UNIVERSIDADE FEDERAL DO AMAZONAS
FACULDADE DE CIÊNCIAS AGRÁRIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS FLORESTAIS E AMBIENTAIS

SOBREVIVÊNCIA, CRESCIMENTO E CARACTERÍSTICAS FOTOSSINTÉTICAS DE ESPÉCIES FLORESTAIS EM RESPOSTA À FERTILIZAÇÃO FOSFATADA

Alaíde de Oliveira Carvalho

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Orientador: Dr. Marciel José Ferreira

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Sinopse: Os efeitos do fornecimento de fósforo via fertilização mineral sobre as taxas demográficas e características fotossintéticas foliares de mudas de dez espécies florestais foram investigados em um plantio misto de dois anos de idade. As respostas à fertilização variaram de acordo com as espécies estudadas ainda dentro do mesmo grupo ecológico. Respostas de crescimento e características fotossintéticas indicaram as espécies pioneiras como mais sensíveis aos efeitos da fertilização.

Palavras chave: Crescimento; sobrevivência; características fotossintéticas; status sucessional; reflorestamento.

Ministério da Educação
Universidade Federal do Amazonas
Coordenação do Programa de Pós-Graduação em Ciências Florestais e Ambientais

Ata da Defesa Pública da Dissertação de Mestrado do Sr. **ALAÍDE DE OLIVEIRA CARVALHO,** mestrando(a) do Programa de Pós-Graduação em Ciências Florestais e Ambientais - PPGCIFA, Faculdade de Ciências Agrárias, Universidade Federal do Amazonas, área de concentraçao em Ciências Florestais e Ambientais (CIFA), realizada no dia 03 de novembro de 2020.

Aos terceiro dias do mês de novembro de 2020, às 09:00 Horas, por meio da plataforma google meets disponibilizada gratuitamente para reuniões ao vivo por vídeoconferência, realizou-se a Defesa de Mestrado, intitulada: **"SOBREVIVÊNCIA, CRESCIMENTO E CARACTERÍSTICAS FOTOSSINTÉTICAS DE ESPÉCIES FLORESTAIS EM RESPOSTA À FERTILIZAÇÃO FOSFATADA"** da discente **ALAÍDE DE OLIVEIRA CARVALHO ,** como parte dos requisitos para obtenção do título de **MESTRE** *"Magister Scientia"* em **CIÊNCIAS FLORESTAIS E AMBIENTAIS (CIFA)**. A Banca Examinadora foi constituída pelos seguintes membros**: DOUTOR MARCIEL JOSÉ FERREIRA** (Orientador/Presidente - UFAM), **DOUTOR JHONY VENDRUSCOLO** (Membro Externo - UFAM) **e o DOUTOR JOÃO BAPTISTA SILVA FERRAZ** (Membro Externo - INPA)**.** Após o fim da apresentação e arguição pelos membros da Banca Examinadora, esta se reuniu para deliberação, emitindo o seguinte parecer:

Marciel José Ferreira - UFAM	Aprovada (X)	Não Aprovada ( )	Suspensão da Sessão ( )
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João Baptista Silva Ferraz - INPA	Aprovada (X)	Não Aprovada ( )	Suspensão da Sessão ( )

Como resultado final da avaliação, a Banca Examinadora decidiu pela APROVAÇÃO da Dissertação de mestrado da ALAÍDE DE OLIVEIRA CARVALHO, que tem até 30 (trinta) dias corridos a partir desta data para enviar a coordenação a versão final da dissertação, conforme as recomendações da Banca. A sessão foi encerrada e eu, Gillieny de Souza Rodrigues, secretária do PPG-CIFA, lavrei esta ata que depois de lida será assinada pelos membros da Banca Examinadora.

em Manaus, 03 de novembro de 2020.

Assinaturas eletrônicas da Banca Examinadora e Ciência da Discente

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Resumo

A baixa disponibilidade de fósforo (P) em solos tropicais pode afetar o estabelecimento inicial de espécies florestais em projetos de reflorestamento em áreas perturbadas. No entanto, os efeitos do suprimento de fósforo via fertilização mineral como uma estratégia para melhorar a sobrevivência, o crescimento e as características fotossintéticas de espécies arbóreas da Amazônia em solos pobres em P permanecem indefinidos. Nesta pesquisa, o objetivo foi investigar como níveis contrastantes de fertilização com fósforo afetam o estabelecimento de espécies florestais nativas pertencentes a diferentes status sucessionais. As espécies pioneiras estudadas foram: *Apuleia leiocarpa* (Vogel) J.F.Macbr, *Erythrina fusca* Lour, *Guazuma ulmifolia* Lam, *Cordia alliodora* (Ruiz & Pav.) Cham, *Cedrela fissilis* L.; e as não pioneiras: *Swietenia macrophylla* King, *Bertholletia excelsa* Bonpl, *Carapa guianensis* Aubl, *Hymenaea courbaril*. L, *Dipteryx odorata* (Aubl.) Willd. As taxas de sobrevivência e crescimento, e as características foliares (índice SPAD, parâmetros de fluorescência da clorofila *a*, nutrientes foliares, razão N/P e trocas gasosas) de dez espécies florestais (pioneiras e não pioneiras) submetidas à fertilização fosfatada (-P = 0 kg P_2O_5 ha^{-1}, controle, e + P = 160 kg P_2O_5 ha^{-1}) foram mensuradas em campo durante 24 meses. As espécies pioneiras foram mais sensíveis à fertilização. *Erythrina fusca* (pioneira) apresentou alta mortalidade sob -P. No entanto, *Apuleia leiocarpa* (pioneira) e *Dipteryx odorata* (não pioneira), apesar dos altos valores da relação N/P foliar, mantiveram as taxas de crescimento em solos pobres em P. Por outro lado, *Cedrela fissilis* e *Cordia alliodora* (pioneiras) exibiram os maiores aumentos nas taxas de crescimento após a fertilização. A fertilização melhorou os teores foliares de P em ambos os grupos sucessionais, enquanto a absorção (valores SPAD) e a eficiência no uso (índice de desempenho total, PI_{total}) da luz e a captura de carbono (condutância estomática) aumentaram apenas nas espécies pioneiras. Por outro lado, não foram observados efeitos positivos na assimilação de carbono em nível foliar, resultando em diminuição da eficiência fotossintética no uso do fósforo em espécies não pioneiras. Portanto, a fertilização com fósforo afeta o estabelecimento inicial de plantações de árvores amazônicas de um modo espécie-específico. As implicações desses resultados para os esforços de reflorestamento na região Amazônica são discutidas.

Palavras chave: Crescimento; Sobrevivência; Características fotossintéticas, Status sucessional; Reflorestamento.

Abstract

The low availability of phosphorus in tropical soils may impair the initial establishment of forest species in reforestation projects in disturbed areas. However, the effects of phosphorus fertilization as a strategy to improve the survival, growth and photosynthesis-related traits of Amazonian tree species in P-limited soils remain elusive. Here, we investigate how contrasting levels of phosphorus fertilization affect the establishment of native forest species belong to different successional status. Pioneers species studied were: *Apuleia leiocarpa* (Vogel) J.F.Macbr, *Erythrina fusca* Lour, *Guazuma ulmifolia* Lam, *Cordia alliodora* (Ruiz & Pav.) Cham, *Cedrela fissilis* L.; and Non-pioneers: *Swietenia macrophylla* King, *Bertholletia excelsa* Bonpl, *Carapa guianensis* Aubl, *Hymenaea courbaril*. L, *Dipteryx odorata* (Aubl.) Willd. We measured the survival, growth and leaf traits (SPAD index, chlorophyll *a* fluorescence parameters, leaf nutrients, N/P ratio and gas exchange) of ten forest species (pioneers and non-pioneers) subjected to contrasting phosphorus supply (-P = 0 kg P_2O_5 ha^{-1}, control, and +P = 160 kg P_2O_5 ha^{-1}) on the field during 24 months. Pioneers species were more sensible to fertilization. *Erythrina fusca* (*pioneers*) showed high mortality under -P. However, *Apuleia leiocarpa* (pioneers) and *Dipteryx odorata* (non-pioneers), despite high values on leaf N/P ratio, remained growth in P-limited soils. On the other hand, *C. fissilis* and *C. alliodora* (*pioneers*) exhibited the highest increase in growth rates after fertilization. Phosphorus supply improved the phosphorus leaf content in both successional groups, while light absorption (SPAD values) and processing (total performance index, PI_{total}) and carbon capture (stomatal conductance) were increased only in pioneers species. Conversely, positive effects on carbon assimilation at leaf-level were not observed, then the phosphorus fertilization reduced the phosphorus use-efficiency of non-pioneers species. Thus, phosphorus fertilization affects the initial establishment of Amazonian trees in a species-specific way. The implications of these results for reforestation efforts in Amazonia are discussed.

Keywords: Growth; Survival; Photosynthesis-related traits; Successional status; Reforestation.

Sumário

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1 Introdução geral

Os solos da Amazônia, em sua grande maioria, possuem baixa fertilidade, que é representada, principalmente, por acidez elevada, baixa capacidade de troca de cátions e baixos teores de fósforo (P) disponível (Walker e Syers, 1975; Moreira e Fageria 2009; Quesada et al. 2012). Fatores antrópicos intensificam a limitação desse nutriente por meio do desmatamento, queimadas, erosão e exportação de nutrientes com a remoção da biomassa aérea (McGrath et al. 2001). Essas ações restringem a mobilização de P e aumentam sua fixação (Ketterings et al. 2002). No estado do Amazonas, em particular, mais de 80% dos solos possuem teores de P considerados baixos ou muito baixos (< 5,4 mg dm^{-3}) (Moreira e Fageria, 2009).

O baixo teor de fósforo no solo geralmente é considerado um fator limitante para a produtividade florestal (Quesada et al. 2012; Fleischer et al. 2019), pois, representa um nutriente essencial à fotossíntese e, portanto, à produção primária (Domingues et al. 2010; Vitousek et al. 2010). No entanto, evidências diretas (manipulação de P no solo e efeitos no crescimento) sobre a limitação de P nos trópicos são escassas e inconclusivas (Waring et al. 2019). Por exemplo, a redução nas taxas de crescimento tem sido observada no nível de espécie, porém não se traduzindo em uma resposta de toda a comunidade, pois algumas espécies crescem rapidamente em solos com baixa disponibilidade de fósforo (Wardle et al. 2004; Turner et al. 2018). O baixo teor de fósforo mostrou-se limitante na produtividade primária em florestas subtropicais da China (Huang et al. 2013) e em florestas do Havaí (Vitousek e Farrington, 1997). Por outro lado, para um estrato de floresta tropical na África Central (Newbery et al. 2002), floresta tropical úmida (Alvarez-Clare et al. 2013) e floresta tropical secundária na Costa Rica, não houve relação entre o crescimento e a disponibilidade do nutriente a nível de comunidade (Waring et al. 2019). Portanto, identificar os mecanismos pelos quais as espécies florestais modulam as variações nas respostas a disponibilidade deste nutriente é o próximo passo em direção à previsão da produtividade em escala de comunidade (Waring et al. 2019).

As exigências nutricionais das espécies florestais podem ser afetadas por suas características ecológicas (Resende et al. 2005). Espécies pioneiras têm maiores taxas de crescimento quando comparadas as espécies não pioneiras (Swaine e Whitmore, 1988), surgem no processo inicial de sucessão das florestas (Dalling e Hubbell, 2002), e podem apresentar maior eficiência no uso dos nutrientes, mantendo suas taxas de crescimento ao longo de seu estabelecimento, mesmo em solos limitados por fósforo (Hidaka e Kitayama, 2013; Zhang et al. 2018). Apesar de tais características, quando cultivadas em ambiente controlado, essas espécies apresentam respostas positivas à adição de fósforo (Resende et al. 1999; Cruz et al. 2011). Espécies não pioneiras, por sua vez, possuem menores taxas de crescimento (Swaine e Whitmore, 1988) e podem apresentar menor eficiência no uso dos nutrientes, quando comparadas as pioneiras (Zhang et al. 2018). Quando cultivadas em ambientes controlados, espécies não pioneiras, podem apresentar menor sensibilidade a adição de nutrientes (Resende et al. 1999; Silva et al. 1997; Tucci et al. 2011), podendo ter essas taxas iniciais mantidas pelas reservas de nutrientes das suas sementes (Huante et al. 1995; Milberg e Lamont, 1997; Resende et al. 1999). Tais espécies podem apresentar comportamento conservativo, com baixas taxas de crescimento, porém alta sobrevivência durante o estabelecimento (Poorter et al. 2008; Chave et al. 2009; Wright et al. 2010).

Características foliares representativas do Espectro de Economia Foliar são consideradas variáveis indicadoras do trade-off entre crescimento e sobrevivência (Sterck et al. 2006; Martínez-Garza et al. 2013; Luo et al. 2016; Guimarães et al. 2018). Em solos com baixos teores de fósforo, as concentrações foliares desse nutriente estão ligadas a mudanças em vários traços foliares (Santiago, 2015). Plantas que crescem em sítios limitados por fósforo podem apresentar maior massa foliar por área (LMA), pois necessitam de folhas com tempo de vida mais longo (Wigrht et al. 2004), menor capacidade fotossintética (Wigrht et al. 2004; Warren et al. 2011) e baixas concentrações de nutrientes foliares (Wigrht et al. 2004; Hidaka e Kitayama, 2009). Consequentemente, essas espécies irão apresentar menores taxas de crescimento (Warren et al. 2011; Zavisic e Polle, 2017). Porém, para algumas espécies, essas características podem apresentar mudanças mais sutis, por serem altamente eficientes no uso dos nutrientes (Hidaka e Kitayama, 2009). Os mecanismos pelos quais as espécies respondem à variação na disponibilidade de P no solo ainda não são completamente entendidos. Do ponto de vista fisiológico, por exemplo, espécies capazes de alocar o P absorvido preferencialmente para funções metabólicas tendem aclimatar à baixa disponibilidade de P (Mo et al. 2019).

Dessa forma, faz-se necessário melhor compreensão dos mecanismos por trás dessas diferentes respostas das espécies florestais a disponibilidade de P no solo.

Portanto, a partir do monitoramento da sobrevivência, crescimento e características fotossintéticas foliares em sítios com disponibilidades contrastantes de fósforo, controlando outros fatores como a idade, espaçamento e disponibilidade de outros nutrientes essenciais, além da utilização de um conjunto de características morfológicas e fisiológicas, nós buscamos compreender as respostas para as seguintes questões principais: i) o estabelecimento de espécies pioneiras em condições de campo submetidas à fertilização com fósforo é mais sensível que as espécies não pioneiras? ii) os efeitos da fertilização com fósforo sobre a sobrevivência, crescimento e características fotossintéticas diferem entre as espécies? iii) as espécies com melhor crescimento em solos pobres em fósforo também exibem bom desempenho dos processos fisiológicos?

2 Objetivos

2.1 Geral

Investigar como a fertilização fosfatada determina o desempenho de espécies florestais dois anos após o plantio em áreas perturbadas.

2.2 Específicos

i) Verificar se o estabelecimento de espécies pioneiras em condições de campo submetidas à fertilização com fósforo é mais sensível que as espécies não pioneiras;

ii) Analisar se os efeitos da fertilização com fósforo sobre a sobrevivência, crescimento e características fotossintéticas dependem das espécies;

iii) Investigar se espécies com melhor crescimento em solos pobres em fósforo também exibem bom desempenho dos processos fisiológicos.

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Short-term effects of phosphorus fertilization on the establishment of Amazonian tree species in a mixed plantation

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Abstract

The low availability of phosphorus in tropical soils may impair the initial establishment of forest species in reforestation projects in disturbed areas. However, the effects of phosphorus fertilization as a strategy to improve the survival, growth and photosynthesis-related traits of Amazonian tree species in P-limited soils remain elusive. Here, we investigate how contrasting levels of phosphorus fertilization affect the establishment of native forest species belong to different successional status. We measured the survival, growth and leaf traits (SPAD index, chlorophyll *a* fluorescence parameters, leaf nutrients, N/P ratio and gas exchange) of ten forest species (pioneers and non-pioneers) subjected to contrasting phosphorus supply (-P = 0 kg P_2O_5 ha^{-1} and +P = 160 kg P_2O_5 ha^{-1}) on the field during 24 months. Pioneers species were more sensible to fertilization. *Erythrina fusca* (pioneers) showed high mortality under -P. However, *Apuleia leiocarpa* (pioneers) and *Dipteryx odorata* (non-pioneers), despite high values on leaf N/P ratio, remained growth in P-limited soils. On the other hand, *C. fissilis* and *C. alliodora* (pioneers) exhibited the highest increase in growth rates after fertilization. Phosphorus supply improved the phosphorus leaf content in both successional groups, while light absorption (SPAD values) and processing (total performance index, PI_{total}) and carbon capture (stomatal conductance) were increased only in pioneers species. Conversely, positive effects on carbon assimilation at leaf-level were not observed, then the phosphorus fertilization reduced the phosphorus use-efficiency of non-pioneers species. Thus, phosphorus fertilization affects the initial establishment of Amazonian trees in a species-specific way. The implications of these results for reforestation efforts in Amazonia are discussed.

Keywords: Growth; Survival; Photosynthesis-related traits; Successional status; Reforestation.

1. Introduction

Phosphorus (P) is a widely limiting nutrient of aboveground plant production in terrestrial ecosystems (Hou et al. 2020). Most of the Amazonian soils, for example, have low fertility natural, characterized mainly by high acidity, low exchange capacity and low phosphorus availability (Walker and Syers 1975; Moreira and Fageria 2009; Quesada et al. 2012). The soils of Amazonas state can exhibit values < 5.4 mg P dm^{-3} (Moreira and Fageria 2009). In addition, the deforestation of mature forests can exacerbate the phosphorus limitation by restricting the mobilization and increase the fixation in soils on disturbed areas (McGrath et al. 2001; Ketterings et al. 2002).

Phosphorus is an essential nutrient for photosynthesis and, therefore, for primary productivity (Domingues et al. 2010; Vitousek et al. 2010). The improving of soil conditions in disturbed areas can be reached by silvicultural treatments (e.g. fertilization) (Campoe et al. 2014; Rubilar et al. 2018). The input of P by fertilization has positively affected the growth and survival of tree species (Resende et al. 1999; Uddin et al. 2009; Tng et al. 2014). However, there are cases in which even with the increase of P available in the soil through the addition of chemical fertilizer, the species did not show a growth response (Driessche 1980). Likewise, different responses between species submitted to fertilization are observed (Barrow 1977). These differences may be associated with successional status (Resende 1999) and may vary between species and their characteristics (Groves and Heraitis 1976; Barrow 1977; Resende et al. 2005).

Pioneers species have higher growth rates than non-pioneers and can show greater nutrient use efficiency maintaining their growth even in soils limited by phosphorus (Hidaka and Kitayama 2013; Zhang et al. 2018). However, when submitted to fertilization treatments, pioneers species tend to show positive responses to the input of phosphorus (Resende et al. 1999; Cruz et al. 2011). Conversely, non-pioneers species, have slow growth and may show low nutrient use efficiency (Zhang et al. 2018). The effects of phosphorus fertilization normally are less significant for the growth of non-pioneers species due to the nutrient reserves of seeds (Huante et al. 1995; Milberg and Lamont 1997; Resende et al. 1999). The conservative strategies of non-pioneers species contrast the low growth rates with high survival during the initial establishment (Poorter et al. 2008; Chave et al. 2009; Wright et al. 2010). These responses are related to the strategy of resource utilization, or the spectrum of the leaf economy, which consists of the leaf strategies of plants, in changing their chemical, structural, and/or physiological properties according to their growth or survival (Wright et al. 2004; Hidaka and Kitayama 2013; Zhang et al. 2018).

Leaf traits representative of the leaf economy spectrum can reflect the trade-off between growth and survival (Sterck et al. 2006; Martínez-garza et al. 2013; Luo et al. 2016; Guimarães et al. 2018). Plants growing in sites limited by phosphorus may have reduced photosynthetic capacity (Wright et al. 2004; Warren et al. 2011) and low leaf nutrients content (Wright et al. 2004; Hidaka and Kitayama 2009) and, consequently, slow growth rates (Warren et al. 2011; Zavisic and Polle 2017). However, tropical tree species adapted to infertile soils can maintain their photosynthetic capacity by altering the allocation of P foliar reducing P allocation to non-metabolic foliar P fractions (Mo et al. 2019). The relevance of nutrient use efficiency to determine the interspecific growth differences during the initial establishment of plants on infertile soils has been highlighted for plantations of Amazonian trees (Santos Jr et al. 2006; Guimarães et al. 2018). However, how the controlled supply of phosphorus by fertilization drives the growth and photosynthetic mechanisms of native species in field is still lacking.

Here, in a mixed plantation using ten Amazonian tree species for protective objective established during 24 months on field condition, we address the following main question: how contrasting levels of phosphorus fertilization affect the survival, growth and photosynthesis-related traits of native forest species belonging to different successional status. Our specific hypothesis were as follows: i) the establishment of pioneers species on field condition as affected by phosphorus fertilization is more sensible than non-pioneers species; ii) the effects of phosphorus fertilization on survival, growth and photosynthesis-related traits are species-dependent; iii) species with the best growth in P-limited soils also exhibits the good performance of physiological mechanisms.

2 Material and methods

2.1 Study site

The experiment was conducted at the Experimental Farm of the Federal University of Amazonas (02 ° 38 ′ S and 60 ° 03 ′ W), Manaus, Amazonas, Brazil. The Central Amazon region is characterized by annual precipitation of 2,350 mm, monthly air temperature ranging from 26.4°C to 28.5°C and air humidity reaching an average value 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 lengths from August to September (Sombroek 2001). The soil is clayey yellow Latosol (Araujo et al. 2002). The surrounding forest is a rainforest with an enclosed canopy (Guillaumet and Kahn 1982). The site planting is a disturbed area where the mature forest was removed in 1985 and the area was submitted to several changes in soil use (mainly agricultural activities) until complete abandonment. The site was dominated by weed (*Brachiaria* spp.) before the planting, acting as a strong barrier to the establishment of natural regeneration.

2.2 Experiment installation: species selection and soil preparation

Ten native forest species were selected according to their socioeconomic and ecological importance for the region and on availability of seeds in the planting year. The species were divided into two contrasting successional status, being five pioneers and five non-pioneers species (Table 1). The average value of clay content in the soil was 75%, pH_{H2O} = 4.4 and available phosphorus (P) = 3.12 mg kg^{-1} priory the experiment installation (Luvison, 2018). For soil acid correction, 108.8 g of dolomitic limestone (PRNT 92%; Ca 32%; Mg 15%) was applied 60 days before planting in each pit. In addition to the correction, cover fertilization was applied to all plants only in the planting. We used 10 g of FTEBR12 (Mo 0.001%, B 1,8%, Cu 0.8%, Mn 2% and Zn 0.7%), 16 g of urea (45% N) and 11.5 g of potassium chloride (58% K_20). The same amount of urea and potassium chloride were also applied thirty, sixty and ninety days after planting. The dosages and methods that guarantee the minimum nutrient requirements of native tropical forest species were obtained from a literature review (Furtini Neto et al. 2000; Resende et al. 2005; Campoe 2014; Alvarado 2015).

2.3 Experimental design and phosphorus fertilization treatments

The experiment consists of 4 x 2 factorial design, with eight treatments in randomized blocks with three replications (Fig.1). The factors consisted of four levels of phosphorus fertilization and two successional status species groups. The layout of each block consisted of four main plots of 32 x 6 m (192 m^2), in which the levels of triple superphosphate (46% P_2O_5) were applied (0, 40, 80 and 160 kg P_2O_5 ha^{-1}). Within the main plots, subplots with 32 m x 3 m (96 m^2) were represented by alternated lines of pioneers and non-pioneers species (Nave and Rodrigues 2007). The planting lines (pioneers or non-pioneers) had a total of 15 saplings, being three pseudo-replicates of each species. To best distinguish the species performance on infertile and fertile soil simulated by fertilization, only the most contrasting levels of phosphorus supply (0 and 160 kg_P ha^{-1}, named -P and +P) were examined in this research. The planting spacing was 3 x 2 m. The planting was carried out in 40 x 50 cm pits prepared with a soil drill attached to a tractor. The control of ants was carried out before and after planting through the application of granulated ant killer and the control of weed competition carried out by crowning with manual weeding and semi-mechanized mowing between the lines every three months.

Table 1 Species, abbreviation, family, successional status, diameter and height of saplings used in the experiment.

n°	Species	Abbreviation	Family	Successional status	Diameter (mm)	Height (cm)
1	*Apuleia leiocarpa* (Vogel) J.F.Macbr.	A.l	Fabaceae	Pioneers	5.43±0.87	83±15.55
2	*Erythrina fusca* Lour.	E.f	Fabaceae	Pioneers	8.69± .79	78±15.66
3	*Guazuma ulmifolia* Lam.	G.u	Malvaceae	Pioneers	6.63±0.77	81±5.63
4	*Cordia alliodora* (Ruiz & Pav.) Cham	C.a	Boraginaceae	Pioneers	6.16±1.10	61±14.93
5	*Cedrela fissilis* L.	C.f	Meliaceae	Pioneers	6.45±1.82	20±8.97
6	*Swietenia macrophylla* King.	S.m	Meliaceae	Non pioneers	5.98±0.78	41±0.37
7	*Bertholletia excelsa* Bonpl.	B.e	Lecytidaceae	Non pioneers	5.15±0.76	48±5.94
8	*Carapa guianensis* Aubl.	C.g	Meliaceae	Non pioneers	7.51±1.41	41±11.43
9	*Hymenaea courbaril.* L.	H.c	Fabaceae	Non pioneers	5.30±0.72	54±10.22
10	*Dipteryx odorata* (Aubl.) Willd.	D.o	Fabaceae	Non pioneers	5.14±1.12	32±8.70

* = Ecological groups of the species used in the experiment based on the classification by Withmore (1989).

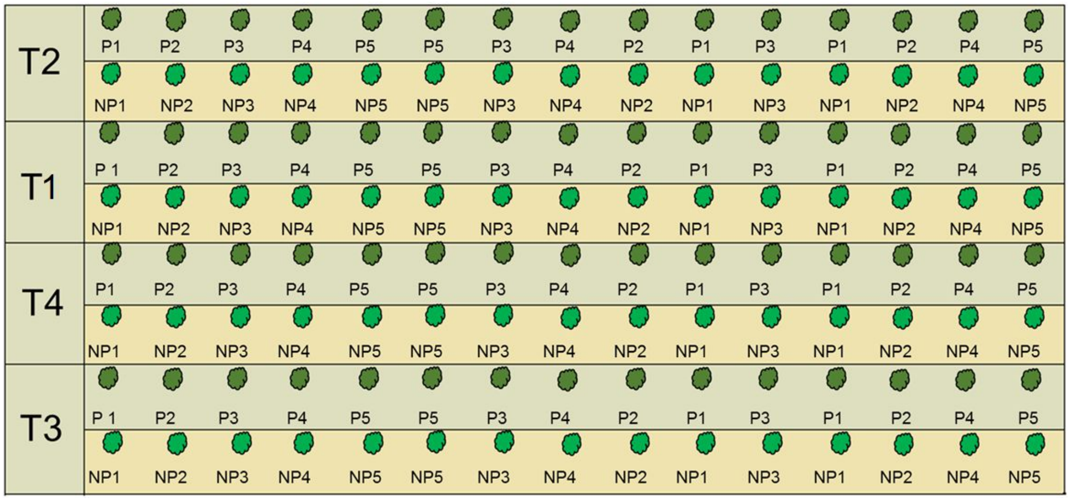

Fig. 1 Layout of one of the experimental blocks showing the distribution of species in the field, following the ecological groups of the pioneers (P) and non-pioneers (NP) in alternate rows of planting, submitted to different levels of phosphorus fertilization (T1 = control, T2 = 40 kg P_2O_5 ha^{-1}, T3= 80 kg P_2O_5 ha^{-1}, T4= 160 kg P_2O_5 ha^{-1}).

2.4 Soil analyses

Two years after planting, soil samples were collected in the pit of both treatments at a depth the 0-20 cm. Three points were collected per planting line to compose a homogeneous sample.

The soil samples were analyzed for pH (H_2O and KCl), potential acidity (H+Al), soil organic matter (SOM) and carbon (C), macronutrients (P, K, Ca and Mg) and micronutrients (Fe, Zn and Mn), subsequently base saturation and the sum of bases and (V%, SB). The pH was determined using an electrode (Thomas 1996). The extraction of potential acidity (H + Al) from the soil was carried out with a solution of calcium acetate and alkalimetric titration of the extract (Mclean 1965). The levels of soil organic matter (SOM) and carbon (C) were determined by the volumetric method using potassium dichromate (Walkley and Black 1934). The concentrations of calcium (Ca) and magnesium (Mg) were obtained by atomic absorption spectrophotometry (Mclean 1965) after the extraction in KCl 1 M (Miyazawa et al. 1999). The macronutrients (P and K) and micronutrients (Fe, Zn, and Mn) were extracted with the Mehlich solution (0.05 M HCl, 0.0125 M H_2SO_4). The P available was determined by visible spectrophotometry

(660 nm), while K and micronutrients were quantified by atomic absorption spectrophotometry (Thomas 1996).

2.5 Demographic measurements

The temporal variation of survival and growth was monitored quarterly from April 2017 to April 2019 for 24 months. In each monitoring campaign, the number of live samplings was counted and the root collar diameter (D) (5 cm above the ground) and total height (H) of each sapling were measured.

2.5.1 Survival rate

We calculated the annual survival rate (SR) according to Poorter and Bongers (2006). The daily seedling survival rate (DSR) for each species consisted of the slope of the log10 regression (percentage of surviving seedlings) against time (in days). The annual survival rate was then calculated as 10^{365DSR}.

2.5.2 Relative growth rates

The relative growth rates were calculated as follow: $RGR_{height} = (\ln H\ 2 - \ln H\ 1) / (t\ 2 - t\ 1)$ and $RGR_{diameter} = (\ln D\ 2 - \ln D\ 1) / (t\ 2 - t\ 1)$ according to Hunt (1990) and Bugbee (1996), where: H 1 = height (cm) at the time of planting, H 2 = height after two years; D 1 = diameter (mm) at the time of planting, D 2 = diameter after two years; t 2 and t 1 = interval between two years.

2.6 SPAD

The chlorophyll index content (SPAD values) was measured in three leaves of each tree and three different regions of the leaf, avoiding the ribs and using a portable chlorophyll meter (SPAD model 502; Minolta, Osaka, Japan). The measurements were made in the field on the same leaves used to determine gas exchange, fully expanded leaves visually in the middle third of the crown.

2.7 Leaf nutrient contents

The nutrients analyses were made by three to six leaves per plant. All leaves of each plant were ground to form a homogeneous composite sample. The leaf nitrogen content was determined by the Kjeldahl method with digestion, distillation and titration (Bremner 1996). Leaf phosphorus was determined by spectrophotometry ($\lambda = 750$ nm) after the molybdate method (Murphy and Riley 1962). The leaf content of potassium, magnesium, calcium, iron, zinc and manganese were determined by atomic absorption spectrometry (1100B, PerkinElmer, Ueberlingen, Germany).

2.8 Fluorescence parameters

Chlorophyll *a* fluorescence analyses were made 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. Measurements were made on three leaves per plant at 4:30 am and 12:00 (noon) (pre-dawn and midday). Before the midday measurements, the leaves were dark acclimated for 30 min for complete oxidation of the photosynthetic electron transport chain using specific leafclips. The chlorophyll *a* fluorescence polyphasic transient and the fluorescence parameters were determined after JIP test application, following Strasser et al. (2010), Strasser, Srivastava et al. (1995), Strasser, Srivastava et al. (1999) and Tsimilli-Michael and 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 have obtained: the reaction centers density (RC/ABS), the 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 in which electron is trapped by PSII (F_V/F_M) and is transferred further than QA^{-} (ET_0/TR_0). PI_{total} is an integrated index of the PI_{ABS} and the efficiency in which electrons reduce the end acceptors at the PSI.

$$PI_{abs}= \left(\frac{RC}{ABS}\right).\left(\frac{F_v/F_m}{1\text{-}F_v/F_m}\right).\left(\frac{ET_0/TR_0}{1\text{-}\ ET_0/TR_0}\right)$$

$$PI_{total}=PI_{abs}.\left(\frac{RE_0/ET_0}{1\text{-}\ RE_0/ET_0}\right)$$

2.9 Photosynthesis and photosynthetic nutrient use efficiency

The net photosynthesis per unit leaf area (A_n), dark respiration (R_d) stomatal conductance (g_s) and transpiration rate (E) were measured by using an infrared gas analyzer (LI-6400XT, LI-COR, USA). The measurements were made on one leaf per plant. However, before carrying out, experimental tests were carried out on several leaves per plant to ensure the selection of leaves with maximum values of photosynthesis at light-saturated (A_{max}). The measurements were made between 08:00 am and 12:00 (noon). The chamber was adjusted to a flow of 400 μmol s^{-1}; CO_2 concentration of 400 μmol mol^{-}

^{1}; 21 mmol mol^{-1} of the H_2O vapor concentration; leaf temperature of 31ºC; 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}). The maximum photosynthesis per unit mass (A_{mass}) was calculated by multiplying the specific leaf area (*SLA*) by A_{max} and by 0.1 depending on the differences between the units of each variable (µmol m^{-2} s^{-1} x cm^{2} g^{-1}). The *SLA* was calculated from the ratio of the fresh leaf area to the dry leaf mass at 65ºC until obtaining constant leaf mass, using leaf discs of known area (0.283 cm^{2}) (Evans and Poorter 2001). The photosynthetic nutrient use efficiency (PnutrientUE) for macro and micronutrients was calculated by the ratio between the rates of photosynthesis per unit mass (A_{max} * *SLA* * 0.1) and the respective leaf nutrient content of each plant (Field and Mooney 1986; Ferreira et al. 2016).

2.10 Statistical analysis

The data were previously submitted to the assumptions of normality and homoscedasticity by Shapiro-Wilk and Lilliefors tests, respectively. Non-normality and heterogeneity were corrected by log transformation. Demographic and photosynthetic traits were analyzed by two-way ANOVA to test for the effects of blocks, fertilization treatments, species and their interactions. In the case of significance ($P < 0.05$), Duncan post hoc test was performed. All analyses were made using Statistica 9.0 software.

3 Results

3.1 Effects of fertilization on chemical properties of the soil

Two years after fertilization, the values of pH increased in both treatments compared priory of the experiment. In addition, there was a seven-fold increase in P available in fertilized treatments and Fe concentrations increased by 27% when fertilized (Table 2).

3.2 Effects of phosphorus fertilization on survival and growth

The species groups showed high survival in both treatments (-P and + P). However, *E. fusca* (pioneer species) under -P, significantly reduced the values of survival after 10 months reaching 0% at 24 months (Fig. 2 a). *A. leiocarpa* exhibited the highest values of height under – P and + P from 15 months after planting. *C. alliodora* and *E. fusca* also increased their height under + P over time (Fig. 2 c,d). The interspecific differences of absolute values in diameter over time were more evident under + P. *C. alliodora*, *E. fusca* and *C. fissilis* showed the highest values of diameter, while *A.*

leiocarpa and *S. macrophylla* exhibited intermediate values and, *H. courbaril*, *D. odorata*, *C. guianensis* and *B. excelsa* had the lowest values (Fig. 2 e,f).

The growth rates in height and diameter were affected in different ways by fertilization and species according to successional status (Fig. 3 a,b). For non-pioneers species (NP), the RGR-height was not affected by fertilization, while there were differences among species. The values of RGR-height for *D. odorota* were approximately two times higher than *C. guianensis*. For RGR-diameter, NP exhibited no significant effect on all treatments. Conversely, the pioneer species (P) showed a significant difference of RGR in height and diameter as affected by fertilization. *C. alliodora* and *C. fissilis* had values 44.5 and 36% higher for height and diameter, respectively, under +P than -P. *A. leiocarpa* showed average values of height 27% and 46% higher than *G. ulmifolia*, for +P and - P, respectively, while the interspecific differences of diameter were not significant.

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Table 2 Chemical characteristics and soil fertility as affected by fertilization treatments after 24 months of planting (n = 3).

Fertilization treatment (P_2O_5)	pH_{H20}	pH_{KCL}	P	K^+	Fe^{2+}	Zn^{2+}	Mn^{2+}	Ca^{2+}	Mg^{2+}	H+Al	C	SOM	SB	V%
					............................mg kg^{-1}............................				................cmolc kg^{-1}................		..........g kg^{-1}..........			
0 kg ha^{-1}	5.4 ± 0.1^{a}	4.4 ± 0.1^{a}	3.0 ± 0.3^{a}	55.9 ± 5.4^{a}	120.4 ± 1.6^{a}	41.2 ± 15.6^{a}	9.5 ± 3.5^{a}	223.3 ± 20.8^{a}	101.7 ± 17.5^{a}	4.9 ± 0.3^{a}	16.7 ± 1.2^{a}	28.8 ± 2.0^{a}	1.9 ± 0.1^{a}	27.9 ± 2.3^{a}
160 kg ha^{-1}	5.4 ± 0.1^{a}	4.4 ± 0.1^{a}	20.9 ± 0.2^{b}	60.2 ± 8.1^{a}	166.1 ± 5.7^{b}	36.9 ± 17.3^{a}	9.9 ± 1.7^{a}	325.0 ± 65^{a}	101.7 ± 12.5^{a}	5.4 ± 0.0^{a}	17.6 ± 1.8^{a}	30.4 ± 3.2^{a}	2.4 ± 0.3^{a}	31.4 ± 3.2^{a}

Carbon (C), soil organic matter (SOM), sum of bases (SB), subsequently base saturation (V%). Equal letters between fertilization treatments show no significant difference according to Duncan's post hoc test ($p > 0.05$).

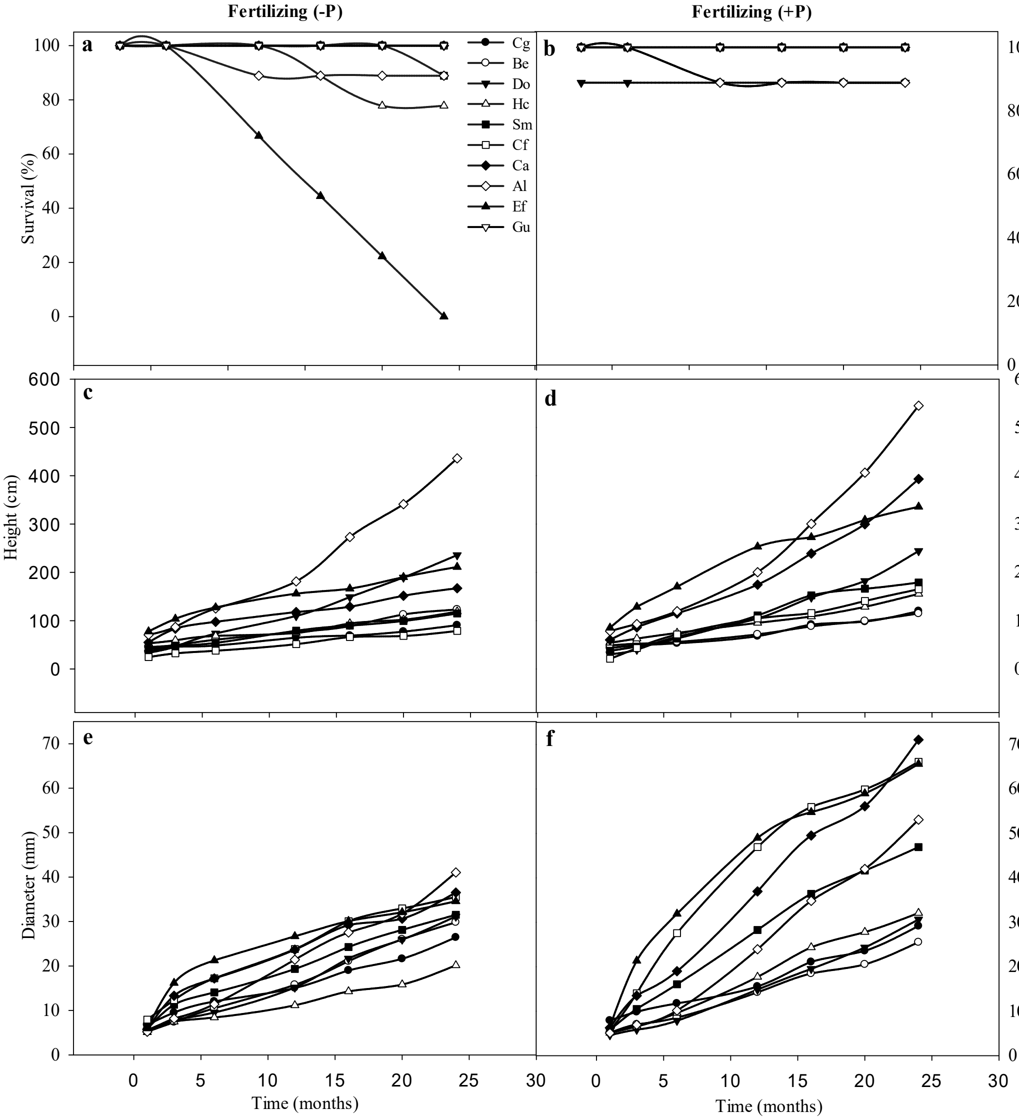

Fig. 2 Survival (-P; a, +P; b) and growth height (-P; c, +P; d) and diameter (-P; e, +P; f) of pioneers and non-pioneers species submitted to contrasting phosphorus fertilization treatments (- P = 0 kg P_2O_5 ha^{-1}; + P = 160 kg P_2O_5 ha^{-1}) over 24 months. *Carapa guianensis*, (C.g); *Bertholletia excelsa*, (B.e); *Dipteryx odorata,* (D.o); *Hymenaea courbaril* (H.c); *Swietenia macrophylla* (S.m); *Cedrela fissilis* (C.f); *Cordia alliodora* (C.a); *Apuleia leiocarpa*, (A.l), *Erythrina fusca*, (E.f); *Guazuma ulmifolia*, (G.u).

Table 3 Survival rates (%) (mean ± standard deviation) 24 months after planting of ten Amazonian forest species submitted to contrasting phosphorus fertilization.

Species	0 kg P_2O_5 ha^{-1} (-P)	160 kg P_2O_5 ha^{-1} (+P)
Pioneers		
C.fissilis	100 ± 0^{a}	100 ± 0^{a}
C.alliodora	100 ± 0^{a}	100 ± 0^{a}
A.leiocarpa	87 ± 23^{a}	87 ± 23^{a}
E.fusca	2 ± 1^{b}	100 ± 0^{a}
G.ulmifolia	100 ± 0^{a}	100 ± 0^{a}
Non-pioneers		
C.guianensis	100 ± 0^{a}	100 ± 0^{a}
B.excelsa	100 ± 0^{a}	87 ± 23^{a}
D.odorata	100 ± 0^{a}	91 ± 17^{a}
H.courbaril	77 ± 23^{a}	100 ± 0.00^{a}
S.macrophylla	95 ± 9^{a}	100 ± 0.00^{a}

Equal letters show no significant difference for the interaction of the two factors according to Duncan's post hoc test ($p > 0.05$). Averages are compared between rows and columns.

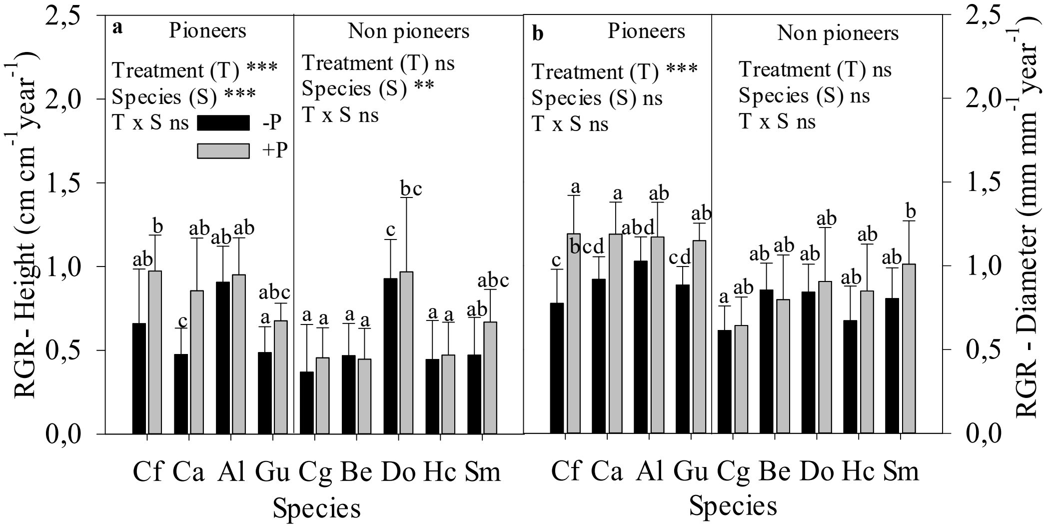

Fig. 3 Relative growth rates in height (a) and diameter (b) (mean ± SD) of nine Amazonian tree species (pioneers and non-pioneers) subjected to contrasting P fertilization (-P = 0 kg P_2O_5 ha^{-1} and +P = 160 kg P_2O_5 ha^{-1}) (n = 3). ($p > 0.05$ ns; $p < 0.05$ *; $p < 0.01$ **; $p < 0.001$***).

Mean values followed by the same letters for the species and treatments are not different at $P < 0.05$ according to Duncan's test. *Carapa guianensis*, (C.g); *Bertholletia excelsa*, (B.e); *Dipteryx odorata,* (D.o); *Hymenaea courbaril* (H.c); *Swietenia macrophylla* (S.m); *Cedrela fissilis* (C.f); *Cordia alliodora* (C.a); *Apuleia leiocarpa*, (A.l), *Erythrina fusca*, (E.f); *Guazuma ulmifolia*, (G.u).

3.3 Effects of phosphorus fertilization on photosynthesis-related traits

3.3.1 SPAD

We observed significant effects of fertilization and species on SPAD measurements only for pioneers group (Fig. 4). Fertilization had a positive effect on the increase of SPAD values. *C. alliodora* had values 17% higher when fertilized. *A. leiocarpa* showed the highest values, being 33% and 28%, higher than *C. fissilis* for -P and + P, respectively.

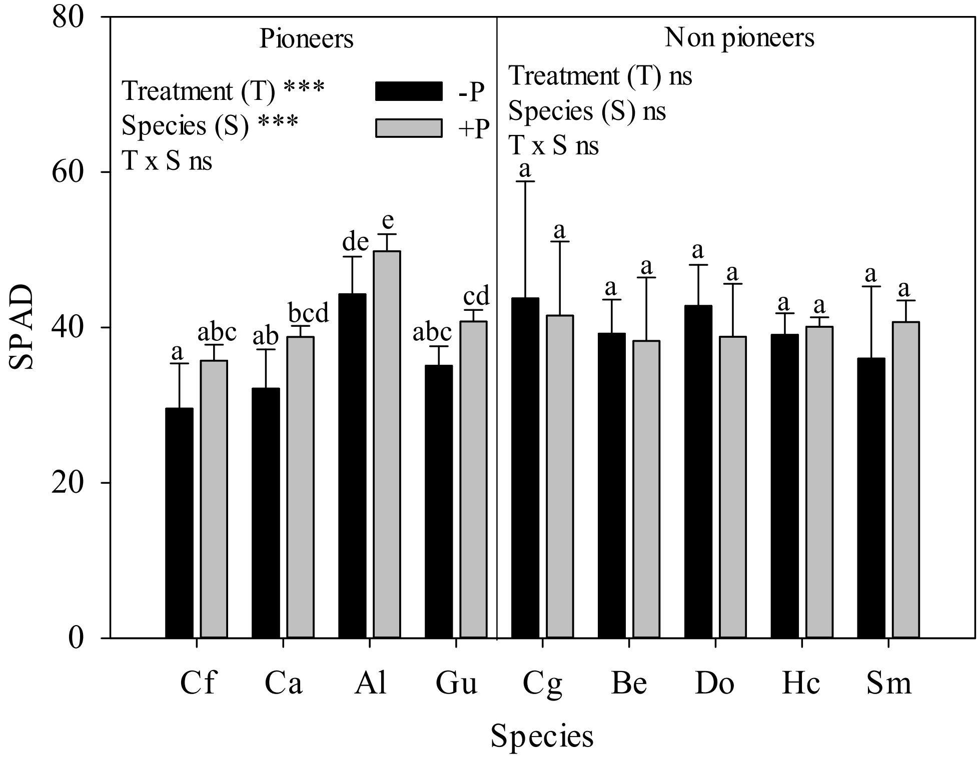

Fig. 4 SPAD values (mean ± SD) of nine Amazonian tree species (pioneers and non-pioneers) subjected to contrasting P fertilization (-P = 0 kg P_2O_5 ha^{-1} and +P = 160 kg P_2O_5 ha^{-1}) (n = 3). ($p > 0.05$ ns; $p<0.05$ *; $p<0.01$ **; $p<0.001$***). Mean values followed by the same letters for the species and treatments are not different at $P < 0.05$ according

to Duncan's test. *Carapa guianensis*, (C.g); *Bertholletia excelsa*, (B.e); *Dipteryx odorata,* (D.o); *Hymenaea courbaril* (H.c); *Swietenia macrophylla* (S.m); *Cedrela fissilis* (C.f); *Cordia alliodora* (C.a); *Apuleia leiocarpa*, (A.l), *Erythrina fusca*, (E.f); *Guazuma ulmifolia*, (G.u).

3.3.2 Fluorescence parameters

The effects of fertilization on photochemical performance across all species were dependent on the fluorescence parameter analyzed and the time of measurements. Fertilization did not significantly affect the maximum quantum yield of photosystem II (F_v/F_m) of species during pre-dawn and midday measurements (Fig. 5 a,b). Interspecific differences were observed for the performance index (PI_{ABS}). *A. leiocarpa* exhibited the highest values across all species during pre-dawn and midday (Fig. 5 c,d). Fertilization had marginal effects on the total performance index (PI_{total}) of pioneers species during midday (Fig. 5 f). The fertilization effect was most evident for *C. fissilis* species, which had values four-fold higher in +P than -P. Similar to PI_{ABS}, the highest values of PI_{total} were also observed for *A. leiocarpa*, which was four-fold higher than *C. alliodora*.

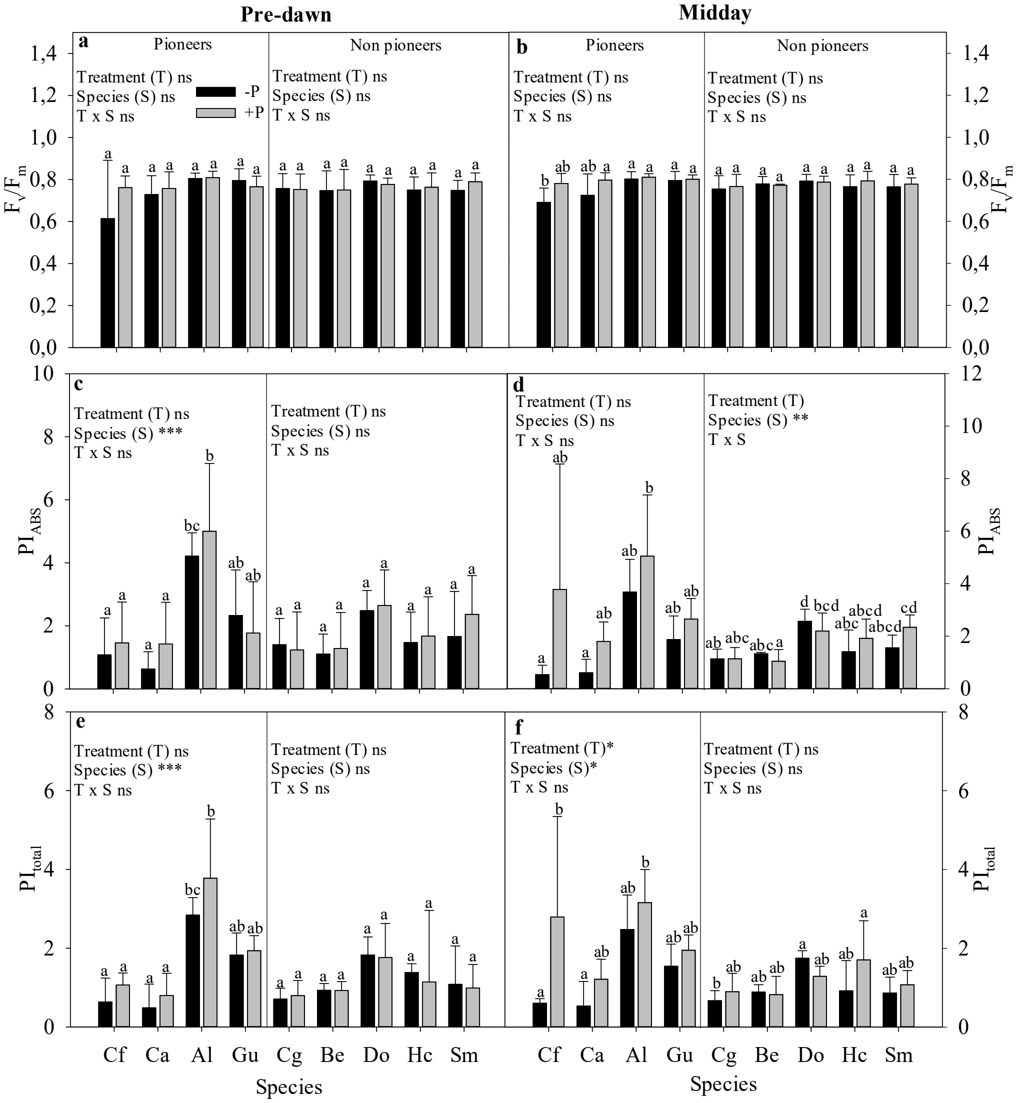

Fig. 5 Maximum quantum yield of photosystem II (Fv/Fm) (pre-dawn: a, and midday: b), photochemical performance index (PI_{ABS}) (pre-dawn: c, and mid-day: d), and total photochemical performance index (PI_{total}) (pre-dawn: e, and mid-day: f) (mean ± SD), of nine Amazonian tree species (pioneers and non- pioneers) subjected to contrasting P fertilization (-P = 0 kg P_2O_5 ha^{-1} and +P = 160 kg P_2O_5 ha^{-1}) (n = 3). ($p > 0.05$ ns; $p < 0.05$ *; $p < 0.01$ **; $p < 0.001$***). Mean values followed by the same letters for the species and treatments are not different at $P < 0.05$ according to Duncan's test. *Carapa guianensis*, (C.g); *Bertholletia excelsa*, (B.e); *Dipteryx odorata,* (D.o); *Hymenaea courbaril* (H.c); *Swietenia macrophylla* (S.m); *Cedrela fissilis* (C.f); *Cordia alliodora* (C.a); *Apuleia leiocarpa*, (A.l), *Erythrina fusca*, (E.f); *Guazuma ulmifolia*, (G.u).

3.3.3 Gas exchange

The values of maximum photosynthesis per unit mass (A_{mass}) were different only for non-pioneer species and were not significantly affected by fertilization (Fig. 6 a). *H. courbaril* had values 43% and 38% higher than *C. guianensis* for -P and + P, respectively. Fertilization affected the stomatal conductance (g_s) and transpiration (E) of pioneers species (Fig. 6 b,c). The species most positively affected by fertilization was *C. alliodora*, with values 37% (g_s) and 31% (E) higher when fertilized. *A. leiocarpa* showed the highest values of g_s and E, that was between 70 and 50% (-P and +P) higher than *C. fissilis* for g_s and, between 42 and 28% (-P and +P) for E compared to the same species. Significant interspecific differences were observed for R_d with *A. leiocarpa* exhibiting the highest values across all species (Fig. 6 d).

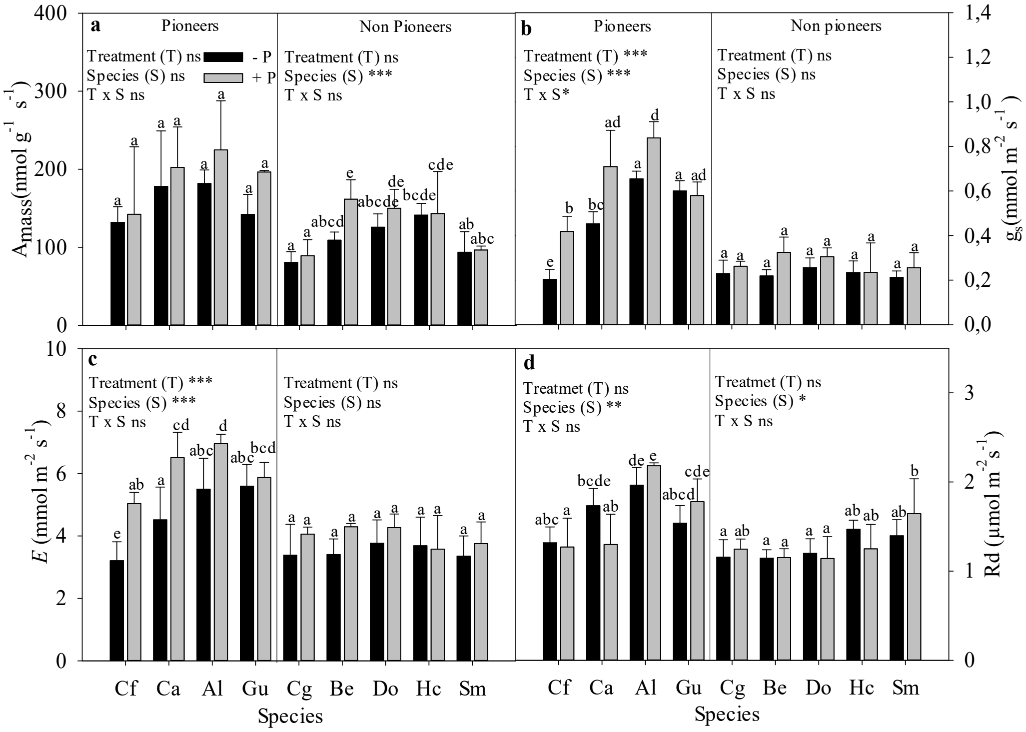

Fig. 6 Maximum photosynthesis per unit mass (A_{mass}; a) stomatal conductance (g_s; b) transpiration (E; c) and dark respiration (R_d; d), (mean ± SD) of nine Amazonian tree species (pioneers and non- pioneers) subjected to contrasting P fertilization (-P = 0 kg P_2O_5 ha^{-1} and +P = 160 kg P_2O_5 ha^{-1}) (n = 3). ($p> 0.05$ ns; $p<0.05$ *; $p<0.01$ **; $p<0.001$***). Mean values followed by the same letters for the species and treatments are not different at $P < 0.05$ according to Duncan's test. *Carapa guianensis*, (C.g); *Bertholletia excelsa*, (B.e); *Dipteryx odorata,* (D.o); *Hymenaea courbaril* (H.c);

Swietenia macrophylla (S.m); *Cedrela fissilis* (C.f); *Cordia alliodora* (C.a); *Apuleia leiocarpa*, (A.l), *Erythrina fusca*, (E.f); *Guazuma ulmifolia*, (G.u).

3.3.4 Leaf nutrient content

The leaf phosphorus content was significantly affected by fertilization treatment for pioneers and non-pioneers species (Fig. 7 b). *G. ulmifolia* and *C. guianensis* exhibited values approximately 39% and 46.5% higher when submitted to phosphorus fertilization. *H. courbaril* had values 21 and 37% higher than *D. odorata* in -P and +P, respectively. The leaf nitrogen content was significantly affected by the species in both pioneers and non-pioneers groups. The phosphorus fertilization (+ P) affected only the group of non-pioneers. Interspecific differences were stronger than the effects of fertilization. *B. excelsa*, *D. odorata* and *H. courbaril* had the highest values of nitrogen leaf content among non-pioneers species, while *C. fissilis*, *A. leiocarpa* and *C. alliodora* did it among pioneers species (Fig. 7 a). The N/P ratio reduced significantly across species as affected by phosphorus fertilization (Fig. 8). The highest reductions were observed for *C. alliodora* and *D. odorata*, which also exhibited the highest values of this parameter under -P.

Phosphorus fertilization decreased the potassium leaf content for all species (Fig. 7 c). *C. alliodora* (under -P) exhibited the highest values among pioneers species. For other nutrients, interspecific differences were more evident than those resulted by fertilization. Overall, *C. alliodora* showed the highest values of Ca, Mg and Zn (Fig. 7 d,e,g). Exception for Mn in pioneers species, the micronutrients were not affected by phosphorus fertilization.

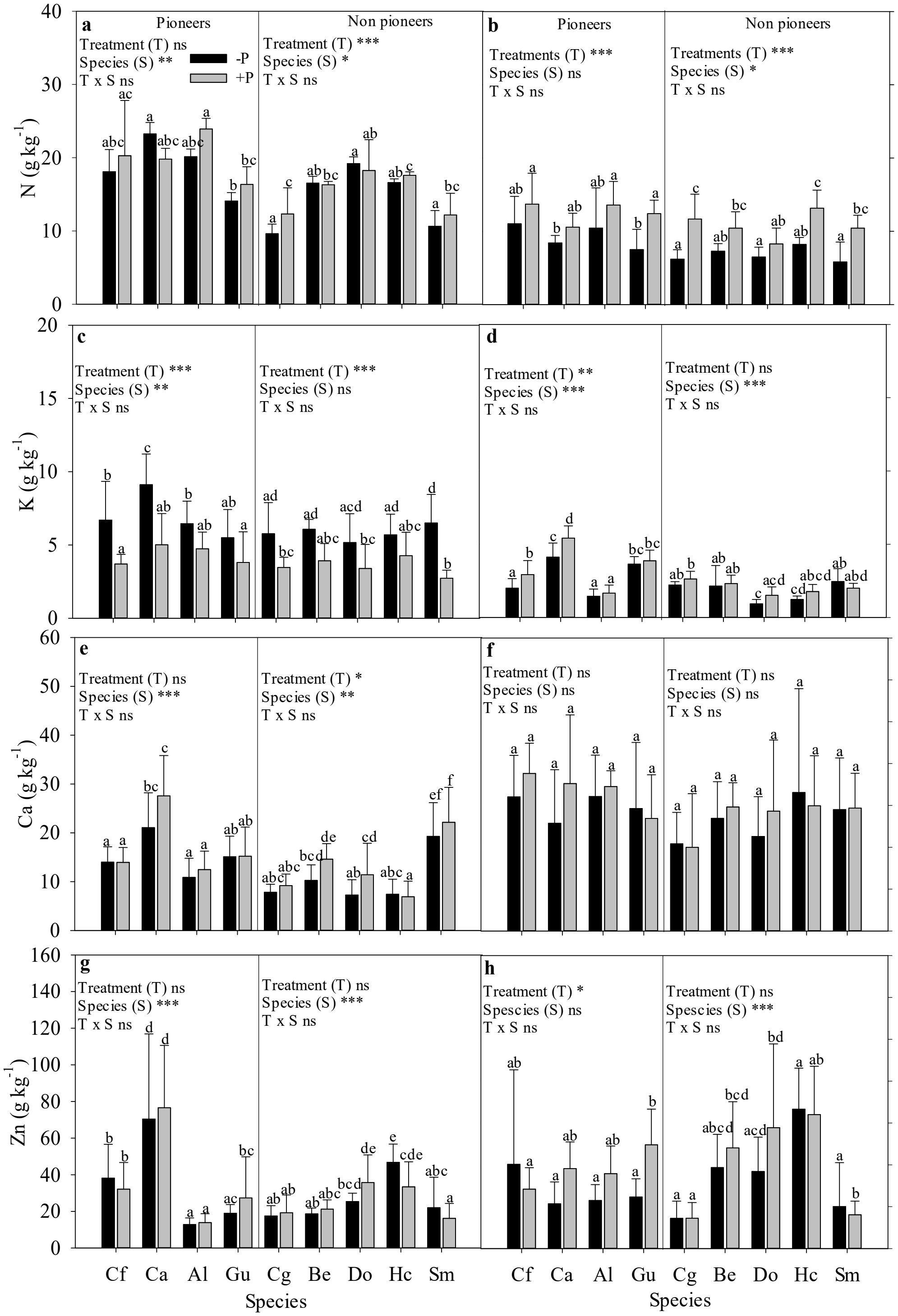

Fig. 7 Macro (N; a, P; b, K; c, Mg; d, Ca; e) and micronutrients (Fe; f, Zn; g, Mn; h) leaf content (mean ± SD) of nine Amazonian tree species (pioneers and non-pioneers) subjected to contrasting P fertilization (-P = 0 kg P_2O_5 ha^{-1} and +P = 160 kg P_2O_5 ha^{-1}) (n = 3). (p> 0.05 ns; p<0.05 *; p<0,01 **; p<0.001***). Mean values followed by the

same letters for the species and treatments are not different at $P < 0.05$ according to Duncan's test. *Carapa guianensis*, (C.g); *Bertholletia excelsa*, (B.e); *Dipteryx odorata,* (D.o); *Hymenaea courbaril* (H.c); *Swietenia macrophylla* (S.m); *Cedrela fissilis* (C.f); *Cordia alliodora* (C.a); *Apuleia leiocarpa*, (A.l), *Erythrina fusca*, (E.f); *Guazuma ulmifolia*, (G.u).

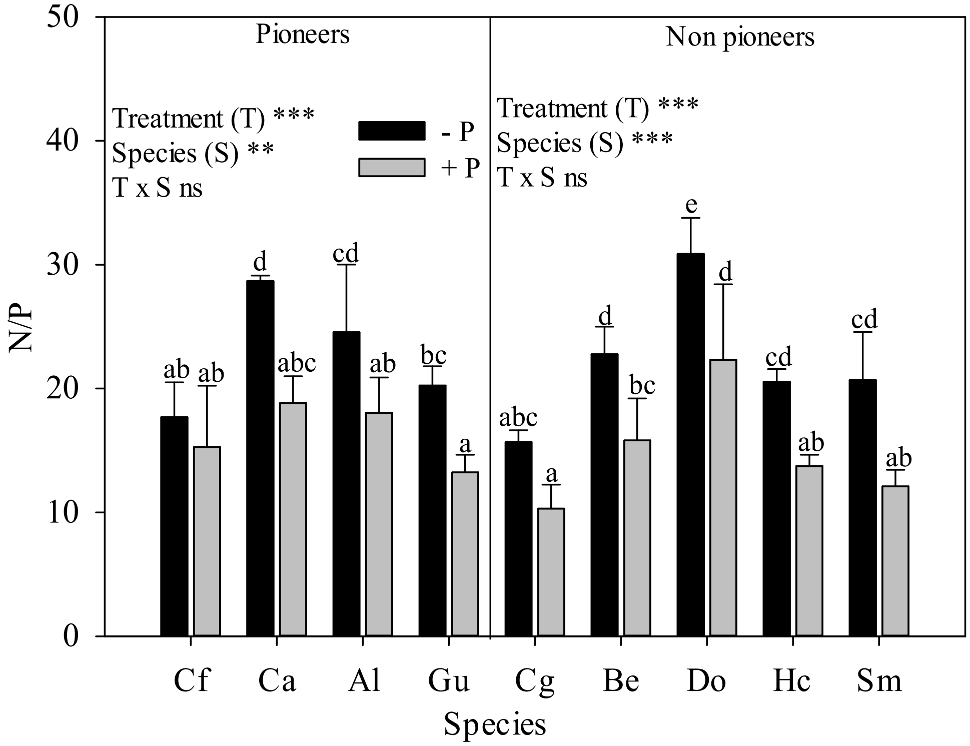

Fig. 8 N/P ratio (mean ± SD) of nine Amazonian tree species (pioneers and non-pioneers) subjected to contrasting P fertilization (-P = 0 kg P_2O_5 ha^{-1} and +P = 160 kg P_2O_5 ha^{-1}) ($n = 3$). ($p > 0.05$ ns; $p < 0.05$ *; $p < 0.01$ **; $p < 0.001$***). Mean values followed by the same letters for the species and treatments are not different at $P < 0.05$ according to Duncan's test. *Carapa guianensis*, (C.g); *Bertholletia excelsa*, (B.e); *Dipteryx odorata,* (D.o); *Hymenaea courbaril* (H.c); *Swietenia macrophylla* (S.m); *Cedrela fissilis* (C.f); *Cordia alliodora* (C.a); *Apuleia leiocarpa*, (A.l), *Erythrina fusca*, (E.f); *Guazuma ulmifolia*, (G.u).

3.3.5 Photosynthetic nutrient use efficiency

Phosphorus fertilization decreased the photosynthetic phosphorus use efficiency of non-pioneer species, with exception for *B. excelsa* and *D. odorata*, which also had the highest values of this parameter among non-pioneers species (Fig. 9 b). *B. excelsa* was the only species increasing the values of nitrogen use efficiency after phosphorus fertilization (Fig. 9 a). Phosphorus fertilization increased the values of potassium use efficiency across all species, mainly for non-pioneer group (Fig. 9 c). For other nutrients, with exception of PZnUE in pioneers species, we observed significant differences only among species. Overall, *A. leiocarpa* (pioneers group) and *D. odorata*, *H. courbaril* and *S. macrophylla* (non-pioneers group) exhibited the highest values of PMgUE, PCaUE, PFeUE, PZnUE and PMnUE (Fig. 9 d,e,f,g,h).

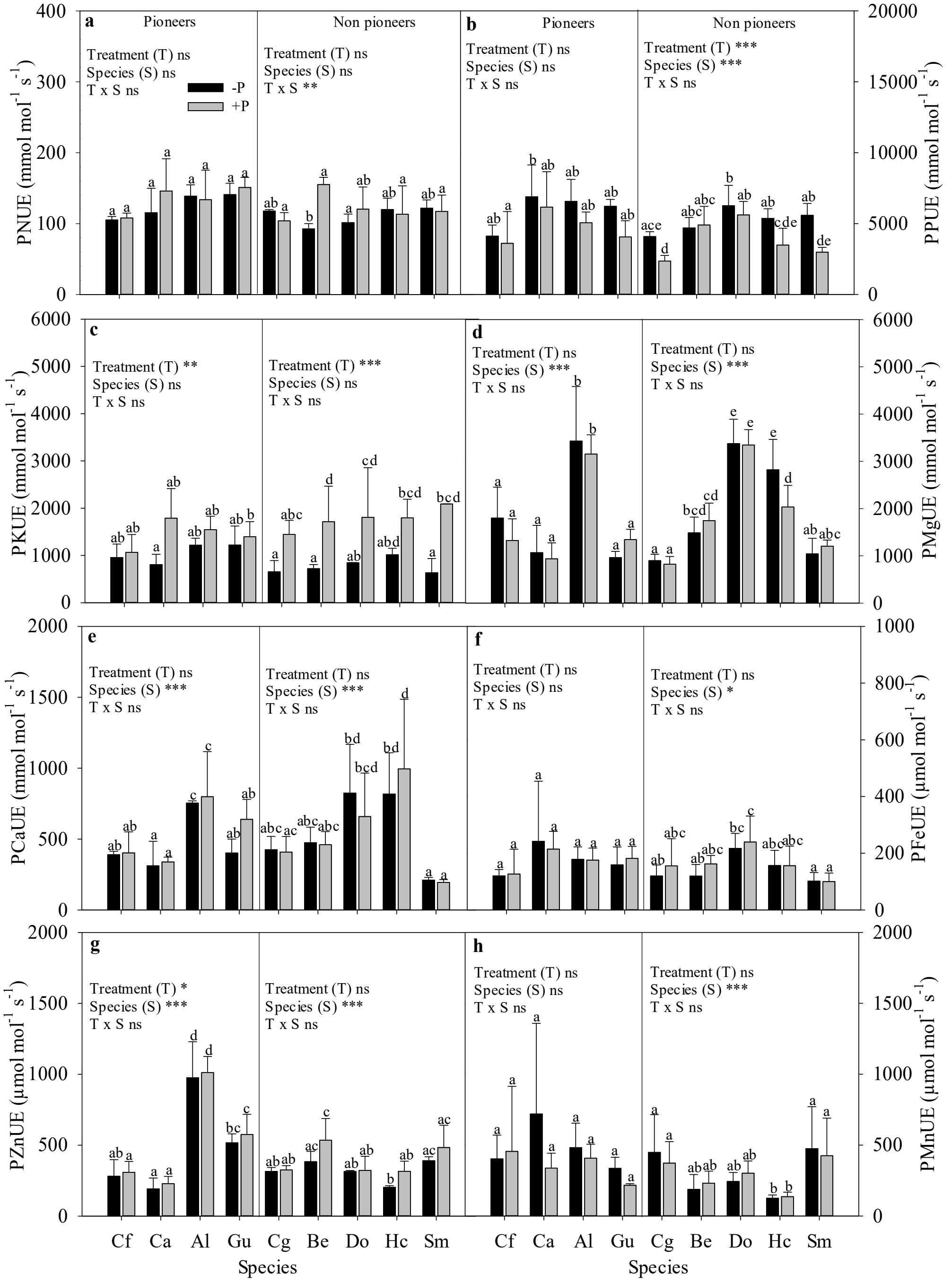

Fig. 9 Photosynthetic nutrient use efficiency (PNUE; a, PPUE; b, PKUE; c, PMgUE; d, PCaUE; e, PFeUE; f, PZnUE; g, PMnUE; h) (mean ± SD) of nine Amazonian tree species (pioneers and non-pioneers) subjected to contrasting P fertilization (-P = 0 kg P_2O_5 ha^{-1} and +P = 160 P_2O_5 kg ha^{-1}) (n = 3). ($p > 0.05$ ns; $p < 0.05$ *; $p < 0.01$ **; $p < 0.001$***). Mean values followed by the same letters for the species and treatments are not different at $P < 0.05$ according to Duncan's test. *Carapa guianensis*, (C.g); *Bertholletia excelsa*, (B.e);

Dipteryx odorata, (D.o); *Hymenaea courbaril* (H.c); *Swietenia macrophylla* (S.m); *Cedrela fissilis* (C.f); *Cordia alliodora* (C.a); *Apuleia leiocarpa*, (A.l), *Erythrina fusca*, (E.f); *Guazuma ulmifolia*, (G.u).

4 Discussion

Phosphorus fertilization improved the availability of P in the soil (Table 2) and allowed greater absorption by trees (Fig. 6 and 7). Positive effects of phosphorus supply on the nutritional status of forest species have been shown in plants cultivated mainly in the greenhouse (Seabra et al. 2017; Araújo et al. 2018). Here, we demonstrated the increase of phosphorus leaf content after fertilization across species belong to different successional groups in field conditions. However, similar patterns of increasing were not observed for other nutrients. Conversely, potassium leaf content reduced in all species after fertilization (Fig. 7 c). Phosphorus supply also induced a decline in the potassium leaf content in *Swietenia macrophylla* seedlings (Seabra et al. 2017). The low concentration of potassium in plants subjected to phosphorus fertilization may be in part due to its role in the growth of meristematic tissues (Mengel 1985), being that the increase in growth rates as affected by fertilization may be induced a higher demand for this nutrient for the growth of different organs. Values of N:P above 20 (Güsewell 2004) suggested high phosphorus limitation for *C. alliodora*, *A. leiocarpa* (pioneers species) and *B. excelsa*, *D. odorata* (non-pioneers species) under control -P. However, *A. leiocarpa* and *D. odorata* kept their growth rates similar to phosphorus fertilization treatment, while *E. fusca*, a fast-growing leguminous species, showed high mortality in -P. Overall, corroborating Resende et al. (1999), the growth of pioneers species was more responsive to phosphorus supply than non-pioneers species. These results indicate that the establishment responses (survival and growth) induced by phosphorus fertilization in Amazonian tree species are species-specific.

Phosphorus fertilization improved the mechanisms of light absorption (SPAD values) and processing (chlorophyll *a* fluorescence parameters) of pioneers species, this last manly at midday according to total performance index. The positive effects of phosphorus supply to enhance light using are substantial for plants growing under full sunlight, since that the excess of energy absorbed not used for photosynthetic pathways may induce photo-oxidative stress in phosphate-starved plants (Hernández and Munné-Bosch 2015). The effects of phosphorus deficiency on the photosynthetic electron transport chain have been related to impair on the ATP production, while the levels of NADPH continue increasing and, hence reduces CO_2 fixation (Carstensen et al. 2018). Contrary to our expectations, in this research, the increase in the leaf P content in response to fertilization did not result in a significant increase in the photosynthesis rates at the leaf-level. The phosphorus fertilization had only marginal effects on photosynthesis across all species despite improving on the carbon capture rate (stomatal conductance) of pioneers species. We believe that the main reasons for not significant effects of phosphorus supply on the carbon assimilation include methodological and functional issues as follow: first, the analysis at individual leaf-level may not represent the real effect on the carbon gain at crown level (Santos et al. 2018), due the changes in total leaf area per plant not measured (Grady et al. 2013); second, the fact of photosynthetic performance may be more influenced by the allocation strategies of nutrients within the leaf than total leaf nutrient content (Dusenge et al. 2015), since that fast-growing species tend to make greater investments in structural P (Villar et al. 2006; Zhang et al. 2018) and slow-growing species tend to invest more P in nucleic and residual acids than in metabolic P (Zhang et al. 2018); third, the significant reduction on the N:P ratios of the species *C. guianensis*, *H. courbaril* and *S. macrophylla* may have contributed to the absence of phosphorus supply effects on the photosynthesis for non-pioneers successional group, where the most of N leaf is an integral part of the proteins of the photosynthetic machinery, especially ribulose – 1.5 - bisphosphate carboxylase oxygenase (Rubisco) (Poorter and Evans 1998) and, thus, an unbalance on the N:P stoichiometric may compromise the effects of phosphorus supply on the photosynthetic performance of plants (Stitt and Schulze. 1994); fourth, the decline of K leaf content after fertilization can also have reduced the significance of increasing on the P leaf content for photosynthesis.

Phosphorus supply reduced the photosynthetic phosphorus use-efficiency mainly for non-pioneers species. This result was partially due to the not significant effects of phosphorus fertilization on photosynthesis at the leaf-level. Cordell (2001) also found that the phosphorus fertilization in an environment limited by P reduced the efficiency of the use of this nutrient. This author associated the decrease in efficiency with the increase in the concentration of leaf P and constant photosynthetic rate. The not significant effects of fertilization on the growth of non-pioneers species may have induced a low demand for this nutrient for trees growth and hence high leaf concentrations. Forest species growing in soils poor in P normally show high nutrient use-efficiency (Zhang et al. 2018).

However, keep this strategy will depend on the biomass increasing at the same ratio as the nutrient uptake and accumulation after fertilization that, in turn, is determined mainly by the successional status, growth rates and seed size (Resende et al. 2005). Interestingly, *A. leiocarpa* and *D. odorota*, species that kept their growth rates in control -P, exhibited the highest values of magnesium and calcium use-efficiency. Amazonian trees, like *Bertholletia excelsa* Bonpl., have shown a significant increase in the growth as affected by improvement in the availability of Mg and Ca (Schroth et al. 2015).

Our findings have important implications for the establishment of plantations using Amazonian tree species in P-limited soils: we showed that the effects of phosphorus supply on the survival and growth are species-specific, suggesting more detailed studies of forest nutrition related to each priority species and not only according to successional status; the positive effects of phosphorus fertilization on the light absorption and processing of pioneers species are important to the establishment of plantations, since that these species are normally the first to be planted in a restoration project in open areas; the capacity of *A. leiocarpa* and *D. odorota* maintain growth despite low soil phosphorus availability reveals the high potential of these species for plantations in P-limited soils and suggest additional research on the mechanisms behind of these responses; the best growth responses of *C. fissilis* and *C. alliodora* to fertilization suggest the importance of phosphorus supply to the planting of these species; the high mortality in short-term of *E. fusca*, a fast-growing leguminous species, can indicate the not sustainability for the planting of leguminous trees in P-limited soils and; future research should be realized accessing the interspecific differences on the above- and belowground biomass as affected by phosphorus fertilization.

5 Conclusions

Phosphorus fertilization affects the initial establishment of Amazonian trees in a species-specific way. The fertilization increases the phosphorus absorption by plants, whereas reduces the use efficiency due to no significant effects on carbon assimilation at the leaf-level. Phosphorus supply improves light absorption and processing of pioneers species suggesting relieve the effects of photo-oxidative stress on the initial establishment of seedlings under full sunlight.

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7 Conclusão geral

Os resultados são importantes para o entendimento do estabelecimento inicial de espécies florestais em áreas com limitação de P. Apesar da fertilização química aumentar a disponibilidade de P, as respostas a esse aumento foram específicas. Apesar dos altos valores na relação N/P foliar, espécies como *Apuleia leiocarpa* (pioneira) e *Dipteryx* *odorata* (não pioneira), mantiveram altas taxas de crescimento em solos limitados por P, apresentando pouca ou nenhuma resposta a fertilização fosfatada. Por outro lado, *Erythrina fusca* (pioneira) apresentou alta mortalidade quando não fertilizada, mostrando limitação a disponibilidade do nutriente. Apesar dos valores de assimilação de carbono em nível foliar não serem afetados pela disponibilidade de P, características de captura de carbono (g_s), absorção (SPAD) e processamento de luz (PI_{total}), tiveram seu desempenho afetado. Esse efeito foi evidenciado principalmente nas espécies pioneiras. As respostas do grupo para essas características são importantes visto que as espécies pioneiras são as primeiras a serem inseridas em plantios a pleno sol. Sugerimos estudos futuros acessando as diferenças interespecíficas em resposta à disponibilidade de fósforo para biomassa acima e abaixo do solo com o objetivo de melhor entender a dinâmica de crescimento das espécies.

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