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FACULDADE DE CIÊNCIAS AGRÁRIAS
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AMBIENTES CONTRASTANTES DE LUZ ALTERAM AS RELAÇÕES ENTRE TAXAS DEMOGRÁFICAS E CARACTERÍSTICAS FOTOSSINTÉTICAS EM MUDAS DE ESPÉCIES ARBÓREAS TROPICAIS?

Guilherme Silva Modolo

MANAUS

Maio, 2020

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Guilherme Silva Modolo

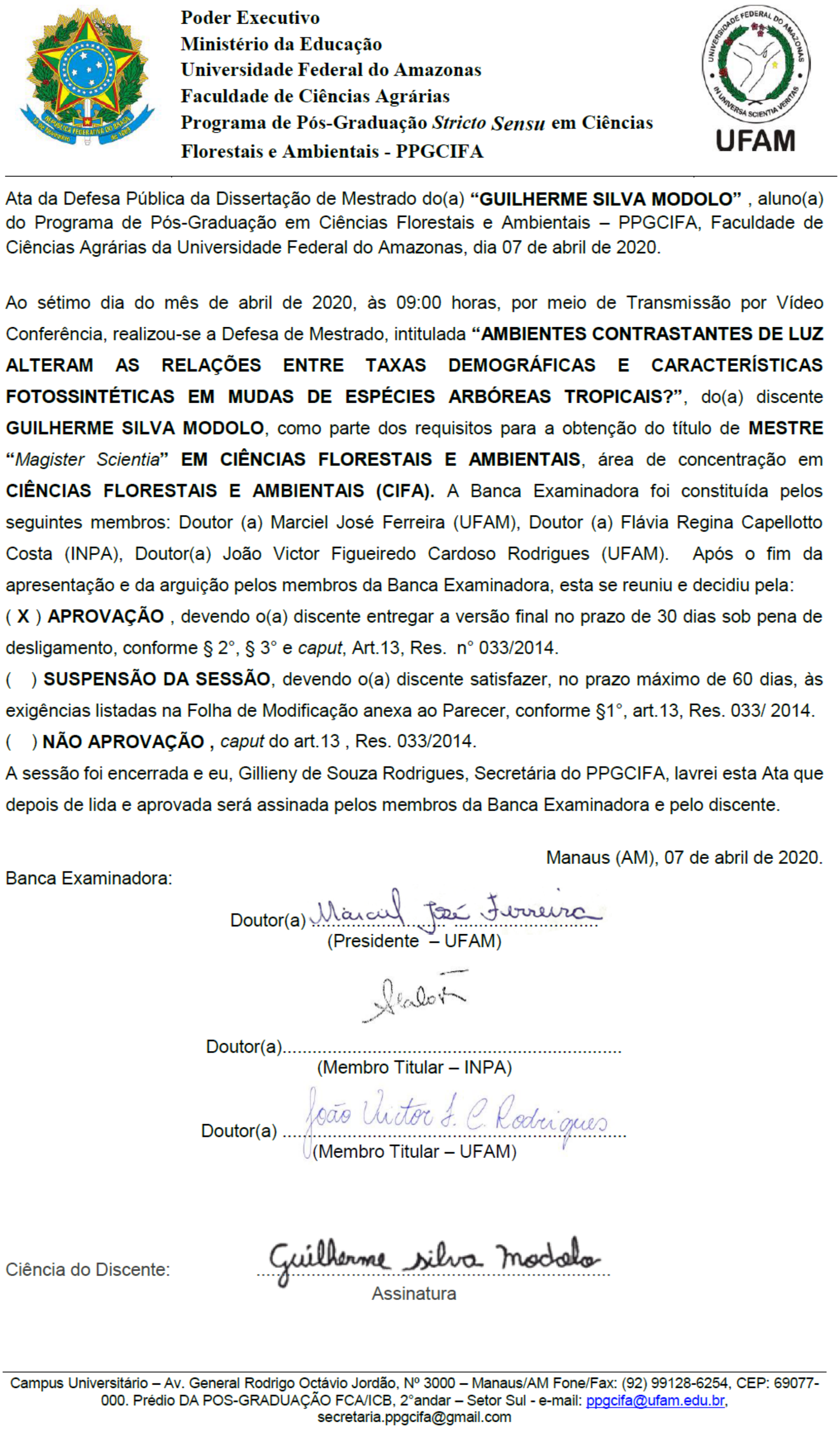
Orientador: Dr. Marciel José Ferreira

Dissertação apresentada ao Programa de Pós-graduação em Ciências Florestais e Ambientais da Universidade Federal do Amazonas (PPG-CIFA/UFAM) como parte dos requisitos para obtenção do título de Mestre em Ciências Florestais e Ambientais.

MANAUS

Maio, 2020

Relação da banca examinadora



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Ata da Defesa Pública da Dissertação de Mestrado do(a) **"GUILHERME SILVA MODOLO"** , aluno(a) do Programa de Pós-Graduação em Ciências Florestais e Ambientais – PPGCIFA, Faculdade de Ciências Agrárias da Universidade Federal do Amazonas, dia 07 de abril de 2020.

Ao sétimo dia do mês de abril de 2020, às 09:00 horas, por meio de Transmissão por Vídeo Conferência, realizou-se a Defesa de Mestrado, intitulada **"AMBIENTES CONTRASTANTES DE LUZ ALTERAM AS RELAÇÕES ENTRE TAXAS DEMOGRÁFICAS E CARACTERÍSTICAS FOTOSSINTÉTICAS EM MUDAS DE ESPÉCIES ARBÓREAS TROPICAIS?"**, do(a) discente **GUILHERME SILVA MODOLO**, como parte dos requisitos para a obtenção do título de **MESTRE "***Magister Scientia***" EM CIÊNCIAS FLORESTAIS E AMBIENTAIS**, área de concentração em **CIÊNCIAS FLORESTAIS E AMBIENTAIS (CIFA).** A Banca Examinadora foi constituída pelos seguintes membros: Doutor (a) Marciel José Ferreira (UFAM), Doutor (a) Flávia Regina Capellotto Costa (INPA), Doutor(a) João Victor Figueiredo Cardoso Rodrigues (UFAM). Após o fim da apresentação e da arguição pelos membros da Banca Examinadora, esta se reuniu e decidiu pela:

(**X**) **APROVAÇÃO** , devendo o(a) discente entregar a versão final no prazo de 30 dias sob pena de desligamento, conforme § 2°, § 3° e *caput*, Art.13, Res. n° 033/2014.

(   ) **SUSPENSÃO DA SESSÃO**, devendo o(a) discente satisfazer, no prazo máximo de 60 dias, às exigências listadas na Folha de Modificação anexa ao Parecer, conforme §1°, art.13, Res. 033/ 2014.

(   ) **NÃO APROVAÇÃO ,** *caput* do art.13 , Res. 033/2014.

A sessão foi encerrada e eu, Gillieny de Souza Rodrigues, Secretária do PPGCIFA, lavrei esta Ata que depois de lida e aprovada será assinada pelos membros da Banca Examinadora e pelo discente.

Manaus (AM), 07 de abril de 2020.

Banca Examinadora:

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(Membro Titular – INPA)

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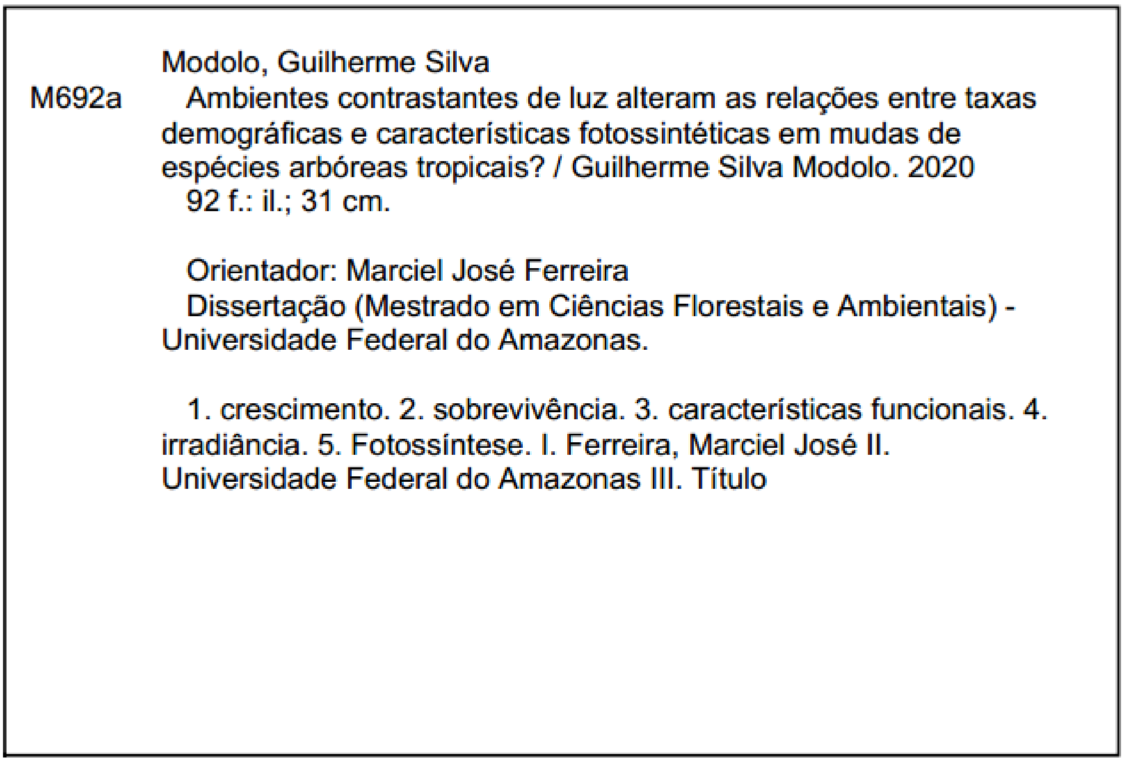

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Sinopse: O efeito da disponibilidade de luz sobre a relação entre taxas demográficas e características fotossintéticas de mudas de seis espécies florestais foi investigado em um plantio de enriquecimento de floresta secundária após dois anos. As abordagens incluíram: o contexto ambiental (disponibilidade de luz), o nível de amostragem (espécie ou indivíduo) e a seleção das características que melhor explicam as taxas de crescimento.

Palavras chave: ecofisiologia, crescimento, sobrevivência, características funcionais, irradiância, fotossíntese, variação intraespecífica.

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Resumo

Características funcionais têm sido utilizadas para explicar taxas demográficas de povoamentos florestais em diversos sítios. No entanto, fracas ou inexistentes relações têm sido frequentemente encontradas, especialmente por desconsideração do contexto ambiental, negligência da variação intraespecífica e pelo baixo significado das características selecionadas para funções mais complexas. Em relação ao contexto ambiental, analisar como a disponibilidade de luz influencia a relação das taxas demográficas com as características funcionais é importante para um melhor entendimento dos principais mecanismos que controlam a dinâmica da floresta. Nesse estudo, o objetivo foi investigar se condições contrastantes de luz alteram as relações entre as taxas demográficas e as características fotossintéticas durante o estabelecimento inicial de seis espécies florestais. O estudo foi realizado em um plantio de enriquecimento de floresta secundária, localizado na fazenda experimental da UFAM. Em março de 2017 foram plantadas 1.800 mudas de seis espécies florestais (*Cedrela fissilis*, *Tabebuia rosea*, *Swietenia macrophylla*, *Bertholletia excelsa*, *Carapa guianensis* e *Hymenaea courbaril*) sob diferentes condições de abertura do dossel resultantes da aplicação de tratamentos de refinamento com diferentes níveis de redução da área basal em árvores do dossel e remoção da vegetação do sub-bosque. Para o presente estudo, foram selecionadas as parcelas com total remoção da área basal (*pleno sol*) e com nenhuma remoção da área basal (*sub-bosque*), ambas com remoção da vegetação natural do sub-bosque. Foram calculadas as taxas de crescimento e sobrevivência das mudas dois anos após o plantio e, em conjunto, foi mensurado uma gama de características divididas em três tipos: copa (*e.g.* área de projeção da copa, profundidade da copa), morfológicas (*e.g.* área foliar total, área foliar específica, conteúdo de matéria seca da folha) e fisiológicas (*e.g.* teor de pigmentos cloroplastídicos, fluorescência da clorofila *a*, trocas gasosas). De maneira geral, as relações, em modelos com uma característica, foram mais fortes no ambiente de *pleno sol* (R^2 m = 0.03 – 0.47) que no *sub-bosque* (R^2 m = 0.03 – 0.33). Embora a área de copa, comprimento de copa, área foliar total e taxa de fotossíntese máxima total tenham tido as relações mais fortes nos dois ambientes, o ambiente de *pleno sol* teve um maior número de características relacionadas às taxas de crescimento além dessas mencionadas. A análise em nível de indivíduo resultou em maior número das relações entre taxas demográficas e características fotossintéticas significativas. Por fim, a capacidade de predição das taxas de crescimento a partir de características fotossintéticas é aprimorada quando analisadas em modelos com múltiplas características diferindo entre os ambientes de *pleno sol* (R^2 m = 0.20 – 0.57) e *sub-bosque* (R^2 m = 0.03 – 0.48).

Palavras chave: ecofisiologia; crescimento; sobrevivência; características funcionais; irradiância; fotossíntese; fluorescência; Amazônia Central.

Abstract

Functional traits have been used to explain demographic rates of forest stands at different site conditions. However, weak or nonexistent relationships have often been found, especially due to a lack of consideration of the environmental context, the neglect of intraspecific variation and poor explanation capacity of selected traits. Furthermore, the effects of environment light availability on the relationship between functional traits, growth and survival are still not well understood. Analyzing how light availability influences the demographic rates-functional traits relationship is important for a better understanding of the main mechanisms that control the dynamics of the forest. In this study, the objective was to investigate whether contrasting light conditions alter the relationship between demographic rates and photosynthetic traits during the initial establishment of a forest stand. The study was carried out in a secondary forest enrichment plantation, located at the UFAM experimental farm. In March 2017, seedlings of six forest species (*Cedrela fissilis*, *Tabebuia rosea*, *Swietenia macrophylla*, *Bertholletia excelsa*, *Carapa guianensis* and *Hymenaea courbaril*) were planted under different conditions of canopy opening resulting from the application of thinning treatments with different levels of basal area reduction in canopy trees and removal of plants from the understory. In the present study, plots with total removal of the basal area (*full sun*) and with no removal of the basal area (*understory*) were selected, both with the removal of the natural vegetation of the understory. Seedling growth and survival rates were calculated two years after planting, together with the measurement of a range of crown (e.g. crown projection area, crown length), morphological (e.g. total leaf area, specific leaf area, leaf dry matter content) and physiological (e.g. chlorophyll pigments content, fluorescence of chlorophyll *a* and gas exchange) traits. Overall, the relationships, in models with a single trais, were more strength at *full sun* (R^2 m = 0.03 – 0.47) than at *understory* (R^2 m = 0.03 – 0.33). Even though the crown projection area, crown length, total leaf area and total maximum photosynthetic rate have had the strongest relationships in both environments, the *full sun* environment had a greater number of related traits. An analysis at the individual-level resulted in the largest number of significative relationships between demographic rates and photosynthetic traits. Finally, the ability to predict growth rates from photosynthetic traits is improved when analyzed in models with multiple traits, both in *full sun* (R^2 m = 0.20 – 0.57) and in the *understory* (R^2 m = 0.03 – 0.48).

Keywords: ecophysiology; growth; survival; functional traits; irradiance; photosynthesis; fluorescence; Central Amazonia.

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Introdução geral

Características funcionais são traços morfológicos, fisiológicos ou fenológicos, mensurados em nível de indivíduo que indiretamente afetam o desempenho por influenciar a sobrevivência, crescimento ou reprodução de plantas (VIOLLE *et al.,* 2007). As relações entre características funcionais e taxas demográficas têm sido analisadas para melhor entender os principais mecanismos que controlam a dinâmica de espécies e povoamentos florestais sujeitos à uma gama de condições ambientais. Entre ambientes com variações na disponibilidade de recursos naturais (luz, água e nutrientes) são observados diferentes espectros de investimento em materiais para construção de madeira e folhas (WRIGHT *et al.,* 2004; CHAVE *et al.,* 2009). Plantas que se estabelecem em ambientes com maior disponibilidade de recursos naturais tendem possuir características que favorecem a acquisição e a utilização desses recursos (*e.g.* alta capacidade fotossintética e rápido crescimento) (WRIGHT *et al.,* 2010; KUNSTLER *et al.,* 2016). Por outro lado, plantas estabelecidas em ambientes com limitação de recursos naturais desenvolvem características que favorecem a conservação de energia e sua permanência no ambiente (*e.g.* baixa capacidade fotossintética e alta sobrevivência) (POORTER *et al.,* 2006; KITAJIMA; POORTER, 2010).

Globalmente, as características que mais têm sido utilizadas para explicar variações demográficas em comunidades florestais são: densidade da madeira, massa de sementes e área foliar específica (CHAVE *et al.,* 2009; WRIGHT *et al.,* 2010; COELHO *et al.,* 2016; GILBERT *et al.,* 2016). No entanto, alguns estudos têm utilizado uma gama de características foliares, além das características tradicionalmente mensuradas, com a intenção de obter um entendimento mais completo sobre os mecanismos que controlam as variações nas taxas demográficas de povoamentos florestais (POORTER; BONGERS, 2006; LIU *et al.,* 2016; GUIMARÃES *et al.,* 2018).

As características foliares em conjunto com outras características mensuradas a nível de indivíduo vêm sendo utilizadas para explicar taxas demográficas em povoamentos florestais naturais ou artificiais, com destaque para o efeito das condições de sítio (MARTÍNEZ-GARZA *et al.,* 2013; LIU *et al.,* 2016; KATABUCHI *et al.,* 2017; GUIMARÃES *et al.,* 2018; POORTER *et al.,* 2018). Em floresta nativa madura, indivíduos com maiores valores de altura, densidade estomática, condutividade hidráulica do xilema e área foliar específica, tiveram maiores taxas de crescimento pelo seu maior potencial de competição por recursos naturais (LIU *et al.*, 2016). No sub-bosque florestal, espécies com maiores valores de características conservativas como, dureza da folha, resistência da lâmina foliar ao cisalhamento, conteúdo de matéria seca foliar e massa foliar por área normalmente possuem maior tempo de vida da folha e maiores taxas de sobrevivência (KITAJIMA; POORTER, 2010). Em um plantio florestal, em sítio com baixa disponibilidade de nutrientes e alta irradiância (≈ 30 mol m^{-2} dia^{-1}), espécies com maior eficiência fotossintética no uso de carbono, fósforo e nitrogênio tiveram maiores taxas de crescimento (GUIMARÃES *et al.*, 2018). Entretanto, outros estudos encontraram fracas ou inexistentes relações entre características de plantas e taxas demográficas em povoamentos florestais (PAINE *et al.*, 2015; POORTER *et al.*, 2018). Por exemplo, características funcionais variaram proporcionalmente a alterações na abundância de indivíduos de um floresta tropical ocasionada por eventos de seca quando analisadas em nível de comunidade, entretanto, quando analisadas em nível de espécie as mudanças na abundância de indivíduos das espécies foram pouco relacionadas as características mensuradas, sendo relacionadas principalmente com um pequeno grupo de espécies, sugerindo que as relações em nível de comunidade foram influenciadas por poucas espécies. (KATABUCHI *et al.*, 2017). Em ambientes de alta irradiância, como uma área desflorestada em processo de recuperação via plantio de espécies florestais nativas, características morfológicas foliares como massa foliar por área, conteúdo de matéria seca da folha e área foliar não tiveram relações com as taxas de crescimento e sobrevivência de espécies introduzidas, por estarem relacionadas à capacidade de aquisição e não de utilização da energia luminosa (MARTÍNEZ-GARZA *et al.*, 2013). De modo geral, características funcionais também foram fracas preditoras das taxas demográficas em modelos globais de dinâmica da vegetação, pelo fato do crescimento vegetal ser afetado pela variação das condições ambientais além das características intrínsecas as espécies e indivíduos (PAINE *et al.*, 2015).

Por que as relações entre características funcionais e as taxas demográficas podem ser fortes em determinados ambientes e fracas ou inexistentes em outros? Ao menos três aspectos metodológicos de amostragem podem influenciar a capacidade de características funcionais predizerem as taxas demográficas (YANG *et al.*, 2018 WORTHY; SWENSON, 2019). Primeiramente, a falta de consideração do contexto ambiental pode levar a fracas relações. Variações temporais e espaciais das condições ambientais podem limitar o potencial de explicação de uma característica. Estudos realizados em grandes áreas podem encontrar fracas relações com as taxas demográficas devido ao fato de que muitos fatores ambientais não controlados podem estar influenciando de modo diferenciado o estabelecimento das plantas. Da mesma forma, estudos de longo prazo que não considerem efeitos de sazonalidade podem encontrar fracas relações entre características de plantas e taxas demográficas (McGILL *et* al., 2006; YANG *et al.,* 2018). O segundo aspecto é o nível de abordagem do estudo (*e.g.* comunidade, espécie ou indivíduo), considerado preponderante para que haja relação entre as características funcionais e as taxas demográficas (YANG *et al.,* 2018). A análise no nível de espécie procura verificar como as espécies diferem em crescimento e quais os principais mecanismos associados, demonstrando seu potencial de crescimento e de expressar suas características. Além disso, atribui o mesmo peso às espécies de um povoamento diminuindo o peso de espécies dominantes nos valores de características no nível de comunidade (KATABUCHI *et al.,* 2017; POORTER *et al.,* 2018). Por outro lado, a análise no nível de indivíduo permite uma visão mais realista da dinâmica da vegetação, pois cada indivíduo contribui igualmente para a dinâmica da floresta, levando em conta o seu potencial de aclimatação e as variações dentro do ambiente (POORTER *et al.,* 2018; SWENSON *et al*., 2020). Em geral, as características funcionais são preditoras mais realistas das taxas demográficas quando analisadas no nível de indivíduo, pois cada indivíduo está diretamente exposto aos fatores microclimáticos (*e.g.* disponibilidade de recursos naturais) e a competição (LIU et al., 2016; KATABUCHI *et al.,* 2017; POORTER *et al.*, 2018; YANG *et al.,* 2018). O terceiro aspecto é a pouca capacidade das características selecionadas explicarem processos funcionais mais complexos envolvidos na variação das taxas demográficas. Muitos estudos optam por características de fácil mensuração (*soft traits*) para explicar as variações demográficas. Apesar do apelo significativo dessas características pela sua fácil aplicabilidade e baixo custo, outras características de mais difícil mensuração (*hard traits*), que explicam processos metabólicos mais complexos, como, a capacidade da planta de absorver da luz (*e.g.* teor de pigmentos cloroplastídicos), utilizar a luz (*e.g.* fluorescência da clorofila *a*) e assimilar carbono (*e.g.* taxa de fotossíntese máxima), podem fornecer uma visão mais completa sobre fatores que controlam a demografia da vegetação (dos SANTOS; FERREIRAb, 2020; SWENSON 2013; KATABUCHI *et al.,* 2017; YANG *et al.,* 2018; WORTHY; SWENSON, 2019). Ademais, o uso de um conjunto integrado de características pode explicar melhor a eficiência na aquisição e no uso dos recursos (LI *et al.,* 2017), uma vez que a performance da planta depende da interação de inúmeras características (MARKS;

LECHOWICZ, 2006). Por último, a uniformidade e baixa disponibilidade de recursos também pode afetar a capacidade das características predizerem as taxas de crescimento. No sub-bosque de floresta tropical úmida, por exemplo, a pequena variação e baixa disponibilidade de luz condiciona os indivíduos de espécies arbóreas a investirem mais energia em estratégias de sobrevivência que de crescimento, resultando em baixas taxas de crescimento dos indivíduos como um todo (KITAJIMA; POORTER, 2010; POORTER *et al.,* 2018). Além disso, essa menor chance dos indivíduos expressarem seu máximo potencial de crescimento ocorre em função do efeito que a limitação por luz causa em suas características. Esses fatores determinam a convergência das taxas de crescimento e dos valores das características funcionais. Com isso, a pequena variação de crescimento e dos valores das características funcionais resulta em uma fraca ou inexistente correlação do crescimento com essas características, levantando a questão se tais características são de fato funcionais (POORTER *et al.*, 2018).

Em florestas tropicais, a luz é o recurso mais limitante ao crescimento das plantas (GOLDSTEIN *et al.,* 2016; WAGNER *et al.,* 2017). A disponibilidade de luz varia tanto no sentido temporal, influenciada principalmente pela sazonalidade de precipitação e presença de nuvens (GRAHAM *et al.,* 2003), quanto no sentido espacial entre os diferentes sítios (WAGNER *et al.,* 2017), e dentro de um mesmo sítio entre as diferentes fases de construção das clareiras e entre as diferentes posições dos estratos florestais (KENZO *et al*., 2015). Em média, do total de irradiância que chega ao dossel da floresta, apenas uma pequena parte (entre 1 e 2%) alcança o sub-bosque (CHAZDON; FETCHER, 1984). Essa variação natural de luz em diferentes sentidos influencia a tomada de decisão sobre a aplicação de tratamentos silviculturais no manejo de florestas nativas, uma vez que a manipulação do ambiente de luz é uma ferramenta importante na mão do silvicultor, a exemplo da implementação dos Sistemas Silviculturais de Enriquecimento (LAMPRECHT, 1990). Muitos estudos têm mostrado que o aumento da disponibilidade de luz sobre mudas introduzidas em plantios de enriquecimento, causado por aberturas artificiais no dossel, resulta em maiores taxas de crescimento comparadas a ambientes sombreados (ADJERS *et al.,* 1995; PEÑA-CLAROS *et al.,* 2002; WIENER, 2010; dos SANTOS; FERREIRA, 2020a). Do mesmo modo, espera-se que características funcionais tenham maior capacidade de predizer taxas de crescimento em ambientes com maior disponibilidade de luz (WRIGHT *et al.,* 2010; KUNSTLER *et al.,* 2016; POORTER *et al.*, 2018). No entanto, em algumas situações as características funcionais explicaram melhor o crescimento de indivíduos no sub-bosque que no dossel, como por exemplo o conteúdo de nitrogênio e fósforo foliar e a área foliar específica, por favorecerem a absorção do recurso luminoso que é limitado nesse ambiente (WILLS *et al.,* 2018).

A ampla variação nas respostas encontradas na literatura sobre as relações entre características funcionais e taxas demográficas (sobrevivência e crescimento) é uma das mais importantes na biologia vegetal (SALGUERO-GÓMEZ *et al.*, 2018). Considerando a luz como o fator mais limitante ao crescimento de plantas em florestas tropicais, ainda não está bem compreendido o papel que a disponibilidade deste recurso exerce sobre as relações entre as características funcionais e as taxas demográficas. Portanto, nesse estudo, foram testadas as relações entre taxas demográficas e características funcionais, em ambientes de luz contrastantes, em um experimento de enriquecimento de floresta secundária com o controle de outros fatores como a idade das mudas e variação espacial na disponibilidade de nutrientes. Junto à essa circunstância foi mensurado um amplo conjunto de características de copa, morfológicas e fisiológicas das espécies plantadas com objetivo de responder as seguintes questões principais: *i) Qual o efeito do ambiente de luz (alta e baixa irradiância) sobre as relações entre as taxas demográficas (crescimento e sobrevivência) e as características fotossintéticas em espécies florestais*? *ii) As relações entre crescimento e características fotossintéticas modificam em função do nível de abordagem (indivíduo ou espécie)? iii) Características fotossintéticas são melhores preditoras de taxas de crescimento quando integradas?*

Objetivos

Geral

Investigar se condições contrastantes de luz influenciam as relações entre taxas demográficas e características fotossintéticas de espécies florestais durante o estabelecimento inicial.

Específicos

i) Avaliar se as relações entre características fotossintéticas e as taxas de crescimento e sobrevivência diferem entre condições de alta (pleno sol) e baixa (sub-bosque) irradiância.

ii) Analisar se o nível de abordagem (espécie ou indivíduo) afeta as relações entre taxas de crescimento e características fotossintéticas.

iii) Analisar se um conjunto integrado de características melhora a capacidade de predição das taxas de crescimento.

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Do contrasting light environments modulate the relationships between demographic rates and photosynthetic traits in tropical tree saplings?

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Abstract

1 – Functional traits have been tested to explain the demographic rates of forest communities at different sites. However, weak or nonexistent relationships have been often found, especially due to lack of an environmental context (*e.g.* light, water or nutrient supply), neglect of intraspecific variation and use of non-functional traits.

2 – In this study, we ask if contrasting light environments modulate the relationships between demographic rates and photosynthetic traits, whether the level of approach (individual or species) changes the strength of the relationships and if an integrated set of traits improves the strength of the relationships. In simulated tree-fall gaps with different sizes, that were created by basal area reduction of natural vegetation, we established an enrichment planting using six tropical tree species. After two years of planting, we measured thirty photosynthetic traits in saplings growing under two light environments, *full sun* (photosynthetic photon flux density (PPFD) = 27.9 mol m^{-2} day^{-1}) and *understory* (PPFD = 1.3 mol m^{-2} day^{-1}), and related with growth rates (biomass, diameter and height) and survival. In addition, the analysis were performed at both individual and species levels. We performed the individual-level analysis with simple and multiple models.

3 – We found that light availability modulates the relationships between demographic rates and photosynthetic traits. Overall, the relationships, in models with single traits, were more significant at the *full sun* (R^2 m = 0.03 – 0.47) than at *understory* (R^2 m = 0.03 – 0.33), although with weak to moderate strength. The individual-level analysis showed a better relationship and a more realistic predict of growth rates in both light conditions, with 67 and 57% of traits related to some growth rate at *full sun* and *understory*, respectively, against 33 and 23% of species-level at *full sun* and *understory*, respectively. The model including a set of photosynthetic traits explained better the growth rates than single-traits at the *full sun* (up to 57%) and *understory* (up to 48%).

4 – We add the knowledge that the light supply is an environmental key factor to be considered when choosing the set of photosynthetic traits and growth rates to be measured. Furthermore, for studies conducted on a smaller scale, in homogeneous environments, the individual-level analysis gives more realistic insights into the mechanisms that drive the plant performance. Finally, photosynthetic traits are better predictors of growth rates when grouped in a set of traits, because they better represent different stages of growth processes.

Keywords: Central Amazonia; functional traits; growth; intraspecific variation; irradiance; photosynthesis; survival.

1. Introduction

Light is one of the main abiotic factors affecting the establishment of plants and the productivity of tropical forests (Goldstein et al., 2016; Nicotra, Chazdon & Iriarte 1999; Wagner et al., 2017). Globally, the light availability in forest communities varies spatially and temporally in function of climate regime and was proposed as the resource most limiting to forest productivity in the Central Amazon (Wagner et al., 2017). Further, light also varies in both vertically and horizontally at the same forest community, due to the dynamics of gaps and the vertical position of the strata, reducing gradually from the gaps to the non-gaps areas, where only 1-2% of total irradiance achieve the plants growing in understory (Chazdon & Fetcher, 1984). Temporally, the availability of light is strongly affected by the seasonality of precipitation, reducing the photosynthetic capacity of plants in the wet season due the reduction on irradiance caused by clouds (Graham et al., 2003).

The light availability affects the growth of tropical plants due their effects in vital processes that can be represented by a set of functional traits (Poorter et al., 2018; Poorter, 1999; Wright et al., 2010). Functional traits are morphological, physiological or phenological measurements, performed at individual level that indirectly affect the *fitness* via their effects on some aspect of plant performance (i.e. growth, survival or reproduction) (Violle et al., 2007). Thus, the relationships between demographic rates (survival and growth) and functional traits have been analyzed in different contexts, specially to better understand the main mechanisms that control the dynamics of species and forest stands subject to variation of environmental factors. Overall, the studies have shown that the environmental conditions, especially light, water and nutrients supply, influence the strength of the relationships and what traits are the best drivers of growth (Guimarães et al., 2018; Liu et al., 2016; Martinez-Garza, Bongers & Poorter, 2013; Poorter et al., 2018).

The effects of light on growth can be better understood based on the framework of the production ecology theory, which states that the productivity of a plant depends on the availability of resources (*e.g.* light) and the efficiency in acquiring and use of these resources (Binkley, Stape & Ryan, 2004; Monteith, 1977). For example, studies showed that at environments with low light availability such as mature native forest, traits related to acquisition of this resource like height and specific leaf area improved the growth rates (Liu et al., 2016). Further, in a same forest typology, a greater leaf dry matter content, leaf mass per area and leaf toughness can improve the survival rates, because of the higher protection against factors of biotic and abiotic stress (Kitajima & Poorter, 2010). On other hand, at high light environment (full sunlight), some studies have demonstrated that traits related to light interception (e.g. leaf area and specific leaf area) are poor predictors of demographic rates (Guimarães et al., 2018; Martinez-Garza, Bongers & Poorter, 2013). Yet, Guimarães et al. (2018) in a disturbed area characterized for high irradiance levels (≈ 30 mol m^{-2} dia^{-1}), showed that plants with higher photosynthetic nutrients-use efficiency had the greatest growth rates, demonstrating the importance of this process (resource use efficiency) for growth in this environment. Thus, the results corroborate with the classical work of Poorter (1999), that observed that nursery seedlings, growing under low light availability, showed the highest growth rates related to light acquisitive strategies as the increasing of leaf area ratio (LAR). However, under high light, the growth rates were most related to light use strategies as the net assimilation rate (NAR). Despite of these evidences, some studies have failed to predict demographic rates through of plant traits (Katabuchi et al., 2017; Paine et al., 2015; Poorter et al., 2018).

Why the relationships between functional traits and demographic rates are strong in certain contexts and weak or nonexistent in others? At least three methodological aspects of sampling may influence the ability of traits to predict demographic rates (Yang, Cao & Swenson, 2018; Worthy & Swenson, 2019). First, lack of environmental context can contribute for weak relationships. For example, many studies at large scales showed the effects of environmental context on trait-demographic rates relationship (Chave et al., 2009; Paine et al., 2015; Wright et al., 2004). However, few studies have tested these effects at smaller scale, especially in tropical forests. These analyses must be also applied to tropical forest to support theory that phenotype-environment interactions result at differential demographic rates (Anderson, 2016; McGill et al., 2006; Nicotra et al., 2010; Valladares et al., 2014), improving knowledge about the factors that drive the dynamics and diversity of tropical forests (Worthy & Swenson, 2019). Second, the neglect of intraspecific variation, since that the most of the studies that analyzed trait-demographic rates relationship were based on mean values of each species (Campoe et al., 2014; Poorter & Bongers, 2006), for believing that the intraspecific variation in these traits is relatively small compared to the interspecific variation (Albert et al., 2010; Hulshof & Swenson, 2010). However, the intraspecific analyses provide a more realistic insight of traits-demographic rates relationship due the individual be directly exposed to variation on environmental factors as resource availability, neighbor competition and herbivory (Violle et al., 2012; Yang, Cao & Swenson, 2018). Despite, Poorter et al. (2018) studying whether trait intraspecific analysis are good predictors to growth performance in an hyperdiverse tropical forest found no significant correlation between growth and the measured traits. The authors attribute this to the fact that at understory of tropical forest the light is a limiting factor, leading the individuals had minor chance to expressed your maximum growth in function of the effect that light limitation cause in their traits. Third, normally the traits analyzed weakly represent the complexity of growth process. Most of the studies developed to date have focused to measure soft-traits due to their easy applicability and the lower investment required (Gilbert et al., 2016; Worthy & Swenson, 2019; Yang, Cao & Swenson, 2018). However, hard-traits are more informative of physiological processes that drive the plant performance, highlighting the different steps of photosynthesis (dos Santos & Ferreira, 2020b; Worthy & Swenson, 2019; Yang, Cao & Swenson, 2018). Furthermore, a set of traits can better explain demographic rates than a single-trait (Li et al., 2017), since that the plant performance depends on the complex interaction among different traits (Marks & Lechowicz, 2006).

The wide variation in responses found in the literature on the functional traits-demographic rates relationships is one of the most important in plant biology (Salguero-Gómez et al., 2018). Considering that the light is the most limiting factor for plant growth in tropical forests, the role that the availability of this resource has on the functional traits-demographic rates relationships remains underdeveloped. Therefore, from an experiment of enrichment planting in secondary forest, we analyzed the relationships between demographic rates and traits of tropical tree saplings growing under contrasting light environments. Our specific objectives were: **First**, *analyze if the light environment (high and low irradiance) modulates the relationships between demographic rates (growth and survival) and photosynthetic traits in tropical tree saplings*, **second**, *investigate if the relationships between growth and traits changes according to the level of approach (individual or species)*, **third**, *investigate if the relationships between growth and traits improve when performed with an integrated set of traits.*

2. Material and Methods

2.1. Study site

This study was realized in an experiment of enrichment planting in Central Amazon. The site is located at Fazenda Experimental da Universidade Federal do Amazonas (02º38’S, 60º03.5’W), 38 km north of Manaus, Amazonas, Brazil. The annual precipitation is of 2350 mm, mensal average air temperature ranging from 26.4ºC to 28.5ºC and air humidity reaching an average of 75% in the dry season and 85% in the wet season (data from 1988-2018; INMET, 2019). The precipitation seasonality is generally moderate with dry season length between the months of August and September (Sombroek, 2001).

In 1986, the mature forest was mostly clear-cut, burned and then abandoned. Eleven years later (1997), a secondary forest that had regrown was cut and burned; a crop of cupuaçu tree (*Theobroma gradiflorum* (Willd. ex Spreng.) K. Schum.) was planted, but the area was once more abandoned. Therefore, the silvicultural treatments of this study were applied to a 19-years-old secondary forest. The secondary forest was established in a well-drained clayed and infertile oxisol (Chauvel, 1982) (Table 1). The secondary forest covers 17 hectares and is neighbored by a wide mature forest along approximately 80% of the edges (details in dos Santos & Ferreira, 2020a; dos Santos, Modolo & Ferreira, 2020).

2.2.Experimental design

The management of secondary forest for productive objectives was established from two silvicultural treatments applied during the last quarter of 2016. The first treatment consisted of understory slashing, with removing all herbaceous plants and small trees (DBH < 5 cm) with a machete–hereafter named understory slashing treatment. All

Table 1. Chemistry and fertility soil characterization in a Central Amazon secondary forest.

pH		Ca^{2+}	Mg^{2+}	Al^{3+}	K^+	t	SB	P	C/N	M
H_2O	KCl	cmolc.kg						ppm	%	
4.19 ± 0.05	3.85 ± 0.02	0.035 ± 0.03	0.084 ± 0.01	1.43 ± 0.08	0.043 ± 0.01	1.6 ± 0.11	0.16 ± 0.05	1.43 ± 0.76	12.32 ± 0.79	89.85 ± 2.24

Values are means ± standard deviation. Soil samples were collected at a depth of 0-20 cm. One composed sample was collected per subplot. Ca^{2+} exchangeable calcium; Mg^{2+} exchangeable magnesium; Al^{3+} exchangeable aluminum; K^+ exchangeable potassium; t effective cation exchange capacity; SB sum of bases; P available phosphorus; C/N carbon and nitrogen ratio; M aluminum saturation.

understory regrowth was cut again during two maintenance campaigns per year. The second treatment, which occurred soon after understory slashing, consisted of thinning trees (DBH > 5 cm) occupying the forest canopy and subcanopy in progressive levels of basal area reduction (0, 20, 40, 60, 80 and 100%) by felling with a chainsaw and was named canopy refinement treatment. Each level of canopy refinement was applied to a plot of 2318 m^2 (61 x 38 m), and understory slashing was applied in a subplot within half of the main canopy refinement plot (Figure 1). The treatment combinations were replicated in five repetitions (blocks), each with 12768 m^2 (114 x 112 m). Six tropical tree species (Table 2) were planted in these plots in March 2017, configuring a silvicultural system of enrichment planting. In each subplot, five seedlings of each species were planted, 3 x 3 m spaced, with an edge of 10 m between plots and 11 m between subplots (Figure 1). During the planting, the soil surrounding each seedling was fertilized with P_2O_5 (46 g), N (11.6 g), KCl (12 g) and micronutrients (10 g of FTE-BR12: 1.8% B; 0.8% Cu; 3.0% Fe; 2.0% Mn; 0.1%Mo). The dosages and applied methods that ensure the minimal nutrient requirements of tropical trees were obtained from a literature review (Alvarado, 2015; Campoe et al., 2014; Furtini Neto, 2000; Resende, Furtini Neto & Curi, 2005). Further details are given in dos Santos, Modolo & Ferreira (2020) and dos Santos & Ferreira (2020a).

For this study, we selected only two subplots combinations with most contrasting light environments: 1) clearcut (100% of canopy refinement) and understory slashed subplots – hereafter named *full sun* (photosynthetic photon flux density (PPFD) = 27.9 mol m^{-2} day^{-1}) and; 2) plots without basal area reduction (0% of canopy refinement) combined with understory slashing-hereafter named *understory* (PPFD = 1.3 mol m^{-2} day^{-1}) (dos Santos, Modolo & Ferreira, 2020) (Figure 1). We selected only subplots with understory slashed with the objective to reduce the eventual effects of herbaceous competition on survival and growth of trees. Considering the total number of seedlings planted and the number of subplots selected, we had a total of 300 plants at the beginning of the experiment.

2.3.Demographic rates measurements

The seedlings planted in this experiment were bimonthly monitored from March 2017 to March 2019, resulting two years of monitoring. In each monitoring campaign, we counted the number of live seedlings and measured the root collar diameter (*D*) (5 cm above the soil) and total height (*H*) of each sapling.

2.3.1 Annual survival rate

We calculate the annual survival rate (***SR***) according to Poorter & Bongers (2006). The daily seedlings survival rate (DSR) for each species consisted of the regression slope of $\log_{10}$(percentage of surviving seedlings) against time (in days). Annual survival rate was then calculated as $10^{365\mathrm{DSR}}$.

2.3.2 Relative growth

The plant aboveground biomass was approximated by D^2H, as proposed by Kohyama & Hotta (1990). Annual relative growth in biomass (***BG***), diameter (***DG***) and height (***HG***) were calculated according to Hunt (1990).

$$\mathrm{RG_x} = \frac{\ln \mathrm{X_2} - \ln \mathrm{X_1}}{\mathrm{T_2} - \mathrm{T_1}}$$

In which RG_x = relative growth in biomass, diameter or height, $\ln X_2 - \ln X_1$ = increment of logarithmic biomass, diameter or height between two measurements and $T_2 - T_1$ = interval between measurements. During the bimonthly monitoring we also observed damage caused by broken accidentally or by insects. Plants that had growth severely affected by these factors, and plants without sufficient leaves to perform all analyses (e.g. deciduos species as *Cedrela fissilis* and *Tabebuia rosea*) were excluded from this study. In total, were removed 19% of live plants at *full sun* and 18% at *understory*.

Table 2. Scientific name, botanical family and ecological group of the six tropical tree species utilized for the secondary forest enrichment planting.

Species	Family	Ecological group*
*Cedrela fissilis*Vell.	Meliaceae	Pioneer (LLP)
Tabebuia rosea (Bertol.) Bertero ex A. DC.	Bignoniaceae	Pioneer (LLP)
Swietenia macrophylla King	Meliaceae	Pioneer (LLP)
Bertholletia excelsa Bonpl.	Lecythidaceae	Non-Pioneer (PST)
Carapa guianensis Aubl.	Meliaceae	Non-Pioneer (PST)
Hymenaea courbaril L.	Fabaceae	Non-Pioneer (PST)

*Ecological group according to Swaine & Whitmore, 1988; Finegan 1992, Poorter, Bongers & Bongers, 2006; Chazdon, 2014. LLP (long-lived pioneer), PST (partial shade-tolerant).

2.4.Competition index and ligth properties measurements

In March 2019, competition index and two light properties (canopy oppeness and transmittance) were measured in all plants located at *full sun* and *understory* subplots selected for this study (Table S1, S2). **Competition index**, was calculated as the sum of diameters at breast height of all trees (DBH > 5 cm) surround 5.64 m (100 m^2) of each individual (Holmes & Reed, 1991; Lorimer, 1983). **Canopy openness**, calculation was

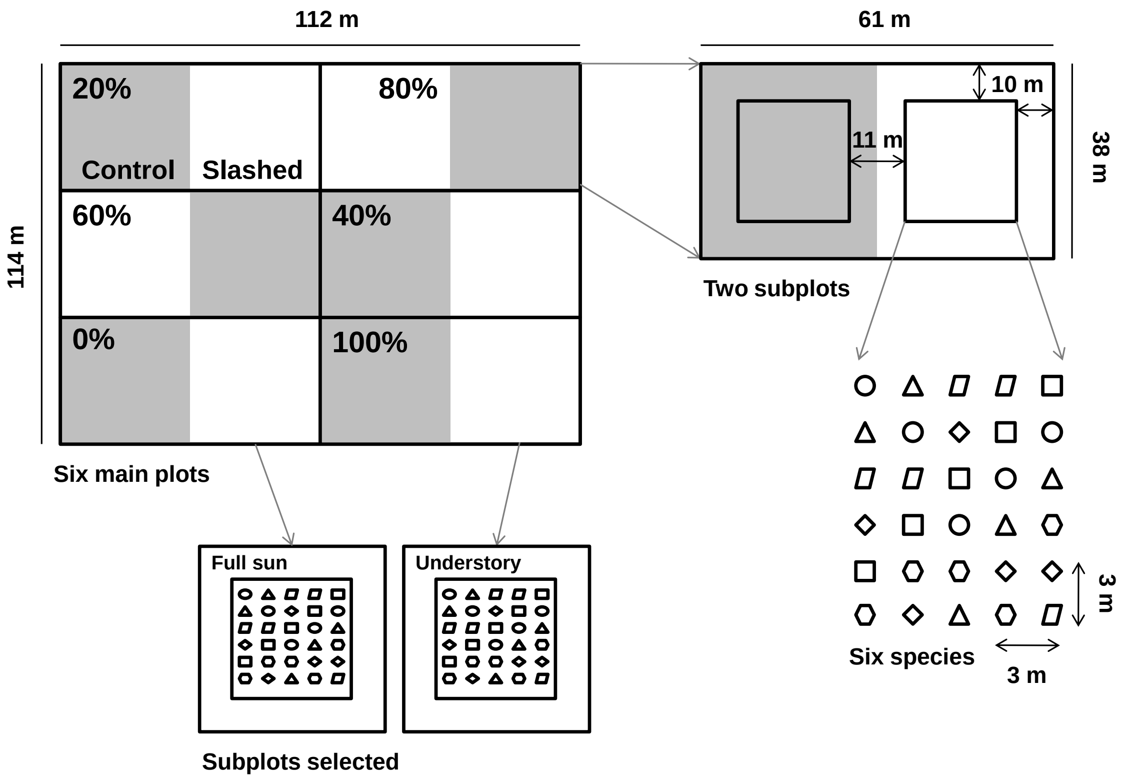

Figure 1. Plot and subplot design where silvicultural treatments were applied and the six tropical tree species were planted in an enrichment planting silvicultural system. The different symbols at the lower left are a representation of the six species. Highlighted subplots represent the subplots selected for the present study.

made from hemispherical photography using a Digital Plant Canopy Imager (CI-110, CID Bio-Science, Camas, WA, USA). The hemispherical photos were taken at the top of each plant and were analyzed using the Plant Canopy Analyses System Software (CID Bio-Science, Camas, WA, USA). The value of canopy open fraction above each plant was registered and utilized for analyses. **Transmittance**, calculation was made by the ratio between photosynthetic photons flux density (PPFD; µmol m^{-2} s^{-1}) measured above each individual and in a full sun area. Measurements in each individual were taken by line sensor (MQ-301: Line quantum with 10 sensors and handheld meter, Apogee, USA). The second PPFD sensor (MQS B/ULM-500 logger, Heinz Walz, Germany) was installed in a full sun area (100 m from the secondary forest), and PPFD values were recorded every

30 seconds for 10 days, throughout the daily photoperiod (from 06:00 to 18:00 hours). Transmittance was calculated by the ratio between the PPFD in the full sun area and the PPFD above each individual at the same time. Measurements were taken on overcast days to avoid the influence of direct irradiance on the measurements, as proposed by Comeau, Gedron & Letchford (1998), Gedron (1998) and Messier & Parent (1997).

2.5. Photosynthetic traits measurements

A set of photosynthetic traits was measured at the end of the second year after planting (Table 3). The measurements were made in 113 individuals at *full sun*, ranging from 16 to 23 per species, and 89 individuals at *understory* subplots, ranging from 7 to 22 per species. All measurements were made on leaves healthy, fully expanded, visually without herbivory and located in the middle third of the crown. When possible, the same leaves were used in all analyzes. The traits measured were grouped in three sets of traits: Crown, morphological and physiological traits.

2.5.1. Crown traits

Crown projection area (*CPA*), was calculated as an ellipse area using crown diameters measured in two orthogonal directions. **Crown length (*CL*)**, was calculated as the length between insertion of the lower branch (or leaf) and the highest branch (or leaf) of the crown. **Crown ratio (*CR*)**, is the ratio of mean crown diameter to root collar diameter. **Crown length ratio (*CLR*)**, is the ratio of *CL* and total sapling height. **Relative crown length (*RCL*)**, was calculated as the ratio of *CL* to mean crown diameter (Li et al., 2017).

2.5.2. Morphological traits

Total leaf area (*TLA*), was estimated through two model of regression. First, was developed for each species, a model that estimated the individual area of one leaf based on the product of length x width. The values of area, length and width of each leaf used for the adjusting were measured using a leaf area meter (CI-202, CID, Inc. Beds, WA, USA). Leaves with a wide range of sizes were used. The models were adjusted for two to four leaf size classes for each species, and the coefficient of determination (R^2) of models ranging from 0.86 to 0.99 (Table S3). Further, was measured length and width in the field with the aid of a measuring tape in all leaves of each plant at *understory*, and 30% of leaves of each plant at *full sun*. Measures at *full sun* plants, were distributed randomly in all thirds of the crown (i.e. low, medium and high). Taking care that, on average, the same number of leaves be measured in each third of the crown. Finally, the total number of leaves of each plant was counted. To estimate *TLA* in *understory*, was applied the first regression in all values of length x width that were later summed to obtain the final value. On other hand, to estimate *TLA* in *full sun*, was applied the first regression in all values of length x width of the 30% of leaves measured in the field, and later was adjust the second regression for each plant at *full sun*, that estimated their increase in leaf area based on increase number of leaves. The second regression was applied in total number of leaves of each plant at *full sun* to estimate *TLA* (R^2 ranging from 0.90 to 0.99; non published data). **Leaf area index (*LAI*)**, was estimated as the ratio of *TLA* to *CPA* (Poorter, 1999). **Individual leaf area (*LA*)**, was calculated by the mean of the area estimated of all leaves of each plant. **Specific leaf area (*SLA*)**, was calculated by the area (cm^2) and oven-dried mass (65 ºC; g) ratio of ten leaf discs. **Leaf dry matter content (*LDMC*)**, was determined by the oven-dry mass (65 ºC; mg) and water-saturated fresh mass (g) ratio of ten leaf discs (Pérez-Harguindeguy et al., 2013). Three leaves per plant were selected to obtain the ten discs used for *SLA* and *LDMC* analysis. The discs were cut avoiding primary and secondary leaf veins.

2.5.3. Physiological traits

To calculate the leaf nutrient concentrations, we collected from three to six leaves per plant. All leaves of each plant were ground to form a homogeneous composite sample. **Leaf nitrogen concentration (N_{mass})**, was determined by the Kjeldahl method with digestion, distillation and titration (Bremner, 1996). **Leaf phosphorus concentration (P_{mass})**, was determined by spectrophotometry (λ=750 nm) following the molybdate method (Murphy & Riley, 1962). **Leaf potassium concentration (K_{mass})**, was determined by atomic absorption spectrometry (1100B, PerkinElmer, Ueberlingen, Germany). We take three leaves of each plant for chloroplastidic pigments analysis. **Chlorophyll *a* (*Chl a*)**, **Chlorophyll *b* (*Chl b*)** and **Carotenoids (Car_{c+x}) concentrations**, were determined with acetone extraction (10 ml of 80% acetone with 0.05 g of $MgCO_3$ per 0.1 g of fresh leaf) followed by filtration, absorbance reading at three wavelengths (663, 645 and 480 nm; Biochrom Libra s50 UV/Vis, Cambridge, UK) and concentrations calculations (Lichtenthaler & Wellburn, 1983; Hendry & Price, 1993). **Total chlorophyll concentration (*Chl a+b*)**, was calculated by sum of *Chl a* and *Chl b* concentrations. **Chlorophyll *a* and *b* ratio (*Chl a/b*)**, was calculated by the ratio of *Chl a* and *Chl b* concentrations. **Maximum Quantum yield of PSII (F_V/F_M)**, **ABS-based performance index (PI_{ABS})** and **Total performance index (PI_{total})**, were measured with a portable fluorimeter (PEA, MK2-9600, Hansatech, Norfolk, UK) adjusted to emitted a saturating light pulse of 3000 µmol m^{-2} s^{-1} at a wavelength of 650 nm during 1 s. Before the measurements, the leaves were dark acclimated during 30 min for complete oxidation of the photosynthetic electron transport chain. The measurements were made on six leaves per plant during two days, and these values were used to calculate an average of each plant. The measurements were performed between 08:00 and 10:00 h. The chlorophyll *a* polyphasic transient stages and the fluorescence parameters were determined after JIP-test application, following Strasser et al. (2010), Strasser, Srivastava & Govindjee (1995), Strasser, Srivastava & Tsimilli-Michael (1999) and Tsimilli-Michael & Strasser (2008). The JIP-test calculate light use performance parameters throughout of the electron transport chain, where: light energy is absorbed by the antenna of PSII (ABS) and a fraction is trapped by open PSII reactions centers (TR), leading to the quinone A (QA^-) reduction; the QA^- electron is transported to intersystem electron acceptors (ET) and to the final electron acceptors of PSI (RE). The following parameters using the JIP-test are obtained: the reaction centers density (RC/ABS), maximum quantum yield of PSII (F_V/F_M), efficiency of intersystem transport (ET_0/TR_0) and efficiency of the electron transport to reducing the final electron acceptors PSI (RE_0/ET_0). PI_{ABS} is an integrated index of the efficiency which electron is trapped by PSII (F_V/F_M) and is transferred further than QA^- (ET_0/TR_0).

$$PI_{ABS} = \left(\frac{RC}{ABS}\right) * \left(\frac{Fv/Fm}{1 - Fv/Fm}\right) * \left(\frac{\mathrm{ETo/TRo}}{1 - \mathrm{ETo/TRo}}\right)$$

PI_{total} is an integrated index of the PI_{ABS} and the efficiency which electrons reduces the end acceptors at the PSI

$$PI_{total} = PI_{ABS} * \left(\frac{\mathrm{ETo/TRo}}{1 - \mathrm{ETo/TRo}}\right)$$

Maximum photosynthetic rate (A_{max}) per unit area, **Dark respiration rate (R_d)**, **Stomatal conductance (g_s)** and **Transpiration rate (E)**, were measured with an infrared gas analyzer (LI-6400XT, LI-COR, USA). The measurements were made on one leave per plant. However, prior to recording, experimental tests were performed on several leaves per plant to ensure the selection of leaves with the maximum values of A_{max} and g_s. The measurements were made between 08:00 and 11:00 h and the gas analyzer chamber adjusted to a flow rate of 400 µmol s^{-1}; 400 µmol mol^{-1} of CO_2 concentration; 21 mmol mol^{-1} of H_2O vapor concentration; 31 ºC of leaf temperature; and photosynthetic photon flux density (PPFD) of 2000 µmol m^{-2} s^{-1} (except for R_d when PPFD was 0 µmol m^{-2} s^{-1}). **Carbon use efficiency (*CUE*)**, was calculated by the ratio between $A_{\max}$ and R_{d}. **Photosynthetic nitrogen (*PNUE*)**, **phosphorus (*PPUE*)** and **potassium (*PKUE*) use efficiency**, were calculated by the ratios between maximum photosynthetic rate per unit mass ($A_{\max}$ * *SLA* * 0.1) and the nutrients concentrations in molar mass units. **Total maximum photosynthesis rate (Total $A_{\max}$)**, was estimated based on the product of *TLA* x $A_{\max}$ per plant.

2.6.Statistical analyses

We performed all statistical analyses for data of *full sun* and *understory* plants, separately. Growth rates and traits values, of each individual, were used for individual-level analysis. Mean of growth rates, traits and survival rates, of each species, were used for species-level analysis. All analyses we subjected to Shapiro-wilk and Levene tests to test normality and homocedasticity, respectively, when the assumptions were not met, we performed logarithmic transformations.

Coefficient of variation in percentage (CV %) was calculated for demographic rates and photosynthetic traits at individual-level and species-level analysis to evaluate variation among species and among individuals. Fifth and ninety-fifth percentiles (5th – 95th) were calculated for each demographic rate and photosynthetic trait to evaluate the breadth of the traits values. To characterize the species, mean values and standard deviation, were calculated for each of them.

For analyze the first specific objective, we adjusted simple linear regressions to test the relationship between survival rates and traits, this analysis was made only at species-level. Coefficient of determination (R^2) and significance level (P-value) were observed to determine the strength of the relationships. To test growth rates-traits relationships, we adjusted generalized linear mixed models (GLMM), with each trait separately, this analysis was made at species-level and individual-level. For species-level, we controled the plots as a random factor, while for individual-level, we controled plots and species as random factors. Coefficient of determination marginal (R^2 m) and significance level (P-value) were observed to determine the strength of the relationships. The GLMM results at species-level and individual-level were compared for test the second specific objective. For test the third specific objective, we adjusted GLMM, at individual-level, with multiples traits, grouped in sets of crown traits, morphological traits, physiological traits and a group with all trait's types. However, before adjusting the models, we standardize the data, whereby individual values, of each variable, is subtracted from the variable mean and then divided by its standard deviation. This allows the slope values to be compared. We controled plots and species as random factors. Coefficient of determination marginal (R^2 m) and significance level (P-value) were observed to determine the strength of the relationships. The best models were selected based on Akaike's Information Criterion (AIC), using the MuMIn package, dredge function. The best models were controlled for collinearity by using the variance inflation factor (VIF < 2.5). All analyses were performed using the statistical program R version 3.5.1 (R Core Team, 2018).

Table 3. Name, abbreviation, units and significance to photosynthesis of thirty photosynthetic traits.

Traits group	Traits	Abbreviation	Units	Significance to photosynthesis
Crown traits	Crown projection area	*CPA*	(m^2)	Light interception
	Crown length	*CL*	(m)	Light interception
	Crown ratio	*CR*		Light interception
	Crown length ratio	*CLR*		Light interception
	Relative crown length	*RCL*		Light interception
Morphological traits	Total leaf area	*TLA*	(m^2)	Light interception
	Leaf area index	*LAI*		Light interception
	Leaf area	*LA*	(cm^2)	Light interception
	Specific leaf area	*SLA*	(cm^2 g^{-1})	Light interception
	Leaf dry matter content	*LDMC*	(mg g^{-1})	Carbon alocation
Physiological traits	Leaf nitrogen	N_{mass}	(g kg^{-1})	Nutrient acquisition
	Leaf phosphorus	P_{mass}	(g kg^{-1})	Nutrient acquisition
	Leaf potassium	K_{mass}	(g kg^{-1})	Nutrient acquisition
	Chlorophyll *a*	*Chl a*	(µmol g^{-1})	Light absorption
	Chlorophyll *b*	*Chl b*	(µmol g^{-1})	Light absorption
	Carotenoids	Car_{c+x}	(µmol g^{-1})	Light absorption
	Total chlorophyll concentration	*Chl a+b*	(µmol g^{-1})	Light absorption
	Chlorophyll *a* and *b* ratio	*Chl a*/*b*		Light absorption
	Maximum Quantum yield of PSII	F_V/F_M		Light use in the first steps of the electron transport chain
	ABS-based performance index	PI_{ABS}		Light use in the first to intermediary steps of the electron transport chain
	Total performance index	PI_{total}		Light use in the first to final steps of the electron transport chain
	Maximum photosynthetic rate	A_{max}	(µmol CO_2 m^{-2} s^{-1})	Carbon assimilation
	Dark respiration rate	R_d	(µmol CO_2 m^{-2} s^{-1})	Carbon consumed by respiration
	Stomatal conductance	g_s	(mol H_2O m^{-2} s^{-1})	Diffusive limitation
	Transpiration rate	*E*	(mmol H_2O m^{-2} s^{-1})	Water lost by transpiration
	Carbon use efficiency	*CUE*		Carbon balance
	Photosynthetic nitrogen use efficiency	*PNUE*	(nmol CO_2 mol^{-1} N m^{-2} s^{-1})	Nutrient allocation for photosynthesis
	Photosynthetic phosphorus use efficiency	*PPUE*	(nmol CO_2 mol^{-1} P m^{-2} s^{-1})	Nutrient allocation for photosynthesis
	Photosynthetic potassium use efficiency	*PKUE*	(nmol CO_2 mol^{-1} K m^{-2} s^{-1})	Nutrient allocation for photosynthesis
	Total maximum photosynthetic rate	*Total* A_{max}	(µmol CO_2 $individual^{-1}$ s^{-1})	Carbon assimilation total

3. Results

3.1. Inter and intraspecific variations in demographic rates and photosynthetic traits

The coefficients of variation (CV%) and ranging (Range 5th - 95th) of the demographic rates and photosynthetic traits were different between light environments (Table 4). Annual survival rate (*SR*) was greater at *full sun* (ranging from 94 to 100%) than *understory* (ranging from 74 to 98%). Furthermore, *SR* was more variable at *understory* (CV = 12%) than *full sun* (CV = 3%). Relative growth in biomass (*BG*), diameter (*DG*) and height (*HG*) were more variable at *understory* than *full sun* at both individual and species-level (Table 4). *CPA*, *CL*, *CLR* (crown traits), *TLA*, *LAI* (morphological traits) and *Total* $A_{\max}$ (physiological trait), had the highest variation among traits measured at both light environments. Specific leaf area (*SLA*) was greater variable at *understory* (ranging from 150.4 to 427.5 cm² g^{-1}) than at *full sun* (ranging from 80.9 to 137.1 cm² g^{-1}) at both individual and species levels (Table 4). Overall, the values of coefficient of variation of demographic rates and photosynthetic traits were greater at individual-level analysis than species-level analysis (Table 4). Individual-level analysis, on average, had a CV for the traits of 42% at *full sun* (ranging from 4% for F_V/F_M to 100% for *Total* $A_{\max}$) and 46% at *understory* (ranging from 1% for F_V/F_M to 103% for *CPA*). While species-level analysis, on average, had a CV for the traits of 26% at *full sun* (ranging from 2% for F_V/F_M to 74% for *LAI*) and 30% at *understory* (ranging from 1% for F_V/F_M to 79% for *RCL*).

3.2.Relationship between demographic rates and photosynthetic traits under contrasting light environments

Annual survival rate (*SR*) – functional traits relationships were strongest at *understory* (Figure 2), while there were no significant relationships at *full sun*, except for

Table 4. Range (5th - 95th percentiles) and coefficient of variation (CV%) of all demographic rates and traits, in two light environments, and two analysis level.

Environments	*Full sun*	*Understory*	*Full sun*		*Understory*	
	Range 5th - 95th		CV (%)			
			Ind.	Sp.	Ind.	Sp.
			Demographic rates			
SR	94 – 100	73 - 98		3		12
BG	1.85 - 3.46	0.33 - 1.45	19	10	44	29
DG	0.70 - 1.28	0.15 - 0.59	18	13	46	33
HG	0.42 - 1.06	0.06 - 0.48	24	11	63	28
			Traits			
CPA	0.40 - 8.31	0.07 - 0.79	80	59	103	67
CL	0.27 - 3.53	0.03 - 1.08	67	53	66	66
CR	1.67 - 5.13	2.78 - 6.97	38	37	29	22
CLR	0.11 - 0.83	0.05 - 0.89	46	47	55	62
RCL	0.17 – 2.15	0.04 – 1.78	65	62	66	79
TLA	1.07 – 15.70	0.03 – 0.40	92	40	80	44
LAI	0.59 - 7.46	0.14 - 0.80	85	74	88	41
LA	21.21 – 156.74	15.57 - 118.45	51	44	57	54
SLA	80.91 - 137.12	150.37 - 427.54	16	12	39	41
LDMC	256.59 - 464 .23	178.06 - 400.25	19	9	24	25
N_{mass}	11.25 - 21.77	10.23 - 19.38	20	15	19	14
P_{mass}	0.51 - 1.02	0.60 - 1.31	25	17	27	18
K_{mass}	4.38 - 14.84	3.09 - 13.18	38	31	42	26
Chl a	0.56 - 2.13	0.92 - 3.08	38	26	34	10
Chl b	0.18 - 0.66	0.36 - 1.13	36	21	35	13
$Car_{\mathrm{c+x}}$	0.29 - 0.81	0.37 - 1.09	32	19	33	12
Chl a+b	0.72 - 2.82	1.26 - 4.21	37	25	34	11
Chl a/b	2.36 - 3.82	2.32 - 3.10	15	11	9	5
$F_{\mathrm{V}}/F_{\mathrm{M}}$	0.738 - 0.827	0.814 - 0.846	4	2	1	1
PI_{ABS}	0.940 - 4.927	1.217 - 3.601	46	29	29	26
PI_{total}	0.737 - 2.793	0.324 - 1.130	38	14	36	29
A_{max}	7.86 - 19.49	4.19 - 11.78	26	12	33	24
R_{d}	0.88 - 2.64	0.18 - 1.23	32	9	66	19
g_{s}	0.12 - 0.53	0.07 - 0.29	40	11	48	25
E	2.57 - 7.50	1.50 - 4.64	30	5	33	18
CUE	5.02 - 16.41	4.95 - 51.37	42	11	71	31
PNUE	82.36 - 191.58	92.44 - 247.40	28	8	30	21
PPUE	3957.48 - 10029.23	2881.22 - 10067.65	29	13	40	17
PKUE	290.57 - 1515.12	390.79 - 1650.62	47	29	45	20
Total A_{max}	10.56 - 272.38	0.18 - 3.24	100	40	94	54

Notes: *SR*., annual survival rate; *BG*., biomass growth; *DG*., diameter growth; *HG*., height growth; Ind., individual-level analysis; Sp., species-level analysis; range (5th - 95th percentiles) were calculated only for individual-level analysis. For abbreviations, see Table 3 in 'Material and Methods'.

total maximum photosynthetic rate (*Total* A_{max}; R^2 = 0.74) (Table S4). In the *understory*, *SR* was positively related to crown length (*CL*; R^2 = 0.70), crown length ratio (*CLR*; R^2 = 0.75) and relative crown length (*RCL*; R^2 = 0.77), and negatively related to specific leaf area (*SLA*; R^2 = -0.70), leaf nitrogen concentration (N_{mass}; R^2 = -0.74), leaf potassium concentration (K_{mass}; R^2 = -0.76) and photosynthetic nitrogen use efficiency (*PNUE*; R^2 = -0.85) (Figure 2). *Tabebuia rosea* and *Cedrela fissilis* had the lowest values of *SR* at *understory* and the highest mean values of negatively survival related traits, and lowest mean values of positively survival related traits (Table S6).

Growth rates-photosynthetic traits relationships differed between light environments from three aspects: strength of relationship, type of growth rate predicted and the traits found as driver. The relationships between growth rates and each one of the functional traits were stronger at *full sun* than *understory* at individual-level analyses (Figure 3 to 8). Overall, photosynthetic traits had a better relationship with diameter growth (*DG*) at *full sun* (Figure 5) and with height growth (*HG*) at *understory* (Figure 8). The trait-biomass growth (*BG*) relationship were very similar to relationships between traits and *DG* at *full sun*, for the most of photosynthetic traits (Figure 3).

Crown length (*CL*; R^2 m = 0.41), crown projection area (*CPA*; R^2 m = 0.33), total leaf area (*TLA*; R^2 m = 0.32) and maximum photosynthetic rate (*Total* A_{max}; R^2 m = 0.29), had the highest relationships with *DG* at *full sun*, followed by total performance index (PI_{total}; R^2 m = 0.19) and ABS-based performance index (PI_{ABS}; R^2 m = 0.18) (Figure 5). Other traits, related to crown architecture (*CLR*, *RCL*), leaf display (*SLA*), nutrient absorption (N_{mass}), light absorption (*Chl a*, *Chl b*, Car_{c+x}, *Chl a+b*, *Chl a/b*) and gas exchange (A_{max}, g_s), showed weak, but significative relationships with *DG* at *full sun* (Figure 5). Similar to *full sun*, crown projection area (*CPA*; R^2 m = 0.33), total leaf area (*TLA*; R^2 m = 0.27), total maximum photosynthetic rate (*Total* A_{max}; R^2 m = 0.17) and crown length (*CL*; R^2 m = 0.17), had the highest relationships with *HG* at *understory*, but in a different order of importance (Figure 8). Furthermore, maximum quantum yield of PSII (F_V/F_M; R^2 m = -0.09) was negatively related with *HG* at *understory*. Others traits, related to crown proportion (i.e. *CR*) nutrient absorbtion (i.e. N_{mass}), light absorption (i.e. *Chl a*, *Chl b*, *Car* $_{c+x}$, *Chl a*+*b*), gax exchange (i.e. A_{max}) and nutrient use efficiency (i.e. *CUE*, *PPUE*, *PKUE*) showed weak, but positive relationships with *HG* at *understory* (Figure 8).

3.3.Relationship between growth rates and photosynthetic traits at individual and species levels

Overall, the individual-level relationships had higher values of coefficient of determination marginal (R^2 m) than species-level relationships at both light environments, but the most were not significant (Figure 3 to 8). Crown length (*CL*) had the highest relationship with *DG* (R^2 m = 0.41) at *full sun* for individual-level. Crown projection area (*CPA*) which had the strongest relationship with *DG* at *full sun*, explained only 29% of the *DG* variation for species-level (Figure 5). Crown projection area (*CPA*) had the highest relationship with *HG* at *understory*, at individual-level and species-level. However, the relationship was stronger at individual-level (R^2 m = 0.33) than species-level (R^2 m = 0.24) (Figure 8). The individual-level analysis had the greatest numbers of significative relationships than species-level at both light environments (Figure 3 to 8). In total, the individual-level analysis had twenty (67% of traits) traits significantly related to some of growth rates at *full sun*, while the species-level analysis had only ten (33% of traits). Similarly, the individual-level analysis had seventeen (57% of traits) traits significantly related to some of growth rates at *understory*, while the specie-level analysis had only seven (23% of traits).

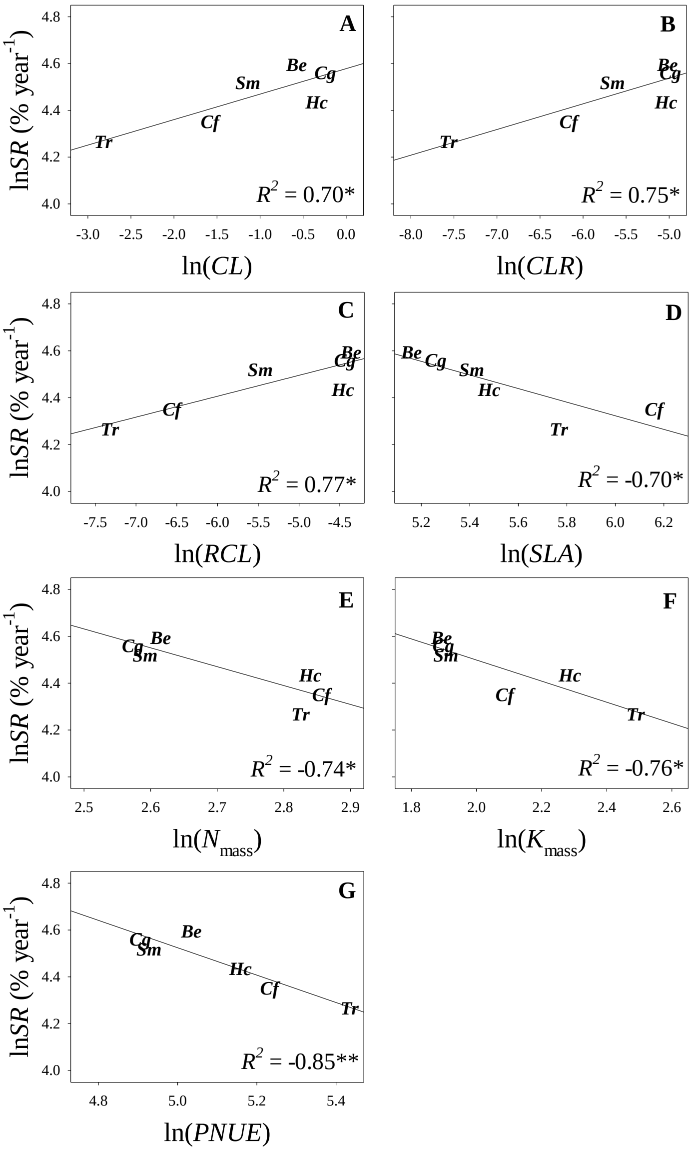

Figure 2. Scatterplot of the relationships between annual survival rate (*SR*, ln values) and *CL*, *CLR*, *RCL*, *SLA*, N_{mass}, K_{mass}, *PNUE* (ln values) at *understory*. Each point represents the average of all individuals (ranging from seven to twenty-three) of each species. (*Cf*) *C. fissilis*, (*Tr*) *T. rosea*, (*Sm*) *S. macrophylla*, (*Be*) *B. excelsa*, (*Cg*) *C. guianensis*, (*Hc*) *H. courbaril*. Coefficient of determination (R^2). The p-values of simple linear regression are inserted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For abbreviations, see Table 3 in 'Material and Methods'.

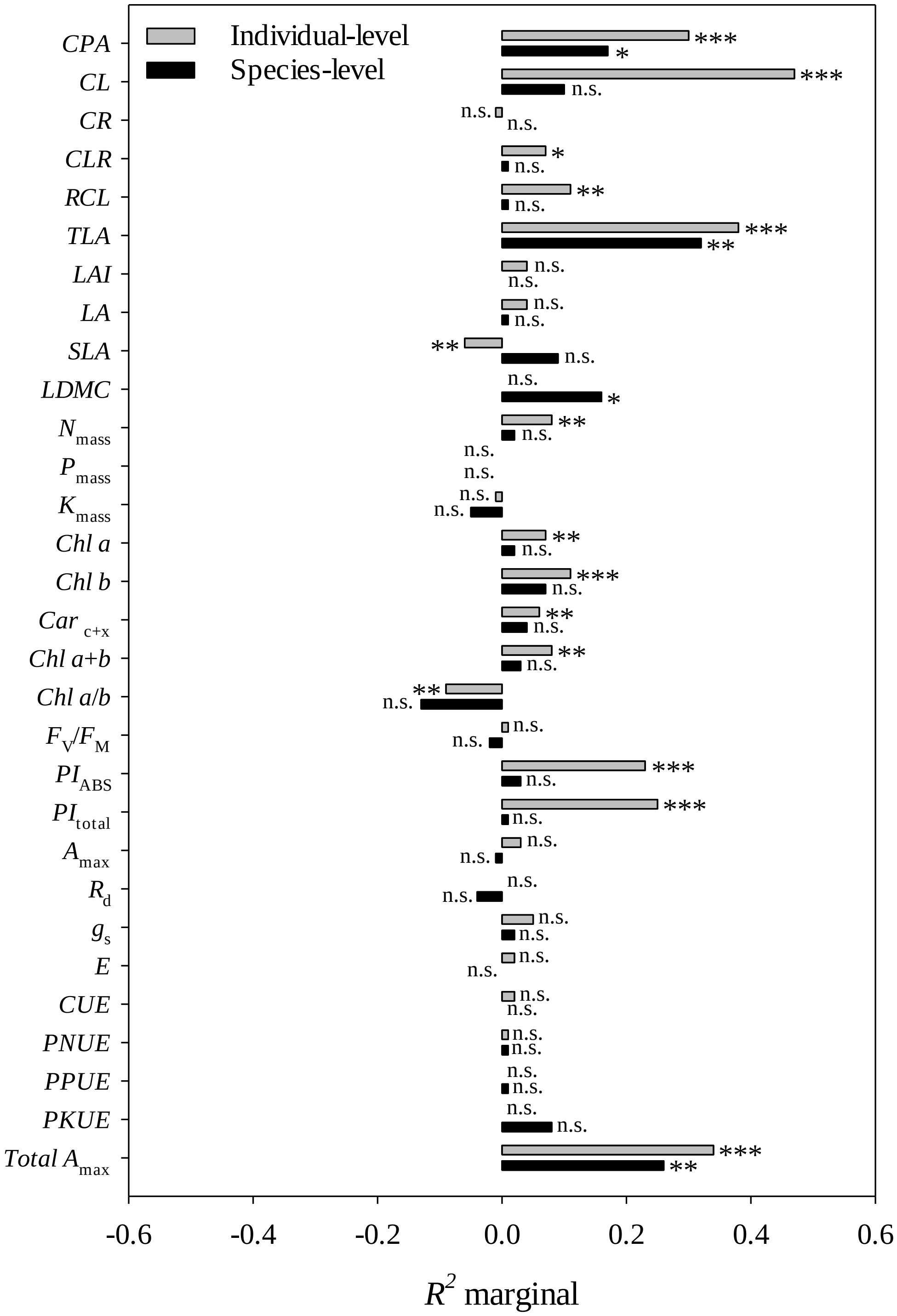

Figure 3. Barplot of the relationships between relative **biomass growth** with all traits at *full sun*, at two level analysis. Coefficient of determination marginal (R^2 marginal). The p-values of relationships are inserted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; (not significant) $P \geq 0.05$. For abbreviations, see Table 3 in ‘Material and Methods’.

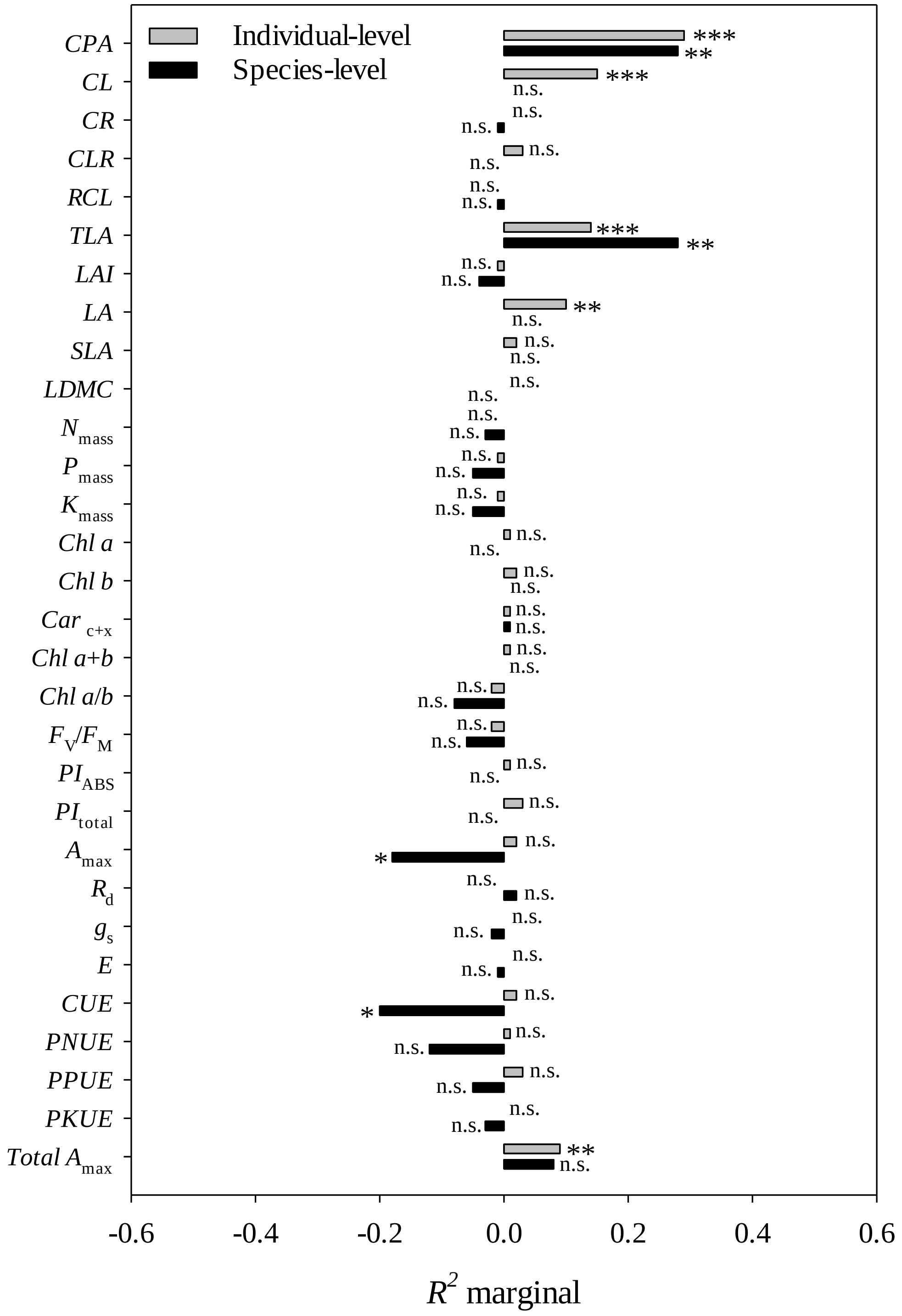

Figure 4. Barplot of the relationships between relative **biomass growth** with all traits at *understory*, at two level analysis. Coefficient of determination marginal (R^2 marginal). The p-values of relationships are inserted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; (not significant) $P \geq 0.05$. For abbreviations, see Table 3 in 'Material and Methods'.

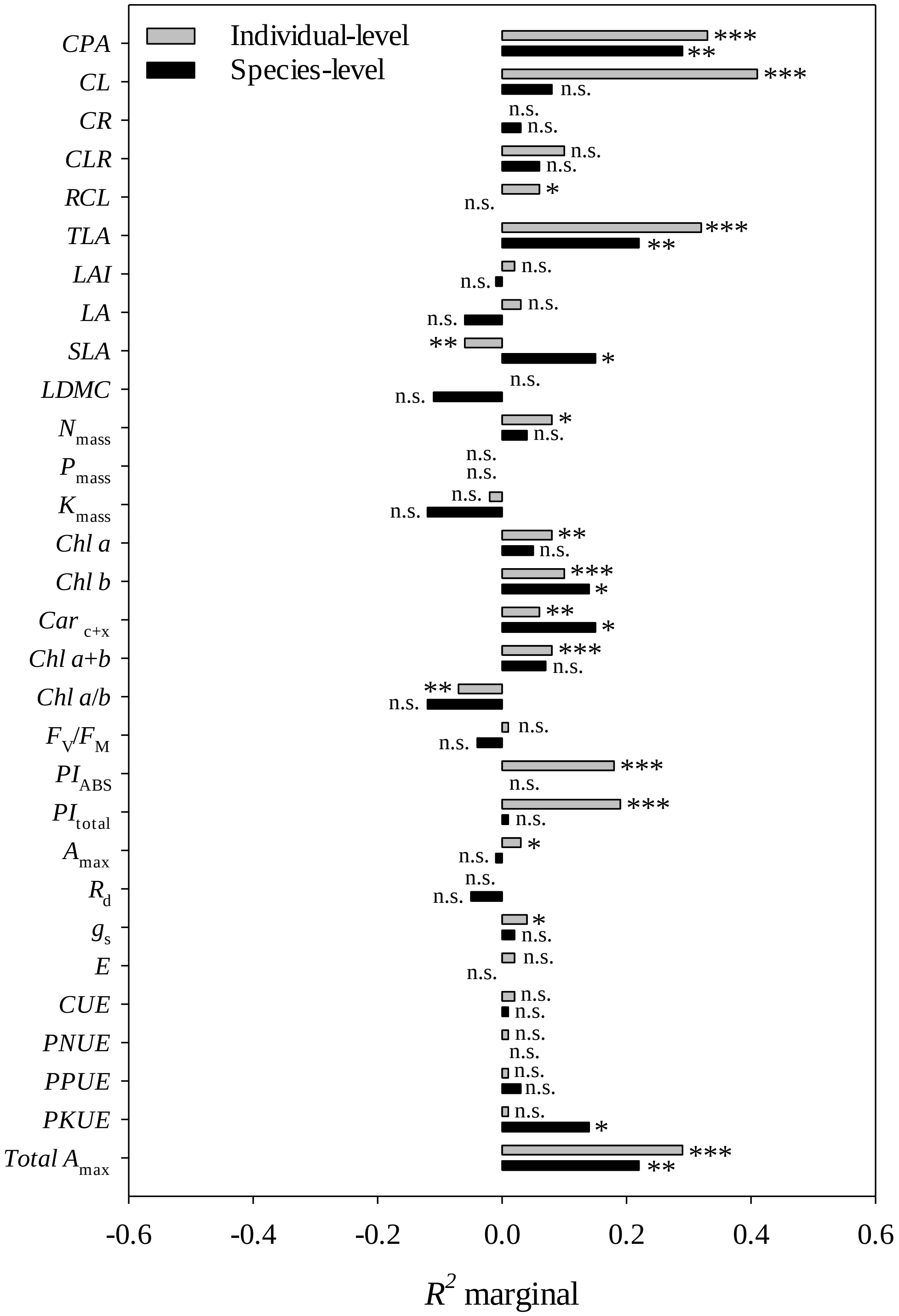

Figure 5. Barplot of the relationships between relative **diameter growth** with all traits at *full sun*, at two level analysis. Coefficient of determination marginal (R^2 marginal). The p-values of relationships are inserted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; (not significant) $P \geq 0.05$. For abbreviations, see Table 3 in 'Material and Methods'.

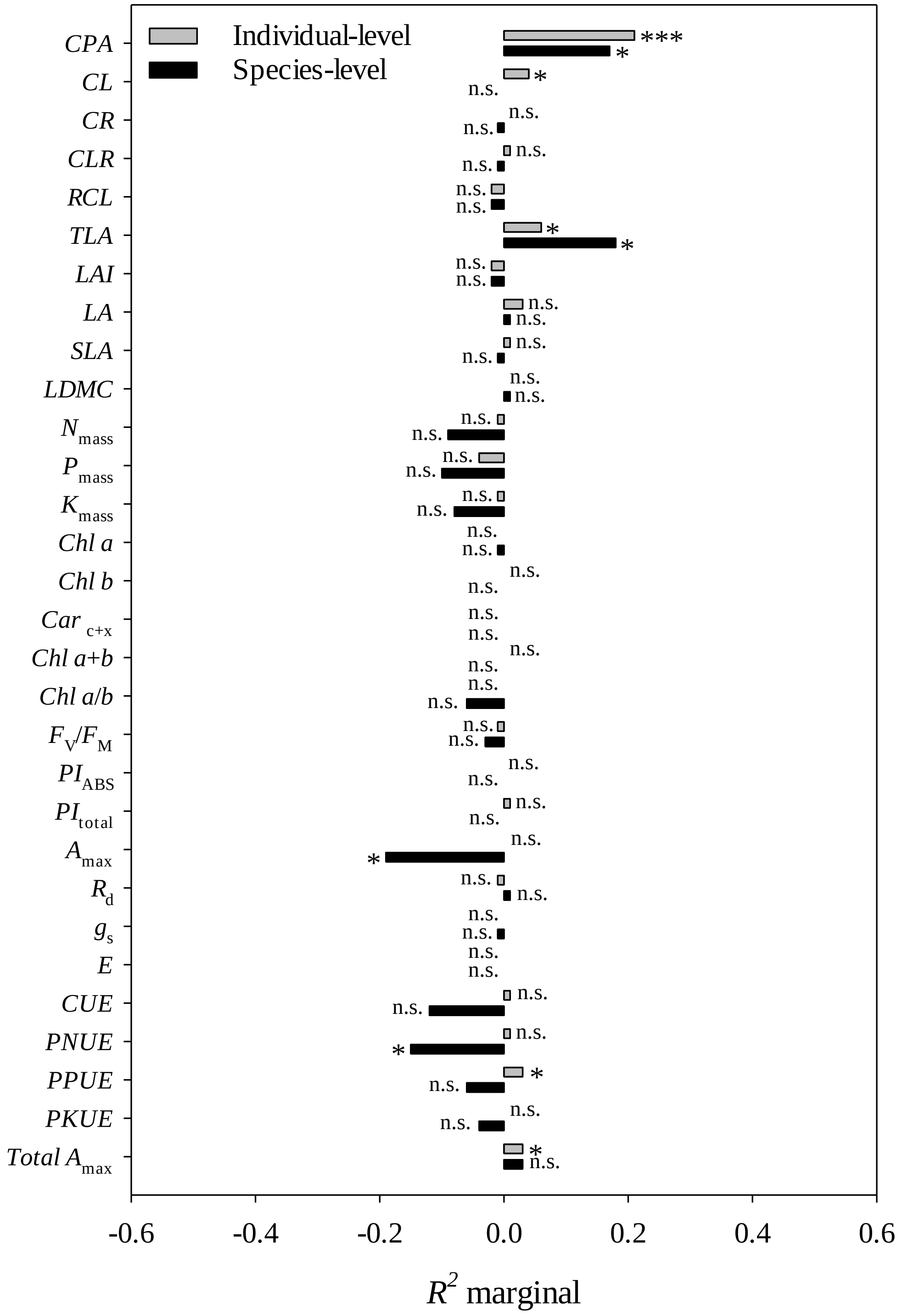

Figure 6. Barplot of the relationships between relative **diameter growth** with all traits at *understory*, at two level analysis. Coefficient of determination marginal (R^2 marginal). The p-values of relationships are inserted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; (not significant) $P \geq 0.05$. For abbreviations, see Table 3 in 'Material and Methods'.

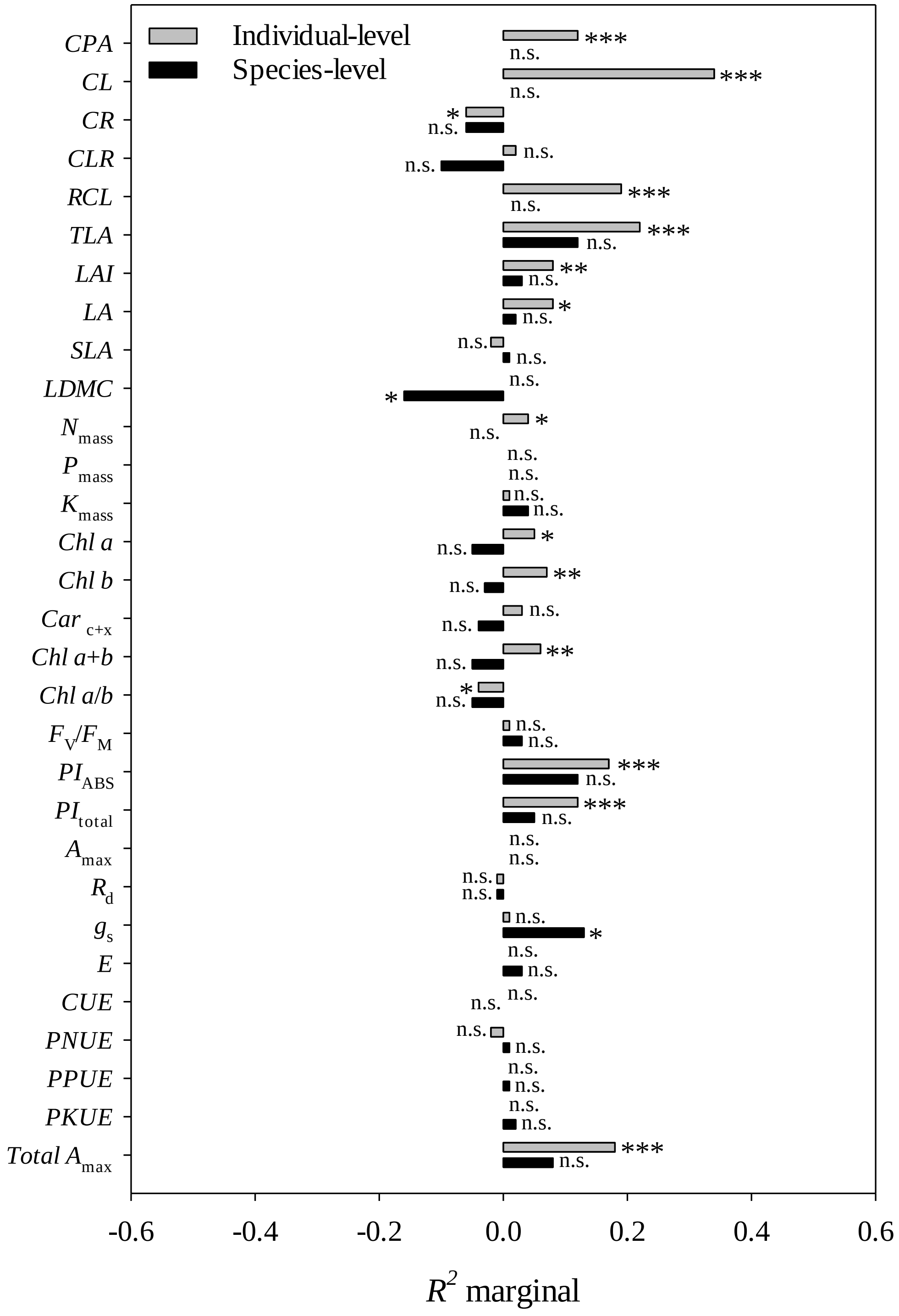

Figure 7. Barplot of the relationships between relative **height growth** with all traits at *full sun*, at two level analysis. Coefficient of determination marginal (R^2 marginal). The p-values of relationships are inserted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; (not significant) $P \geq 0.05$. For abbreviations, see Table 3 in 'Material and Methods'.

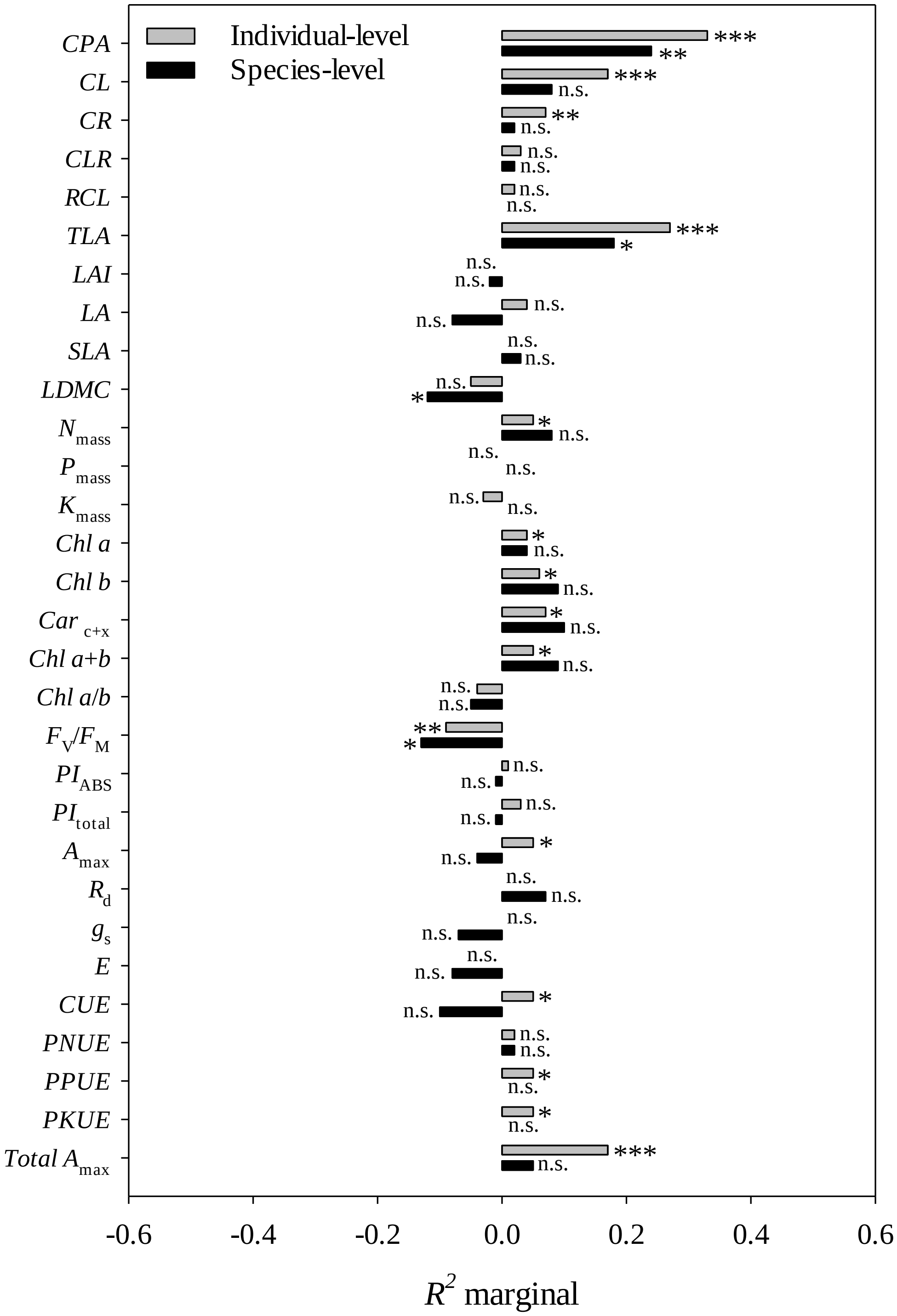

Figure 8. Barplot of the relationships between relative **height growth** with all traits at *understory*, at two level analysis. Coefficient of determination marginal (R^2 marginal). The p-values of relationships are inserted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; (not significant) $P \geq 0.05$. For abbreviations, see Table 3 in 'Material and Methods'.

3.4.Multiple regression models for growth estimative from different sets of traits

The best models of multiple regression for growth estimative had one to four predictors for each set of traits. The models that best explain each growth rate through each set of traits are presented in Table 5. Similar to observed in the single traits-growth relationship, multiple regression, overall, explained better the growth rates at *full sun* (R^2 m = 0.20 – 0.57) than at *understory* (R^2 m = 0.03 – 0.48). Furthermore, the models explain better the variation of growth in diameter (*DG*) and biomass (*BG*) at *full sun* and height (*HG*) at *understory*. The model based on crown traits (*CPA*, *CL* and *CLR*) explained 42% of *DG* variation at *full sun*. On other hand, the model including crown projection are (*CPA*) and crown length (*CL*) explained 33% of *HG* variation at *understory*. The best model with morphological traits showed that total leaf area (*TLA*) leaf area index (*LAI*) and specific leaf area (*SLA*), combined explained 37% of *DG* variation at *full sun*. On other hand, the model based on morphological traits (*TLA* and *LAI*) explained 33% of *HG* variation at *understory.* Additionally, the best model including only physiological traits explained in a similar way *DG* at *full sun* (*Chl a*/*b* and PI_{total}; R^2 m = 0.20) and *HG* at *understory* (F_V/F_M, PI_{total}; R^2 m = 0.19). *Total* A_{max} was not included because it was measured in a different scale (whole plant) of the other physiological traits. Finally, when were added traits of all groups as predictors, around 46% of the *DG* variation at *full sun* was explained by the best model (*CPA*, *CL* and PI_{total}), and 48% of *HG* variation at *understory* was explained by the best model (*CL*, *TLA* and F_V/F_M). However, models included all groups of traits, explained better *BG* at *full sun* (*CPA*, *CL*, *CR*, PI_{total}; R^2 m = 0.57) than *understory* (*CPA*, *CL*, *CR*; R^2 m = 0.34).

Table 5. Results of gereralized linear mixed models, with multiples traits for predicting biomass (*BG*), diameter (*DG*) and height (*HG*) growth from a set of crown, morphological and physiological traits and the combinations of all traits types.

	Environment	*RGR*	Predictors included	AIC	R^2 m
Crown traits	*Full sun*	*BG*	(0.560***) CPA + (0.475***) CL + (-0.498***) CR	234	0.54
		DG	(0.267***) CPA + (0.835***) CL + (-0.456***) CLR	231	0.42
		HG	(1.003***) CL + (-0.654***) CLR	261	0.37
	Understory	*BG*	(0.558***) CPA + (0.304***) CL + (-0.222**) CR	199	0.34
		DG	(0.555***) CPA	205	0.29
		HG	(0.316***) CPA + (0.463***) CL	222	0.33
Morphological traits	*Full sun*	*BG*	(0.618***) TLA	267	0.38
		DG	(0.686***) TLA + (-0.351***) LAI + (-0.211**) SLA	252	0.37
		HG	(0.469***) TLA	288	0.22
	Understory	*BG*	(0.476***) TLA + (-0.272***) LAI	217	0.23
		DG	(0.363***) TLA + (-0.257**) LAI	220	0.14
		HG	(0.595***) TLA + (-0.224*) LAI	226	0.33
Physiological traits	*Full sun*	*BG*	(-0.214**) Chl a/b + (0.490***) PI_{total}	281	0.28
		DG	(-0.192*) Chl a/b + (0.433***) PI_{total}	275	0.22
		HG	(-0.285**) F_V/F_M + (0.598***) PI_{ABS}	294	0.20
	Understory	*BG*	(0.184*) PI_{total}	236	0.03
		DG			n.s.
		HG	(-0.470***) F_V/F_M + (0.362***) PI_{total}	241	0.19
All traits	*Full sun*	*BG*	(0.478***) CPA + (0.396***) CL + (-0.411***) CR + (0.278***) PI_{total}	218	0.57
		DG	(0.267***) CPA + (0.459***) CL + (0.266***) PI_{total}	226	0.46
		HG	(1.003***) CL + (-0.654***) CLR	261	0.37
	Understory	*BG*	(0.558***) CPA + (0.304***) CL + (-0.222**) CR	199	0.34
		DG	(0.555***) CPA	205	0.29
		HG	(0.440***) CL + (0.334***) TLA + (-0.370***) F_V/F_M	206	0.48

Notes: *RGR*., relative growth rate; *BG*., biomass growth; *DG*., diameter growth; *HG*., height growth. Akaike's Information Criterion (AIC); Coefficient of determination marginal (R^2 m). The p-values of estimated parameters are inserted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; (not significant) $P \geq 0.05$. For abbreviations, see Table 3 in 'Material and Methods'.

4. Discussion

The relationship between functional traits and demographic rates is one of the major challenges in studies of community ecology (Wright et al., 2004; Chave et al., 2009; Wright et al., 2010). These relationships have shown frequently weak or nonexistent, particularly in tree communities (Yang, Cao & Swenson, 2018; Poorter et al., 2018; Worthy & Swenson, 2019). Contextual information (e.g. environmental gradients) frequently ignored, focus on species relative to individuals, functional processes (e.g. photosynthesis) that determined the plant performance are not completely explained only from soft traits or with a single trait; have been the three core reasons for unsuccessful of the functional traits determine demographic outcomes in trait-based community ecology (Yang, Cao & Swenson, 2018; Worthy & Swenson, 2019). Here, we added evidence on the importance of, first, considering the context of plants growing (i.e. light supply), second, determination of trait variation within species and, third, the use of a set of morphophysiological traits representing different phases of photosynthetic process.

4.1. Relationships between demographic rates and photosynthetic traits are modulated by light environment

The effects of light environment on demographic rates-photosynthetic traits relationships were analyzed from the aspects of plant performance survival and growth. Species annual survival rate (*SR*) was not related to photosynthetic traits at *full sun* (except for *Total* A_{max}) (Table S4), as there was little variation in *SR* (CV = 3%) in this environment (Table 4). On the other hand, at *understory*, *SR* was negatively related with acquisitive (*SLA*, N_{mass}, K_{mass}) and resource-use efficiency (*PNUE*) traits, and positively related with crown traits (*CL*, *CLR* and *RCL*) (Figure 2). In general, under low light environments, high survivorship is a more important strategy for seedlings establishment because of the resource's limitation (Kitajima, 1994; Poorter, Bongers & Bongers, 2006; Poorter et al., 2018). Poor resources environment (e.g. light supply in understory) select for more conservative strategies, as low growth rates, low photosynthetic capacity and more physically structured leaves to protection against herbivores (Montgomery & Chazdon, 2002; Kitajima & Poorter, 2010). In this sense, species with the highest values of acquisitive traits and consequently higher growth are more susceptible to death in conditions of very little light as *understory* of tropical rainforests (Kitajima, 1994.). In the same experiment, a trade-off was observed between growth at high light and mortality in shade environments one year after planting (dos Santos & Ferreira 2020a; dos Santos & Ferreira 2020b). The authors attribute this to a high cost that light-demanding species have to adapt their physiological machinery to light variation (photosynthetic plasticity), losing their capacity to invest resources in traits that promote survival. This same trade-off also has been shown in temperate forest, where gap-demanding species may acquire photosynthetic plasticity, sacrificing shade tolerance from acquisitive traits (Oguchi, Hiura & Hikosaka, 2017). The positive relationships found in this study between crown related traits and *SR*, may be related to interspecific variation on leaf lifespan. We observed that plants with deep crowns had older leaves and inserted at the minor height of the stem, some kept since the planting. Plants growing in poor environments exhibiting longer leaf lifespans tend to have more successful in surviving for compensate the high payback times need to return carbon investments on leaf construction (Poorter & Bongers, 2006; Poorter, Bongers & Bongers, 2006; Kitajima & Poorter, 2010).

As already mentioned, the relationship between growth rates and photosynthetic traits differed between light environments from three aspects: strength of relationship, type of growth rate predicted and the traits found as driver. First, the relationship between growth rates and photosynthetic traits, when analyzed in individual-level, for most traits, was stronger at *full sun* than *understory*. Moreover, *full sun* had a greater number of significative growth-traits relationships than *understory* (Figure 3 to 8). Under high light supply as *full sun* the plants can express their maximum growth potential due the effects that higher energy availability cause in their traits (Wright et al., 2010; Kunstler et al., 2016; Poorter et al., 2018). For example, due the higher light supply over the photoperiod at *full sun*, plants can express their maximum daily photosynthetic capacity. However, the maximum performance of plants depends on individual acclimation capacity to optimize the use of high energy supply without damage to the photosynthetic apparatus (Niinemets, 2010; Oguchi, Hiura & Hikosaka, 2017; dos Santos & Ferreira 2020b). The weakest relationship at *understory* can be due the fact that light limitation inhibits photosynthetic traits expression (Poorter et al., 2018). Second, the traits were more related to diameter (*DG*) (Figure 5) and biomass (*BG*) (Figure 3) growth at *full sun* and to height growth (*HG*) at *understory* (Figure 8). This result can be associated with the influence of the light environment on the specie's growth strategies. In *full sun*, plants have a large amount of energy to activate their physiological processes, allowing the plant to invest this energy in the carbon allocation on non-photosynthetic tissues (stems and roots) (Adjers et al., 1995; Peña-Claros et al., 2002; Wiener, 2010) for don't need investing so much in the light interception. Some studies demonstrate that increase of the length of photoperiod (i.e. daily irradiance) improve xylogenesis capacity and carbon allocation to xylem growth (Cafarra & Donnelly, 2011; Lemay et al., 2017; Pérez-de-Lis et al., 2017). On the other hand, under very little light as *understory*, the plants tend to invest more energy for primary growth (i.e. height), as a way to access the light available at upper stratus of forest (Finegan, 1992; Poorter, Bongers & Bongers, 2006; Chazdon, 2014). Third, *CPA*, *CL*, *TLA* and *Total* A_{max} (Figure 5, 8) were commonly most linked to growth rates at *full sun* and *understory*, demonstrating the importance of improving on light interception for growth in both environments and, consequently, achieve a greater whole photosynthetic capacity. Specifically, *CL* had the best relationship at *full sun* (Figure 5), while *CPA* exhibited the best relationship at *understory* (Figure 8). In *full sun*, it becomes more important for growth to have a deep crown (i.e. higher *CL*) to intercept the maximum amount of incident light. On the other hand, at *understory*, due to the heterogeneity of microsites with different intensity of light (Table S1), a higher *CPA* can be crucial to optimize the interception of diffuse light or sun-flecks reaching the forest floor, without increase the leaf area index (Delagrange et al., 2006; Iida et al., 2014b; Niklas, 1989). The microsite variation may have been one of the main growth factors at *understory*. The competition index, canopy openness and transmittance were more variable at *understory* (Table S1), and were more related to growth at this environment (Table S2), especially, transmittance was the best property related to *HG* (R^2 m = 0.17). Montgomery & Chazdon (2002) found that, at low light environments, the microsites of light can improve seedlings growth, however, different functional groups can have different growth strategies other than height growth (e.g. leaves and roots biomass).

The photosynthetic traits analyzed separately, contrary to our expectations, didn't have strong relationships with growth in both light environments (Figure 5 to 8). We believe that biological and methodological aspects affected the ability of the traits to predict growth rates. Growth and functional traits of forest species have species-specific response to light variation (Laughlin & Messier, 2015; dos Santos & Ferreira, 2020a; dos Santos & Ferreira, 2020b; Wiener, 2010), leaving expectations that magnitude to response of growth to traits variation can be species-specific, which can weaken relationships when individuals in the community are not separated by species or ecological groups. In addition, the growth rates measured in this study (i.e. dendrometric measurerements) none detect real carbon allocation strategies of these species with different wood densities

(Chave et al., 2009; dos Santos & Ferreira, 2020b), which can lead to weak relationships. Moreover, species can allocate carbon in belowground growth, especially at low light environments (Montgomery & Chazdon, 2002). In our study, photosynthetic traits were measured in a one campaign with one-off measures on plants in single life stage (sapling) with broad genetic variation. Traits-demographic rates relationships may change throughout plant's life stage and static measures cannot capture this dynamic (Iida et al., 2014a; Iida et al., 2014b; Swenson et al., 2020). Further, we measure only leaf-level traits, and growth can also be influenced by hydraulic, stem and root traits (Worthy & Swenson, 2019). Finally, quantify traits in a one-off measure can neglect effects of diurnal variations and leaf age on plant whole photosynthetic capacity (Graham et al, 2003, Kitajima et al., 2002). For example, $A_{\max}$ measured from an individual leaf was weak or not related to growth at both environments, while *Total* $A_{\max}$ although it was better related (Figure 3 to 8). Even though considering total leaf area of the plant can improve the relationship between photosynthesis rates and growth rates (Yang, Cao & Swenson, 2018), *Total* $A_{\max}$ no quantify the effects of self-shading, diurnal variation and leaf age on whole-plant photosynthetic capacity (Delagrange et al., 2004; Sendall, Reich & Lusk 2018). Long-term studies comprising the effects of age, time and seasonality on traits-demographic rates relationship, and that also relate traits with growth rates that occur before and after traits collection campaing, will be required (Swenson et al., 2020; Tripathi et al., 2020).

4.2.Traits measured at the individual-level are more linked to growth rates under contrasting light environments

The level of analysis (individual or species) is an important factor that can affect the relationship between demographic rates and traits (Yang, Cao & Swenson, 2018).

Many studies have used species mean values based on expectative of a higher variation in traits among species than within species (Albert et al., 2010; Hulshof & Swenson, 2010; Poorter et al., 2018). However, the effects of intraspecific variation on the traits-demographic rates relationship must not be neglected under different aspects (Albert et al., 2010; Messier, McGill & Lechowicz, 2010; Violle et al., 2012). Here, the analyses of traits made at the individual-level showed be more determinants of the growth rates in both light environments (Figure 3 to 8). When the individual is used as a sample unit, hence the real competition for resources (light, water and nutrients) and the susceptibility to herbivore attack also are considered (Liu et al., 2016; Yang, Cao & Swenson, 2018). This approaching can lead to better insights into the main traits that drive plant performance within a community and, consequently, the demographic outcomes.

The greater number of significant relationships observed at individual-level may be associated to the higher variation (CV %) intraspecific of growth rates and traits than interspecific (Table 4). Overall, many studies agree with the fact that the variation in functional traits is greater between species than within species (Albert et al., 2010; Hulshof & Swenson, 2010). However, the most of these studies were realized in large areas with significant microclimate variations (heterogeneous environment) (Albert et al., 2010; Paine et al., 2015; Poorter & Bongers, 2006). We observed from an experiment realized at small spatial scale that, under homogeneous light conditions, the interspecific variation of traits tend to be lower than intraspecific variation (Table 4), since that the environmental filtering can lead the species a convergence on values of growth and traits (Keddy, 1992; Kraft et al., 2015; Laliberté, Zemunik & Turner, 2014; Lebrija-Trejos et al., 2010). Moreover, the absence of nutritional limitation of plants (dos Santos & Ferreira, 2020a), due to planting fertilization, can lead species to a convergence of growth rates and photosynthetic traits values. Even though environmental filtering and fertilization effects also leads individuals a convergence of growth and traits values, the genotypic variation can contribute to greater variation at individual-level. Our results corroborate with the findings of Albert et al. (2010), that showed that due to the habitat filtering, in a homogeneous environment, the interspecific differences were reduced leading to a strong relative importance and not negligible of intraspecific functional variability.

Deciding when to choose for individual or species analyses depend among other factors on the study objectives. Individual-level analyses provides a more realistic view of the communities' dynamics, because traits are related with realized growth of individuals, while species-level analysis demonstrates the potential of growth and of traits expression of species, through mean values (Poorter et al., 2018). Individual-level analyses adding stochastic (*e.g.* competition, herbivory damage) and deterministic (*e.g.* genetic composition, environmental gradient) factors of community assembly (Albert et al., 2011), being a more useful approach for trait-based community ecology studies by comprising important aspects of evolutionary biology (Caruso et al., 2020; Swenson et al., 2020). On the other hand, species-level analyses are important for the detect response of species acclimation to environmental gradients and resource supply (Chave et al., 2009; Wright et al., 2004), besides to be an important tool to screen species for silvicultural objectives (Campoe et al., 2014; dos Santos & Ferreira, 2020b), for show the potential of growth and traits expression of species (Poorter el al., 2018). However, utilizing species mean values precludes the ability to link the plant performance to trait differences, a core base in phenotypic selection explanation that can't be neglected (Swenson et al., 2020).

4.3. Set of traits explaining the growth rates as affected by light environments

Multiple leaf traits representing relevant functional process (e.g. photosynthesis) can improving the predictions of growth rates and, consequently, to be more sustainable to determine the fitness of individuals and species (Guimarães et al., 2018; Li et al., 2017; Liu et al., 2016; Rosas, et al., 2019; Worthy & Swenson, 2019; Yang, Cao & Swenson, 2018). However, how much the environmental context (e.g. light supply) affect which set of traits better explain the growth rates still is unclear.

Based on production ecology theory, the resources availability, the fractions of resources acquired and the resource use efficiencies are process that may affect the growth of plants (Binkley et al., 2010; Binkley, Stape & Ryan, 2004; Forrester, 2017; Monteith, 1977). From this framework, our expectations were that the main related growth traits differ between contrasting light environments. After to test for four set of traits (crown, morphological and physiological traits and all photosynthetic traits together) separately, was observed that the traits predictors included in the best models were dependent of light environments. In *full sun*, for example, the best model of physiological traits included as light absorption (*Chl a*/*b*) and light use (PI_{total}) traits, and at *understory*, the model including only light use (F_V/F_M and PI_{total}) traits better explained *HG* variation among physiological traits models (Table 5). Moreover, the strength of the relationships was greater at *full sun* (Table 5), similar to found in the single-traits relationships.

Poorter (1999) found that, at low light, the interspecific variation in relative growth rates was determined mainly by differences in a morphological trait, whereas at high light it was mainly determined by differences in a physiological trait. Our results do not support this proposition, because physiological traits are presents in the models of the both light environments, even though with that different predictors (traits). We believe that microsite variation at understory, especially on light availability (see Table S1), may have been important to increasing the role of physiological mechanisms on the performance of plants at *understory*.

A highlight of this study, is the result that photosynthetic traits are better predictors of growth rates when grouped in a set of traits. We observed that, photosynthetic traits in models with multiples traits explain from 20 to 57% of growth rates at *full sun* and from 4 to 48% at *understory*, while models with single traits explain from 3 to 47% at *full sun* and from 3 to 33% at *understory*. Showing the importance to use integrate traits to explain growth rates (Li et al., 2017; Yang, Cao & Swenson, 2018). A viewpoint more attractive to ecologists is that phenotype constitution depends of the values of many traits (Enquist et al., 2007; Marks & Lechowicz, 2006), as well as the local environment context (Liu et al., 2016). Saplings growing in the same environments with similar fitness can have alternative functional designs, according with their growth strategies (Marks & Lechowicz, 2006), making it difficult to predict growth rates for many species and individuals with single-traits.

4.4.Ecological implications

Studies that relate functional traits to demographic rates can help to uncover mechanisms that control the dynamics of forest communities (Salguero-Gómez et al., 2018). Following this approach, our results highlight the importance to consider the environmental context (e.g. light supply) during the screening of traits and demographic rates to be measured. Moreover, we confirmed that the intraspecific variation is critically important for a more realistic prediction of demographic rates, especially when working at smaller spatial scales. Finally, a complex process as growth is better represented when functional traits are grouped in a composed model. However, further studies that analyze the effects of life stage, seasonality, biomass allocation and species or phylogenetic groups on traits-demographic rates relationships are critical to improving this important groundwork in trait-based community ecology.

5. Conclusions

In summary, this study adds evidence about the importance of considering the environmental context (light supply) when deciding which traits and growth rates to measure in futures functional ecological researches. In this sense, photosynthetic traits seem be better predictors of plant performance at high light environments, especially when grouped in multiple traits, whereas crown traits are good predictors under high and low light. Finally, we confirmed from an experiment realized at small spatial scale, that the intraspecific variation cannot be neglected contributing significantly with key ecological questions related to the main mechanisms behind of demographic responses of forest communities.

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8. Supplementary material

Table S1. Overview of competition index and light properties, units of measurement, range (5th - 95th percentiles) and coefficient of variation in percentage (CV %) of all variables in two light environments (*Full sun* and *Understory*) at individual-level analysis.

Environments		*Full sun*	*Understory*	*Full sun*	*Understory*
Variable	Units	Range 5th - 95th		CV (%)	
Competition index	(cm²)	0.00 - 0.00	106.98 - 270.13	0	28
Transmittance	(%)	86.11 - 95.58	1.58 - 6.38	5	42
Canopy openness	(%)	73.00 - 94.00	3.00 - 7.00	9	31

Table S2. Coefficients of determination marginal for the relationships among competition index, light properties and three demographic rates at individual-level analysis.

Environments	*Full sun*			*Understory*		
Variables	*BG*	*DG*	*HG*	*BG*	*DG*	*HG*
Competition index	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Canopy openness	0.14*	0.13***	0.09**	0.04*	n.s.	n.s.
Transmittance	n.s.	n.s.	n.s.	0.10***	0.05*	0.17***

Notes: Relative growth rate in: *BG*., biomass; *DG*., diameter; *HG*., height. The p-values of simple linear regression are inserted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s. (not significant) $P \geq 0.05$.

Table S3. Parameters of the regressions adjusted to estimate the area of a one leaf, for each species.

Species	Range LxW	β0	β1	R^2	p-value	Std error	DF	F
C. fissilis	23.1 - 38.0	-0.01459	0.69379	0.8648	< 2.2e-16	1.095	56	358.1
	38.1-56.9	-0.7383	0.71402	0.8791	< 2.2e-16	1.364	77	559.8
	57.0 - 136.9	-2.63345	0.744736	0.967	< 2.2e-16	3.039	399	1.17E+04
	137.0 - 475.3	2.766736	0.71138	0.9904	< 2.2e-16	6.533	81	8358
T. rosea	58.4 - 163.8	3.25187	0.6376	0.9396	< 2.2e-16	4.003	179	2783
	163.9 - 361.7	5.02413	0.64781	0.9558	< 2.2e-16	7.885	161	3483
S. macrophylla	16.9 - 112.1	-2.86202	0.72619	0.9687	< 2.2e-16	2.56	291	9012
	112.2 - 421.9	17.05773	0.578442	0.9574	< 2.2e-16	7.706	190	4.27E+03
B. excelsa	36.5 - 94.1	4.12882	0.55897	0.9125	< 2.2e-16	2.465	67	698.8
	94.2 178.1	4.7726	0.5869	0.8925	< 2.2e-16	4.296	158	1312
	178.2 - 333.8	-6.2446	0.68529	0.9274	< 2.2e-16	8.654	101	1289
C. guianensis	29.1 - 91.4	0.5227	0.66241	0.9658	< 2.2e-16	1.974	88	2485
	91.5 - 194.8	-2.9776	0.718	0.9558	< 2.2e-16	4.237	177	3831
	194.9 298.2	1.1304	0.7114	0.8776	< 2.2e-16	7.588	60	430.1
H. courbaril	18.6 - 36.5	2.46984	0.62902	0.901	< 2.2e-16	0.8464	118	1074
	36.6 - 99.2	0.818776	0.703005	0.9644	< 2.2e-16	1.773	673	1.83E+04
	99.3 - 401.2	9.1313	0.6032	0.9651	< 2.2e-16	11.52	57	1.57E+03

Notes: Range of length x width measures used for adjusted each model; Range LxW., intercept; β0., slope; β1., coefficient of determination; R^2., signifficance level; p-value., standard error; Std error., degrees of freedom; DF., F-value; F.

Table S4. Coefficients of determination (R^2) of the relationships among thirty traits and survival rates

Environments		*Full sun*	*Understory*
Trait groups	Traits	*SR*	*SR*
Crown traits	*CPA*	n.s.	n.s.
	CL	n.s.	0.70*
	CR	n.s.	n.s.
	CLR	n.s.	0.75*
	RCL	n.s.	0.77*
Morphological traits	*TLA*	n.s.	n.s.
	LAI	n.s.	n.s.
	LA	n.s.	n.s.
	SLA	n.s.	-0.70*
	LDMC	n.s.	n.s.
Physiological traits	N_{mass}	n.s.	-0.74*
	P_{mass}	n.s.	n.s.
	K_{mass}	n.s.	-0.76*
	Chl a	n.s.	n.s.
	Chl b	n.s.	n.s.
	$Car_{\mathrm{c+x}}$	n.s.	n.s.
	Chl a+b	n.s.	n.s.
	Chl a/b	n.s.	n.s.
	$F_{\mathrm{V}}/F_{\mathrm{M}}$	n.s.	n.s.
	PI_{ABS}	n.s.	n.s.
	PI_{total}	n.s.	n.s.
	A_{max}	n.s.	n.s.
	R_{d}	n.s.	n.s.
	g_{s}	n.s.	n.s.
	E	n.s.	n.s.
	CUE	n.s.	n.s.
	PNUE	n.s.	-0.85**
	PPUE	n.s.	n.s.
	PKUE	n.s.	n.s.
	Total A_{max}	0.74*	n.s.

Notes: Annual survival rate (*SR*). The p-values of simple linear regression are inserted as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s. (not significant) $P \geq 0.05$. For abbreviations, see Table 3 in 'Material and Methods'.

Table S5. Mean and standard deviation values of demographic rates and all photosynthetic traits of the six species at *full sun*.

Environment	*Full sun*					
Species	*C. fissilis*	*T. rosea*	*S. macrophylla*	*B. excelsa*	*C. guianensis*	*H. courbaril*
SR	98	96	93	98	100	100
BG	3.02 ± 0.47	2.30 ± 0.18	2.88 ± 0.61	2.62 ± 0.44	2.48 ± 0.53	2.68 ± 0.38
DG	1.13 ± 0.15	0.80 ± 0.07	1.06 ± 0.18	0.98 ± 0.15	0.87 ± 0.17	1.03 ± 0.13
HG	0.82 ± 0.18	0.72 ± 0.12	0.82 ± 0.26	0.65 ± 0.18	0.73 ± 0.21	0.62 ± 0.13
CPA	4.71 ± 2.16	2.13 ± 1.43	0.92 ± 0.46	4.96 ± 3.02	1.35 ± 0.99	4.64 ± 2.39
CL	0.97 ±0.55	0.48 ± 0.26	1.04 ± 0.58	1.63 ± 0.67	2.29 ± 1.24	2.45 ± 0.77
CR	2.86 ± 0.67	2.33 ± 0.41	1.89 ± 0.27	4.59 ± 0.88	1.95 ± 0.29	3.80 ± 0.62
CLR	0.33 ± 0.12	0.15 ± 0.07	0.36 ± 0.11	0.56 ± 0.11	0.59 ± 0.12	0.76 ± 0.10
RCL	0.39 ± 0.18	0.30 ± 0.14	0.95 ± 0.33	0.71 ± 0.28	1.76 ± 0.55	1.03 ± 0.13
TLA	6.72 ± 4.47	2.49 ± 1.61	3.65 ± 2.28	5.44 ± 3.77	8.53 ± 8.73	7.12 ± 5.28
LAI	1.61 ± 1.70	1.23 ± 0.50	3.93 ± 1.04	1.16 ± 0.68	5.58 ± 2.12	1.40 ± 0.52
LA	80.94 ± 25.91	97.46 ± 28.05	76.85 ± 18.89	123.88 ± 26.91	135.47 ± 31.61	24.26 ± 4.55
SLA	128.07 ±12.67	107.17 ± 13.59	104.89 ± 18.54	117.57 ± 10.82	90.77 ± 12.55	116.82 ± 8.55
LDMC	301.62 ± 32.46	365.42 ± 97.59	371.67 ± 89.13	394.64 ± 68.59	376.02 ± 47.74	359.47 ± 37.37
N_{mass}	18.47 ± 2.63	16.62 ± 3.20	13.30 ± 2.28	18.91 ± 2.03	13.21 ± 1.84	17.69 ± 1.88
P_{mass}	0.84 ± 0.16	0.82 ± 0.14	0.56 ± 0.09	0.71 ± 0.09	0.61 ± 0.06	0.84 ± 0.23
K_{mass}	10.33 ± 2.55	13.73 ± 2.91	7.45 ± 2.36	7.65 ± 1.98	6.51 ± 1.85	7.18 ± 2.01
Chl a	1.04 ± 0.35	0.88 ± 0.24	1.14 ± 0.49	1.77 ± 0.42	1.17 ± 0.38	1.50 ± 0.39
Chl b	0.38 ± 0.11	0.26 ± 0.09	0.42 ± 0.16	0.52 ± 0.13	0.39 ± 0.13	0.45 ± 0.13
$Car_{\mathrm{c+x}}$	0.50 ± 0.13	0.39 ± 0.09	0.54 ± 0.22	0.68 ± 0.15	0.50 ± 0.16	0.55 ± 0.12
Chl a+b	1.42 ± 0.47	1.14 ± 0.32	1.56 ± 0.64	2.29 ± 0.54	1.56 ± 0.51	1.95 ± 0.51
Chl a/b	2.71 ± 0.31	3.44 ± 0.27	2.74 ± 0.33	3.45 ± 0.37	3.10 ± 0.37	3.39 ± 0.40
$F_{\mathrm{V}}/F_{\mathrm{M}}$	0.77 ± 0.05	0.79 ± 0.03	0.80 ± 0.02	0.79 ± 0.04	0.80 ± 0.02	0.79 ± 0.03
PI_{ABS}	2.46 ± 0.99	2.30 ± 0.87	3.65 ± 1.52	1.71 ± 0.70	3.61 ± 1.11	2.47 ± 1.05
PI_{total}	1.58 ± 0.49	1.63 ± 0.57	1.77 ± 0.79	1.39 ± 0.61	1.87 ± 0.72	2.06 ± 0.64
A_{max}	12.26 ± 3.07	14.30 ± 4.72	12.18 ± 3.04	14.96 ± 3.50	12.36 ± 2.19	15.94 ± 3.05
R_{d}	1.46 ± 0.45	1.79 ± 0.65	1.58 ± 0.50	1.58 ± 0.51	1.60 ± 0.37	1.85 ± 0.57
g_{s}	0.33 ± 0.15	0.26 ± 0.16	0.34 ± 0.12	0.32 ± 0.08	0.28 ± 0.09	0.28 ± 0.10
E	4.76 ± 0.89	4.22 ± 2.03	4.88 ± 1.04	4.87 ± 1.25	4.52 ± 1.45	4.70 ± 1.60
CUE	9.05 ± 3.03	8.88 ± 4.23	8.24 ± 2.71	10.91 ± 5.95	8.10 ± 2.57	9.47 ± 3.53
PNUE	119.73 ± 30.99	131.25 ± 53.53	135.78 ± 40.05	130.12 ± 29.13	119.52 ± 24.07	148.68 ± 33.49
PPUE	5931.66 ± 1667.36	5830.44 ± 2108.76	7106.28 ± 1895.58	7717.91 ± 1983.39	5626.51 ± 1072 74	7207.88 ± 1901.47
PKUE	646.45± 313.63	452.36 ± 187.87	757.76 ± 413.78	953.57 ± 324.31	727.06 ± 274.23	1068.55 ± 313.77
Total A_{max}	81.73 ± 63.50	38.68 ± 37.68	46.09 ± 32.30	89.67 ± 75.84	109.27 ± 117.88	116.09 ± 96.57

Notes: Relative growth rate in: *BG*., biomass; *DG*., diameter; *HG*., height, and Annual survival rate (*SR*). For abbreviations, see Table 3 in ‘Material and Methods’.

Table S6. Mean and standard deviation values of demographic rates and all photosynthetic traits of the six species at *understory*.

Environment	*Understory*					
Species	*C. fissilis*	*T. rosea*	*S. macrophylla*	*B. excelsa*	*C. guianensis*	*H. courbaril*
SR	78	71	92	99	96	85
BG	0.84 ± 0.49	0.74 ± 0.21	1.28 ± 0.38	0.63 ± 0.26	0.79 ± 0.24	0.64 ± 0.20
DG	0.33 ± 0.17	0.28 ± 0.07	0.52 ± 0.14	0.26 ± 0.11	0.27 ± 0.08	0.23 ± 0.08
HG	0.26 ± 0.13	0.19 ± 0.11	0.26 ± 0.11	0.11 ± 0.09	0.27 ± 0.15	0.26 ± 0.14
CPA	1.11 ± 1.12	0.58 ± 0.19	0.44 ± 0.18	0.17 ± 0.10	0.36 ± 0.21	0.32 ± 0.16
CL	0.21 ± 0.26	0.06 ± 0.03	0.32 ± 0.25	0.56 ± 0.26	0.79 ± 0.33	0.71 ± 0.18
CR	5.80 ± 1.55	3.61 ± 0.65	4.57 ± 1.13	4.37 ± 0.88	4.15 ± 0.99	6.37 ± 1.27
CLR	0.21 ± 0.17	0.05 ± 0.03	0.35 ± 0.17	0.66 ± 0.23	0.67 ± 0.17	0.65 ± 0.11
RCL	0.14 ± 0.13	0.07 ± 0.03	0.42 ± 0.29	1.27 ± 0.56	1.18 ± 0.33	1.15 ± 0.21
TLA	0.13 ± 0.06	0.25 ± 0.14	0.17 ± 0.11	0.09 ± 0.07	0.20 ± 0.14	0.08 ± 0.04
LAI	0.17 ± 0.07	0.42 ± 0.13	0.39 ± 0.22	0.62 ± 0.71	0.55 ± 0.17	0.29 ±0.12
LA	23.39 ± 10.03	90.73 ± 23.05	46.37 ± 12.99	82.08 ± 35.58	61.16 ± 21.78	21.13 ± 3.72
SLA	473.42 ± 98.54	319.80 ± 45.23	223.29 ± 34.52	174.05 ± 34.62	192.42 ± 24.37	239.75 ± 24.40
LDMC	167.68 ± 32.16	217.60 ± 24.70	274.67 ± 29.25	359.69 ± 58.71	267.15 ± 30.39	255.21 ± 31.38
N_{mass}	17.40 ± 3.04	16.87 ± 2.01	13.36 ± 2.23	13.67 ± 2.54	13.11 ± 1.54	17.11 ± 1.95
P_{mass}	1.02 ± 0.25	1.18 ± 0.29	0.70 ± 0.15	0.87 ± 0.22	0.88 ± 0.20	1.09 ± 0.13
K_{mass}	8.06 ± 3.84	12.05 ± 3.38	6.73 ± 2.60	6.64 ± 2.71	6.68 ± 2.66	9.84 ± 2.35
Chl a	2.24 ± 0.96	1.81 ± 0.66	2.23 ± 0.95	2.05 ± 0.77	1.87 ± 0.51	2.28 ± 0.29
Chl b	0.85 ± 0.33	0.64 ± 0.24	0.88 ± 0.38	0.70 ± 0.26	0.68 ± 0.19	0.79 ± 0.10
$Car_{\text{c+x}}$	0.86 ± 0.33	0.61 ± 0.22	0.84 ± 0.32	0.71 ± 0.26	0.70 ± 0.19	0.74 ± 0.12
Chl a+b	3.09 ± 1.28	2.46 ± 0.90	3.11 ± 1.33	2.68 ± 1.04	2.55 ± 0.69	3.08 ± 0.38
Chl a/b	2.60 ± 0.22	2.82 ± 0.06	2.56 ± 0.22	2.93 ± 0.29	2.75 ± 0.19	2.89 ± 0.17
$F_{\text{V}}/F_{\text{M}}$	0.81 ± 0.01	0.84 ± <0.01	0.83 ± 0.01	0.84 ± <0.01	0.84 ± 0.01	0.84 ± 0.01
PI_{ABS}	1.15 ± 0.27	2.57 ± 0.46	2.61 ± 0.60	2.76 ± 0.87	2.82 ± 0.49	2.37 ± 0.51
PI_{total}	0.29 ± 0.08	0.79 ± 0.20	0.71 ± 0.21	0.79 ± 0.32	0.76 ± 0.18	0.72 ± 0.20
A_{max}	4.87 ± 1.11	8.63 ± 1.59	5.98 ± 1.70	8.71 ± 2.68	6.62 ± 1.59	8.97 ± 2.42
R_{d}	0.40 ± 0.27	0.32 ± 0.11	0.57 ± 0.32	0.47 ± 0.38	0.47 ± 0.31	0.52 ± 0.32
g_{s}	0.14 ± 0.02	0.20 ± 0.05	0.13 ± 0.05	0.21 ± 0.09	0.13 ± 0.07	0.14 ± 0.05
E	3.06 ± 0.44	3.95 ± 0.90	2.66 ± 0.91	3.86 ± 0.89	2.61 ±1.12	2.98 ± 0.75
CUE	16.84 ± 9.51	30.13 ± 13.32	13.50 ± 8.38	29.96 ± 22.11	18.62 ± 10.54	23.63 ± 15.34
PNUE	187.19 ± 55.70	229.21 ± 41.79	138.14 ± 30.94	153.61 ± 43.41	135.06 ± 31.52	173.89 ± 37.20
PPUE	7450.94 ± 2973.23	7369.80 ± 1492.01	6357.44 ± 3312.11	5775.06 ± 2655.61	4696.15 ± 1524.68	6006.06 ± 1076.25
PKUE	1368.02 ± 797.63	949.69 ± 335.59	855.39 ± 337.88	1007.76 ± 457.27	858.06 ± 376.60	874.67 ± 212.55
Total A_{max}	0.61 ± 0.28	2.33 ± 1.74	1.11 ± 0.87	0.80 ± 0.79	1.39 ± 1.14	0.78 ± 0.50

Notes: Relative growth rate in: *BG*., biomass; *DG*., diameter; *HG*., height, and Annual survival rate (*SR*). For abbreviations, see Table 3 in 'Material and Methods'.

9. Conclusão geral

Estudos de ecologia funcional que encontrem fortes relações entre características funcionais e taxas demográficas parecem ser mais uma excessão do que uma regra. A falta de consideração de importantes aspectos metodológicos pode ser o fator que levou ao fracasso de parte desses estudos. Entre os principais aspectos metodológicos estão, a não consideração do contexto ambiental, a negligência da variação intraespecífica e a fraca capacidade de explicação das características selecionadas. Este estudo acrescenta evidências sobre a importância de considerar o contexto ambiental (disponibilidade de luz) ao decidir quais características e taxas demográficas medir em futuras pesquisas de ecologia funcional. Nesse sentido, as características fotossintéticas parecem ser melhores preditores de desempenho da planta em ambientes de alta irradiância, devido esse ambiente possibilitar a máxima expressão dessas características. Entretanto, características da copa são boas preditoras sob alta e baixa irradiância. Ademais, confirmamos a partir de um experimento realizado em pequena escala espacial, que a variação intraespecífica não pode ser negligenciada, contribuindo significativamente com questões ecológicas importantes relacionadas aos principais mecanismos associados às respostas demográficas das comunidades florestais. Por fim, observamos que características fotossintéticas são melhores preditoras do crescimento quando reunidas em modelos múltiplos, pois espécies convivendo em um mesmo ambiente podem ter estratégias alternativas de crescimento, dificultando a predição de taxas de crescimento a partir de uma única característica.

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