.0198489

Voesenek LACJ, Blom CWPM, Pouwels RHW (1989) Root and shoot development of *Rumex* species under waterlogged conditions. Can J Botany 67(6):1865-1869. https://doi.org/10.1139/b89-236

Yaffar D, Norby RJ (2020) A historical and comparative review of 50 years of root data collection in Puerto Rico. Biotropica 52:563–576. https://doi: 10.1111/btp.12771

Zhou L, Hong Y, Li C, Lu C, He Y, Shao J, Sun X, Wang C, Liu R, Liu H, Zhou X (2020) Responses of biomass allocation to multi-factor global change: A global synthesis. Agriculture, Ecosystems and Environment 304:1-10. https://doi.org/10.1016/j.agee.2020.107115

Zipper SC, Evren Soylu M, Booth EG, Loheide SP (2015) Untangling the effect of shallow groundwater and soil texture as drivers of subfield-scale yield variability. Water Resour Res 51:6338–6358. https://doi.org/10.1002/2015WR017522

Zuur A, Ieno EN, Walker N, Savellev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R, Springer, New York, NY, USA, 584 pp

Supplemental material

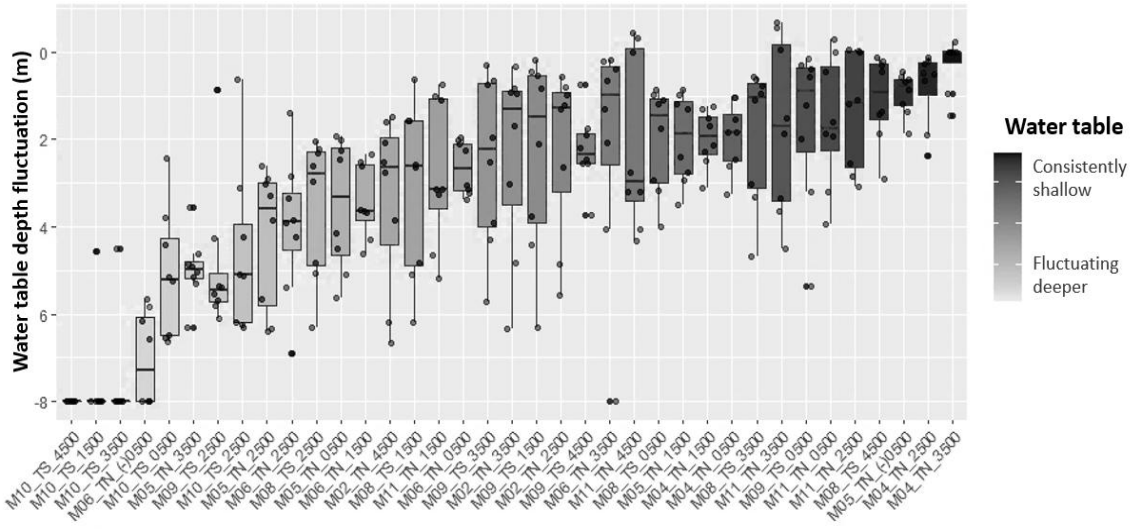

Fig. S1. Temporal fluctuation of the water table depth for Amazonian terra-firme forests with shallow water tables. High variability in WT depth, both spatially (between plots) and temporally (within each plot) was observed, with a general mean (±SD) WT depth of 3.1 ± 2.4 m across the region, and fluctuations of 3.8 ± 1.7 m and up to 5 m within some plots. Each box plot represents the temporal WT fluctuation in each of the 37 study 1-ha plots during the monitoring period, measured with 7m deep piezometers. Overall, the WT is within 7 m of soil depth, ranging from areas where the WT regime is is consiste ntly shallow year-round (WT within the first meters of soil depth, dark gray boxes), to areas where it is more fluctuating and reaching deeper levels (fluctuating between 4-7m, light gray boxes).

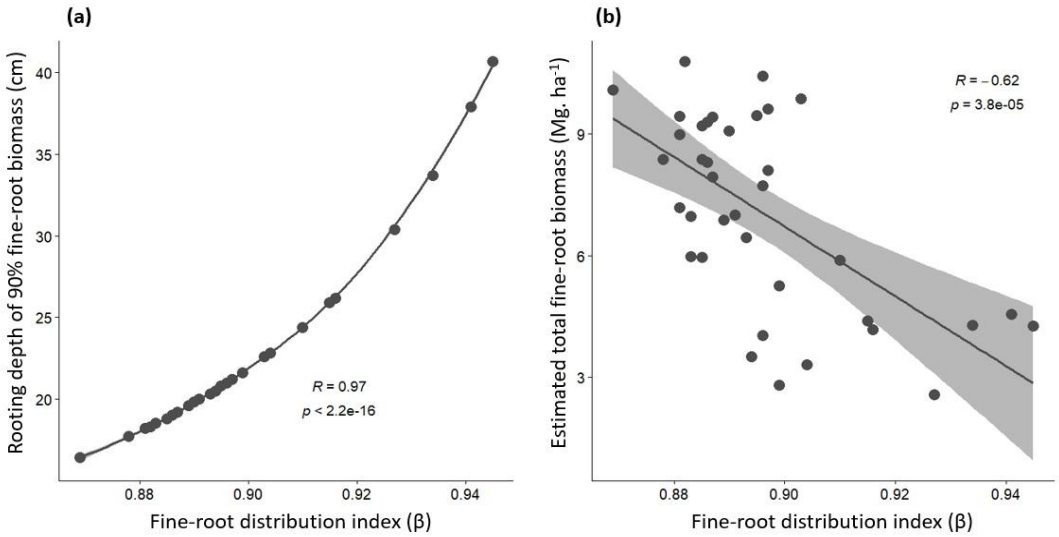

Fig. S2. Relationships between the fine-root biomass distribution with rooting depth or estimated total fine-root biomass in Amazonian terra-firme forests with shallow water tables. Plots show significant correlation effects between the index of fine-root biomass vertical distribution (β) and: (a) the soil depth (cm) at which 90% of this biomass is accumulated, and (b) the total fine-root biomass stock ($Mg.ha^{-1}$).

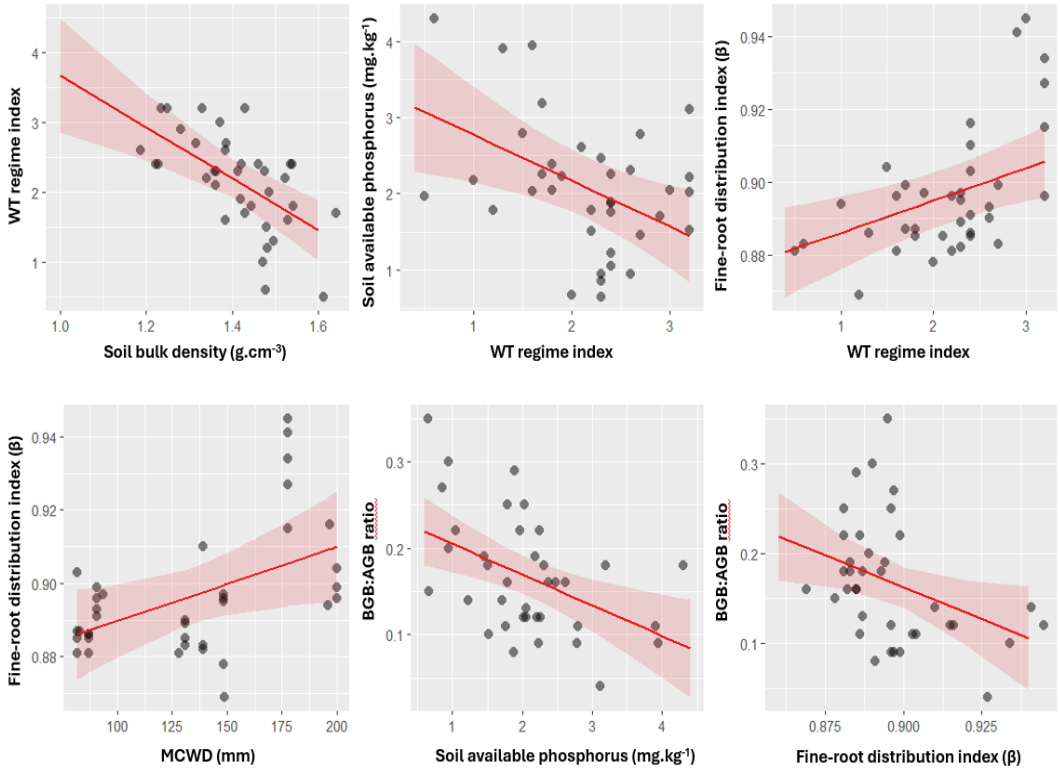

Fig. S3. Significant effects retained in the final piecewise Structural Equation modeling (pSEM) using soil available phosphorus as a proxy for soil nutrient availability. Plots show the partial effects derived from the Structural Equation Modeling to investigate the combined effects of precipitation-related water deficit (MCWD), soil physical restrictions (soil bulk density), soil nutrient availability (phosphorus) and water table regime on fine-root biomass distribution and biomass allocation to below- and aboveground components (BGB:AGB ratio) along Amazonian terra-firme forests with shallow water tables.

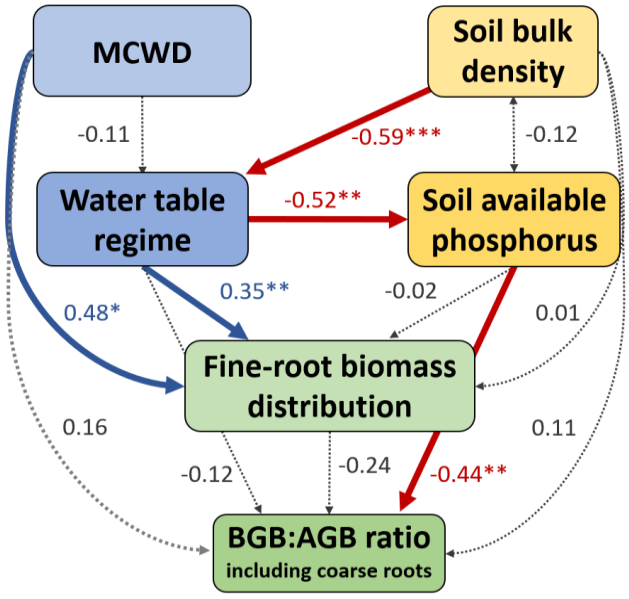

Fig. S4. Result of piecewise SEM model to understand the distribution of fine-roots and the BGB:AGB ratio of Amazonian terra-firme forests (37 plots) characterized by shallow WTs along the Purus-Madeira interfluve. Results shown here are for the model using soil available P as a proxy of soil nutrient availability and BGB values considering coarse root biomass. The model was fitted to test: (i) the effect of cumulative water deficit and soil density on WT regime (lower values indicate consistently shallow WT levels year-round); (ii) the influence of WT regime on soil nutrient availability; (iii) their combined effects on vertical fine-root biomass distribution (lower values indicate a higher concentration of fine-root biomass in the upper soil layers) and, (iv) the interplay of these factors in shaping biomass allocation to below- and aboveground components (BGB:AGB ratio). Blue and red arrows denote significant positive and negative relationships, respectively. Dashed gray arrows represent paths included in our general conceptual model that were not retained as significant effects in the final model. Numbers are the standardized coefficients of determination for each predictor. (*) $p<0.05$, (**) $p<0.01$, (***) $p<0.001$.

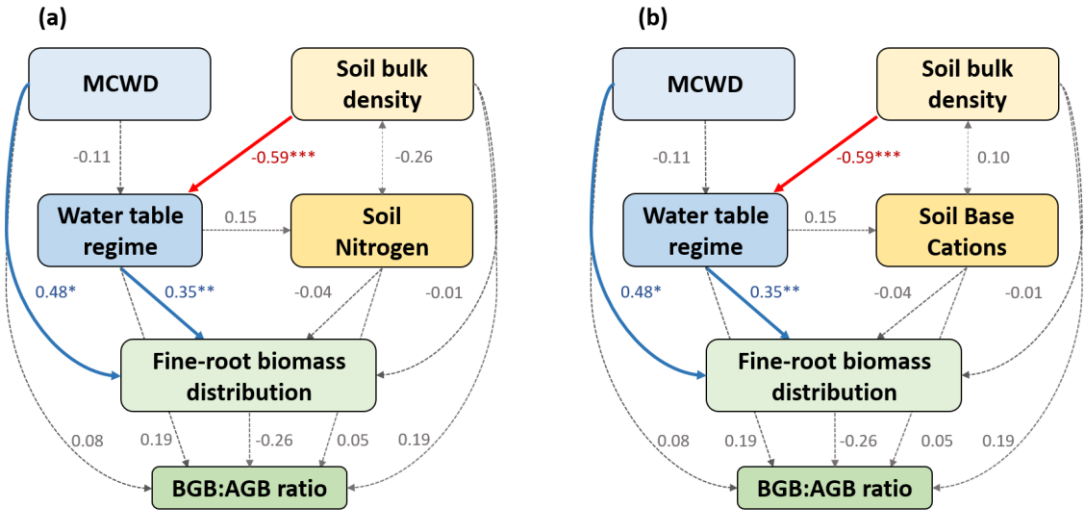

Fig. S5 . Results of piecewise SEM modeling using soil available nitrogen and the concentration of exchangeable base cations as proxies for soil nutrient availability. Both pSEMs were fit to test: (i) the effect of MCWD and soil density on water table regime; (ii) the influence of water table regime on soil nutrient availability; (iii) their combined effects on vertical fine-root biomass distribution and, (iv) the interplay of these factors in shaping biomass allocation to below- and aboveground components (BGB:AGB ratio) across Amazonian terra-firme forests characterized by predominantly shallow water table levels. Blue and red arrows denote significant positive and negative relationships, respectively. Dashed gray arrows represent paths included in the general conceptual model that were not retained as significant effects in the final model. Numbers are the standardized coefficients of determination for each predictor. (*) p<0.01, (**) p<0.005, (***) p <0.001.

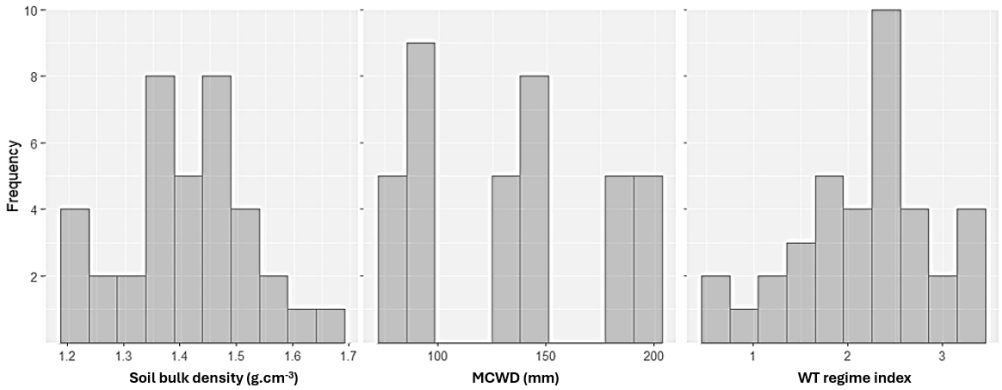

Fig. S6. Soil bulk density, MCWD and WT regime index for Amazonian terra-firme forests with shallow water tables. Frequency histograms for values of soil bulk density (g.cm^{-3}), precipitation-related water deficit (MCWD, mm), and temporal behavior of the water table (WT regime index) across the 37 1-ha study plots. Soil bulk density ranges from low values (1.2 g.cm^{-3}) to the highest value of 1.7 g.cm^{-3}, with most plots having soil density between 1.4-1.6 g.cm^{-3}. MCWD varies from values <100 mm, meaning low levels of climate-related water deficit, up to a cumulative of 200 mm water deficit, indicating areas exposed to moderate dry periods. The WT

regime index varied across plots from low values (0.5) representing areas where the WT remains consistently shallow throughout the year, up to higher values (3.2) indicating more fluctuating WT levels.

Table S1. Summary of piecewise structural equation model (pSEM) results when using soil nitrogen (N) as a proxy for soil nutrient availability . In the table, *Std. est* denotes the standardized estimation values for each predictor; *P* is the probability p-value, with values in bold indicating significant effects; R^2_m is the fixed-effects coefficient of determination, representing the proportion of the variance for a response variable explained by all fixed effects included in the model; R^2_c is the conditional-effect coefficient of determination, representing the proportion of the variance explained by the random effects included in the model. Model fit statistics Fisher's C, AIC (Akaike information criteria) and P (p-value) are also shown.

Path	Response	Std. est	P	R^2_m	R^2_c
Predictor					
MCWD	WT regime	-0.11	0.616		
Soil bulk density	WT regime	-0.59	**<0.001**	0.35	0.54
WT regime	Soil N	0.15	0.406	0.02	0.07
MCWD	Fine-root distribution	0.48	**0.038**		
Soil bulk density	Fine-root distribution	-0.01	0.929		
WT regime	Fine-root distribution	0.35	**0.003**		
Soil N	Fine-root distribution	-0.04	0.696	0.41	0.75
MCWD	BGB:AGB ratio	0.08	0.792		
Soil bulk density	BGB:AGB ratio	0.19	0.459		
WT regime	BGB:AGB ratio	0.19	0.453		
Soil N	BGB:AGB ratio	0.05	0.758		
Fine-root distribution	BGB:AGB ratio	-0.26	0.348	0.05	0.35
Correlation					
Soil bulk density	Soil N	-0.26	0.06		
Fisher's *C*		3.99			
AIC		-363.71			
P		0.996			

Table S2. Summary of piecewise structural equation model (pSEM) results when using the concentration of exchangeable base cations (Base Cations) as a proxy for soil nutrient availability. In the table, *Std. est* denotes the standardized estimation values for each predictor; *P* is the probability p-value, with values in bold indicating significant effects; R^2_m is the fixed-effects coefficient of determination, representing the proportion of the variance for a response variable explained by all fixed effects included in the model; R^2_c is the conditional-effect coefficient of determination, representing the proportion of the variance explained by the random effects included in the model. Model fit statistics Fisher's C, AIC (Akaike information criteria) and P (p-value) are also shown.

Path	Response	Std. est	P	R^2_m	R^2_c
Predictor					
MCWD	WT regime	-0.11	0.616		
Soil bulk density	WT regime	-0.59	**<0.001**	0.35	0.54
WT regime	Soil Base Cations	0.15	0.406	0.02	0.07
MCWD	Fine-root distribution	0.48	**0.038**		
Soil bulk density	Fine-root distribution	-0.01	0.929		
WT regime	Fine-root distribution	0.35	**0.003**		
Soil Base Cations	Fine-root distribution	-0.04	0.696	0.41	0.75
MCWD	BGB:AGB ratio	0.08	0.792		
Soil bulk density	BGB:AGB ratio	0.19	0.459		
WT regime	BGB:AGB ratio	0.19	0.453		
Soil Base Cations	BGB:AGB ratio	0.05	0.758		
Fine-root distribution	BGB:AGB ratio	-0.26	0.348	0.05	0.35
Correlation					
Soil bulk density	Soil Base Cations	0.10	0.28		
Fisher's *C*		5.96			
AIC		-322.75			
P		0.968			

Table S3. Summary of piecewise structural equation model (pSEM) results when using soil available phosphorus (P) as a proxy for soil nutrient availability and considering the interaction effect between WT regime and soil P. In the table, *Std. est* denotes the standardized estimation values for each predictor; *P* is the probability p-value, with values in bold indicating significant effects; R^2_m is the fixed-effects coefficient of determination, representing the proportion

of the variance for a response variable explained by all fixed effects included in the model; R^2_c is the conditional-effect coefficient of determination, representing the proportion of the variance explained by the random effects included in the model. Model fit statistics Fisher's C, AIC (Akaike information criteria) and P (p-value) are also shown.

Path	Response	Std. est	P	R^2_m	R^2_c
Predictor					
MCWD	WT regime	-0.11	0.616		
Soil bulk density	WT regime	-0.59	**<0.001**	0.35	0.54
WT regime	Soil available P	-0.52	**0.004**	0.23	0.46
MCWD	Fine-root distribution	0.48	**0.038**		
Soil bulk density	Fine-root distribution	0.01	0.961		
WT regime	Fine-root distribution	0.35	**0.003**		
Soil available P	Fine-root distribution	-0.02	0.859	0.41	0.75
MCWD	BGB:AGB ratio	0.16	0.368		
Soil bulk density	BGB:AGB ratio	0.11	0.552		
WT regime	BGB:AGB ratio	0.48	0.234		
Soil available P	BGB:AGB ratio	0.16	0.665		
Fine-root distribution	BGB:AGB ratio	-0.27	0.121		
WT regime* Soil available P	BGB:AGB ratio	-0.83	**0.041**	0.44	0.44
Correlation					
Soil bulk density	Soil available P	-0.12	0.234		
Fisher's *C*		7.02			
AIC		-104.23			
P		0.934			