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O PAPEL DA VEGETAÇÃO RESIDENTE NO ESTABELECIMENTO DE PLÂNTULAS COM DIFERENTES CARACTERÍSTICAS FUNCIONAIS

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Manaus, Amazonas

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Sinopse:

Realizou-se um experimento para investigar como a vegetação residente interage com plântulas, influenciando no desempenho de espécies com tamanhos de sementes variados.

Palavras-chave: competição e facilitação, gradiente ambiental, florestas secundárias.

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Resumo

A competição entre raízes é tida como um importante processo em florestas com solos pobres em nutrientes. Espécies com diferentes características funcionais podem responder diferentemente à competição de raízes ao longo de um gradiente ambiental. Este estudo teve como principal objetivo investigar como três espécies arbóreas com diferentes características funcionais respondem à competição de raízes com a vegetação residente ao longo de um gradiente ambiental. Um segundo objetivo deste estudo foi investigar se a cobertura de plantas no sub-bosque das florestas diminui o consumo de herbívoros em plântulas recém estabelecidas, reduzindo o efeito negativo da competição de raízes. O estudo foi conduzido em seis florestas secundárias com diferentes idades na Amazônia Central. Em cada floresta foram instalados cinco blocos que contava por sua vez com um par de parcelas: uma parcela controle e outra tratamento, totalizando 30 blocos. O tratamento correspondeu à remoção da vegetação do sub-bosque e a construção de trincheiras em todo o perímetro da parcela. Em cada parcela foram plantados dois indivíduos cada de *Bertholletia excelsa*, *Hevea brasiliensis* e *Handroanthus serratifolius*, totalizando 120 indivíduos por espécie. As plântulas foram monitoradas a cada três meses e as causas de mortalidade foram registradas quando possível. Após 10 meses foram calculados, índices de competição, de qualidade de sítio e de dano biótico (ex: herbivoria) para cada espécie baseado na biomassa final e monitoramento das plântulas. Também foram medidas algumas características funcionais de todas as plantas vivas, abertura de dossel nas parcelas e nutrientes disponíveis no solo. Para todas as espécies, os índices de competição variaram de positivo (facilitação) à negativo (competição) e a importância da competição de raízes foi positivamente relacionada com o índice de qualidade de sítio. A competição de raízes afetou características funcionais relacionadas à captura de luz de todas as espécies. O dano biótico explicou a maior parte da variação do índice de qualidade de sítio para *B. excelsa* e *H. brasiliensis* e a disponibilidade de recursos parece ter um papel secundário para todas as espécies. A intensidade do dano biótico não se relacionou negativamente com a cobertura da vegetação do sub-bosque. Os resultados demonstram que a competição de raízes é mais importante em locais onde as plântulas têm um maior potencial de crescimento. Facilitação ocorreu na metade mais severa do gradiente ambiental e esta relacionada com a diminuição do dano biótico para indivíduos de *B. excelsa* e de *H. brasiliensis*. As plantas foram consumidas por diferentes herbívoros e a atratividade da vegetação para diferentes espécies de herbívoros deve ter influenciado mais nesta relação do que a cobertura de plantas no sub-bosque.

Abstract

Root competition is considered an important process in forests with nutrient-poor soils. Species with different functional traits may have distinct responses to root competition along an environmental gradient. The main objective of this study was to investigate how three plant species with different functional traits respond to root competition with the neighboring vegetation along an environmental gradient in secondary forests. A second objective was to investigate if the resident understorey vegetation cover reduces seedlings consumption by herbivores, ameliorating the negative effects of root competition. The study was conducted in six secondary forests with distinct ages in Central Amazonia. At each forest, five blocks were established for a total of 30 blocks in the experiment. Each block included a pair of plots: control and treatment. The treatment plot was trenched and the understorey vegetation was removed. In each plot two individuals each of *Bertholletia excelsa*, *Hevea brasiliensis* and *Handroanthus serratifolius* were planted, totaling 120 individuals per species. The seedlings were monitored every three months and causes of death were registered whenever possible. After 10 months of records, for each species, competition indexes, site suitability indexes and biotic disturbances intensity were calculated based on final biomass and seedling monitoring. Functional traits of all live seedlings, canopy openness above the plots and available nutrients in the soil were also measured. For all species, the indexes of competition varied from positive (facilitation) to negative (competition) and the importance of root competition was associated with species-specific site suitability indexes. Root competition affected functional traits by reducing the light capture efficiency for all species. Biotic disturbances explained most of the variation among the species-specific site suitability indexes for seedlings of *B. excelsa* and *H. brasiliensis*. The availability of resources seems to play a secondary role for all species. The intensity of biotic disturbances was not negatively associated with understorey vegetation cover. These results highlight that root competition is more important in sites where seedlings become more developed. Facilitation occurred at the most severe level of the environmental gradient and may be related to reduced biotic damage in plants in control plots when damage is high for seedlings of *B. excelsa* and *H. brasiliensis*. Individuals of each species were consumed by distinct herbivores and the attractiveness of the understorey vegetation for different herbivores may have influenced more than the vegetation cover when facilitation occurred.

Sumário

INTRODUÇÃO GERAL

A perda de habitat é considerada a principal causa de extinção no mundo. Na Amazônia Legal, as taxas de desmatamento nos últimos 20 anos têm variado em torno de 10 mil à quase 30 mil km^2 ao ano (Instituto Nacional de Pesquisas Espaciais – INPE, 2008), onde as principais causas que levam ao desmatamento são o corte de madeira e a abertura de pastagens para a criação de gado. No primeiro caso, após corte e sem posterior queima, a floresta é capaz de regenerar relativamente rápido (Mesquita *et al*., 2001), porém, no segundo caso, para o estabelecimento de pastagens, vastas áreas de floresta são cortadas e queimadas e após 3 a 5 anos, com o declínio da produtividade das pastagens, estas áreas são abandonadas (Uhl, 1987). Logo após o abandono, inicia-se um processo de regeneração florestal secundária e há então uma maior probabilidade de ocorrer dominância de espécies florestais do gênero *Vismia* que restringem o estabelecimento de muitas outras espécies (Mesquita *et al*., 2001). O conhecimento dos fatores que inibem ou promovem o estabelecimento das diferentes espécies vegetais nessas áreas, tem importantes implicações para estratégias de manejo que visam à reabilitação florestal e o enriquecimento das capoeiras para uso agro-silvicultural.

Atualmente, muito tem sido discutido sobre os fatores que podem influenciar a direção positiva ou negativa do efeito que a vegetação residente exerce sobre as plantas colonizadoras. A *hipótese do gradiente de estresse* prevê que em ambientes menos produtivos e com condições abióticas adversas, processos de facilitação seriam mais evidentes (Bertness & Callaway, 1994). Ao contrário, em ambientes caracterizados por alta produtividade e condições ambientais mais amenas, a competição por recursos seria mais intensa (Bertness & Callaway, 1994). Outros estudos sobre as interações entre plantas têm encontrado suporte para a *hipótese da disponibilidade e demanda de recursos* (Taylor *et al*., 1990, Davis *et al*., 1998). De acordo com essa hipótese, a competição é mais intensa quando a disponibilidade dos recursos limitantes está abaixo da demanda da vegetação residente, entretanto, se a disponibilidade de recursos está acima da demanda, a competição é reduzida e até mesmo facilitação pode ocorrer (Davis *et al*., 1998). Note que se a competição é amenizada quando a disponibilidade de recursos é alta, contrariamente ao exposto pela hipótese do gradiente de estresse, a competição pode ser negativamente relacionada com a produtividade.

Mais recentemente, estudos têm focado na distinção entre a intensidade e a importância da competição e como ambas variam ao longo de gradientes de produtividade ou severidade ambiental (Brooker *et al*., 2005, Gaucherand *et al*., 2006, Brooker & Kikvidze, 2008). Como proposto por Welden e Slauson (1986), a *intensidade* da competição é o efeito da vegetação residente sem levar em conta outros fatores do ambiente. Por outro lado, a importância da competição reflete o efeito da vegetação residente relativo à outros fatores ambientais que limitam o desempenho de indivíduos de espécies distintas. Brooker e colaboradores (2005) propuseram dois índices para distinguir a intensidade da importância da competição em experimentos pareados com tratamento (sem competição) e controle e demonstraram que os índices não são necessariamente correlacionados. A distinção entre esses dois conceitos tem levado a novas interpretações de como as interações entre plantas mudam ao longo de gradientes de produtividade (Sammul *et al*., 2000, Brooker *et al*., 2005, Gaucherand *et al*., 2006, le Roux & McGeoch, 2009, Lamb *et al*., 2009).

Em florestas tropicais, a disponibilidade de luz tem sido considerada o principal recurso limitante para as plantas que ocupam ou compõem o sub-bosque (Clark *et al*., 1995, Nicotra *et al*., 1999, Balderrama & Chazdon, 2005). No entanto, em florestas com solo pobres em nutrientes, a competição de raízes pode ser tão importante quanto a disponibilidade de luz (Coomes & Grubb, 2000). Mais recentemente, foi proposto que a detecção da competição de raízes deve ser interpretada levando em consideração outros fatores que restringem o desempenho das plantas (Schenk, 2006). Não há evidências que algum estudo tenha diferenciado a intensidade e a importância da competição de raízes em florestas tropicais ao longo de gradientes de produtividade.

Geralmente, a produtividade de uma comunidade é inferida indiretamente usando a biomassa da parte aérea das plantas de diferentes localidades, o que foi demonstrado ser inversamente relacionado com a severidade do ambiente (Grime, 1977). Em florestas secundárias, este padrão pode não ser encontrado pois a produtividade pode ser maior em estádios iniciais de sucessão (onde a biomassa da parte aérea é menor) e decrescer a medida que a sucessão prossegue (Horn, 1974). No entanto, a severidade do ambiente também pode ser maior em estádios iniciais de sucessão por causa das maiores temperaturas que o solo atinge e a maior exposição aos ventos que levam às plantas a uma maior dessecação. Outro problema é que a tolerância a qualquer tipo de estresse geralmente é espécie-específica, como tolerância à seca por exemplo ou ao desempenho das plantas ao longo de gradientes de disponibilidade de recursos; então a importância das interações entre plantas deve diferir entre florestas secundárias com diferentes idades. Por causa destas particularidades, neste estudo a biomassa da parte aérea da comunidade foi substituída por um índice de qualidade de sítio para cada espécie que está relacionado com a severidade do ambiente (Berkowitz *et al.*, 1995).

Sabendo que espécies com diferentes características funcionais podem responder diferentemente a situações de estresses impostos pelo ambiente (Myers & Kitajima 2007), eu formulei uma hipótese que a resposta das espécies a competição de raízes com a vegetação residente poderia variar entre espécies distintas. Por isso, eu escolhi três espécies com uma alta variação no tamanho de sementes e características foliares, como área foliar. Como o dano por herbívoros é tido como uma das principais causas de mortalidade e redução do crescimento de plantas em florestas tropicais (Benitez-Malvido et al. 2005), eu também formulei outra hipótese que, se ocorrer facilitação nesse sistema de estudo, a influência positiva da vegetação estabelecida vai ser causada por uma redução de dano dos herbívoros nas parcelas onde a vegetação foi mantida intacta.

OBJETIVO GERAL

Investigar como a vegetação residente influencia o desempenho de plântulas de espécies arbóreas com diferentes atributos funcionais ao longo de um gradiente ambiental composto por florestas secundárias com várias idades.

OBJETIVOS ESPECÍFICOS

- Investigar como a competição com a vegetação residente influencia a sobrevivência, crescimento e características funcionais das espécies estudadas;
- Investigar se espécies com distintas características funcionais experienciam a competição diferentemente;
- Analisar qual a relação da importância da competição com o índice de qualidade de sítio de cada espécie;
- Caracterizar como as variáveis ambientais influenciam o índice de qualidade de sítio de cada espécie;
- Investigar se o efeito benéfico da vegetação residente é relacionado a uma redução de dano por animais nas parcelas com vegetação.

CAPÍTULO ÚNICO

Root competition and positive interactions on tree seedlings along an environmental gradient in Central Amazonia

(capítulo a ser submetido à revista *Journal of Ecology*)

Root competition and positive interactions among tree seedlings along an environmental gradient in Central Amazonia

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Summary

1. Root competition is considered an important process in forests with nutrient-poor soils. Species with varying seed masses may have distinct responses to root competition along an environmental gradient. The main objective of this study was to investigate if tropical tree seedlings with different seed masses respond differently to root competition with the neighboring vegetation along an environmental gradient in secondary forests. A second objective was to investigate if the resident understorey vegetation cover reduce seedlings consumption by herbivores, ameliorating the negative effects of root competition.

2. We conducted a trenching and vegetation removal experiment in six secondary forests with distinct ages in Central Amazonia. Three species with varying seed masses were planted. For each species, competition indexes, site suitability indexes and biotic damage by animals were calculated based on final biomass and seedling monitoring. Functional traits of all live seedlings, canopy openness above the plots, available nutrients in the soil and understorey vegetation cover were also measured.

3. Root competition affected functional traits by reducing the light capture efficiency for all species. The responses to trenching and vegetation removal were similar among species independently of seed masses. The indexes of competition varied from positive (facilitation) to negative (competition) and root competition importance increased when site suitability indexes was high. Biotic damage reduced site suitability indexes for two species, suggesting that when biotic damage was low, the importance of root competition increased.

4. Facilitation occurred at the most severe level of the environmental gradient and may be related to reduced biotic damage for two species. However, the damage by animals was not lower in plots with higher cover of the understorey vegetation. Individuals of each species were consumed by distinct herbivores and the attractiveness of the understorey vegetation for

different herbivores may have influenced more than the vegetation cover when facilitation occurred.

5. *Synthesis*: These results highlight that when a site is not particular suitable for a given species, the importance of root competition in tropical forests may decrease and even facilitation may occur. Facilitation by the understorey neighboring vegetation may also contribute to tree seedling coexistence.

Key-words: Tropical forests, seed mass, facilitation, stress-gradient hypothesis, competition importance, secondary forests

Introduction

Plant-plant interactions are recognized as important mechanisms determining the persistence of species at local scales (Huston 1999). In tropical forests, competition for light (or light heterogeneity) is believed to be the central mechanism controlling seedling performance (Balderrama & Chazdon 2005; Nicotra, Chazdon & Iriarte 1999; Clark *et al.* 1996). However, in some forests root competition experienced by establishing seedlings with an already established vegetation can be more important than light availability in controlling seedling performance (e.g. Coomes & Grubb 1998). In their review, Coomes and Grubb (2000) concluded that root competition in forests is mostly due to nutrient foraging and hypothesized that root competition was more important in nutrient-poor forests compared to nutrient-rich forests. More recently, Schenk (2006) proposed that the detection of root competition should be interpreted considering its importance relative to other factors that limit plant performances. This study intends to assess the importance of root competition for three tropical tree species with different functional traits along an environmental gradient in a nutrient-poor forest.

The stress-gradient hypothesis (SGH) states that competition is more frequent in high productivity environments and facilitation occurs more commonly under stressful conditions (Bertness & Callaway 1994). The generality of this hypothesis has been a theme of much debate because empirical data do not always support expectations (Maestre, Valladares & Reynolds 2005; Lortie & Callaway 2006; Maestre, Valladares & Reynolds 2006). A recent refinement of the SGH acknowledges that the relationship of competition and productivity should not always be negative or linear (Maestre *et al.* 2009). The need to incorporate both life-history traits of target species and the type of stress involved was addressed as important variables in evaluating the SGH (Maestre *et al.* 2009). For example, in water limited environment the intensity of competition was more or less pronounced according to the species stress-tolerances or competitive ability, respectively (Liancourt, Callaway & Michalet. 2005). Specifically, the most stress-tolerant species experience more competition than less tolerant species (Liancourt, Callaway & Michalet. 2005, Corcket, Callaway & Michalet. 2005). Similarly, in alpine communities, competition was more common in locations where species were near to their distributional optima (Choler, Michalet & Callaway 2001). The general conclusion from these studies is that if site suitability is high for a given species, competition is expected.

On the contrary, other studies showed competition under a resource supply and demand hypothesis, which states that competition intensifies if limiting resource supply is below the demand of the resident vegetation (Taylor, Aarssen & Loehle 1990; Davis, Wrage & Reich 1998); however, if resource supply is above the demand, competition intensity is reduced and facilitation may occur (Davis, Wrage & Reich 1998). Note that if competition is reduced at high resource conditions, then competition should be negatively related with site suitability.

In an undisturbed forest near to the location of the present study, a positive association between trenching (to avoid root competition) and light availability was documented (Lewis & Tanner 2000). It seems that when light is not limiting survival and growth, then one would expect that the importance of root competition to increase. However, one species was more responsive to both trenching and light than the other (Lewis & Tanner 2000). This result was probably because the less responsive species had morphological and physiological traits that enable it to tolerate lower levels of resource availability. For tropical tree seedlings, it is possible that competition is lower when a species can tolerate lower levels of resource availability.

Tolerance to any given constrain depends on specific morphological and physiological traits, and tolerances to multiple factors depend on a combination of several traits (Grime 2001). Carbohydrate reserves in seeds enable their derived seedlings to survive for a longer period when mass increment is low or even negative, which is itself related to tolerance to multiple stresses (Walters & Reich 2000, Kidson & Westoby 1990). Carbohydrate reserves in seeds also enable seedlings survive and grow with resource shortages whereas small seeded species are more responsive to enhanced availability of soil resources (Milberg, Perez-Fernandez & Lamont 1998). Additionally, in order to grow in a shaded understorey, seedlings must adjust their physiology and morphology in a way to maximize light capture and exploit light efficiently (Valladares & Niinemets 2008). Seed mass is correlated with seed carbohydrate reserves and is also correlated with general traits that enable seedlings to survive in deep shade (Ganade & Westoby 1999, Valladares & Niinemets 2008). Models of competition among species with different seed sizes when there is an already established vegetation only predict coexistence if large seeded species suffer less competition from the established vegetation, however, this relation have been poorly reported for tropical tree species (Coomes & Grubb 2003).

In order to investigate how tropical tree species with different seed masses would differ in their responses to root competition along an environmental gradient we performed a trenching experiment in secondary forests with different ages. We selected secondary forests with a wide range of ages to assess a greater variation in environmental variability and to represent some possibilities that seedlings would face when disperse in most of the secondary forests in Central Amazon. The specific questions are: i) How do species respond to root competition in terms of survival, growth and functional trait values? ii) Do large-seeded species experience less root competition than small-seeded species? iii) What is the relationship between competition importance and the suitability of a site for species with varying seed masses? iv) How do different factors modulate the suitability of a site for each species? We hypothesized that root competition will be less important for the large-seeded species because its larger seed provide storage reserves that enable them to grow and prolong survival with resource shortages (Hypothesis 1). Also, we hypothesized that the relationship between competition importance and the suitability of a site will differ among the species with different functional traits (Hypothesis 2).

Nevertheless, herbivory may also differentially constrain survival and growth of tree seedlings (Gerhardt 1998, Benitez-Malvido *et al*. 2005). Plant species are frequently consumed by different herbivores, particularly in tropical regions, and the responses to herbivory also differ among plant species (Myers & Kitajima 2007). Some studies reported that competition among understorey vegetation are weak (Svenning, Fabbro & Wright 2008), however, facilitation among understorey plants in tropical forests is rarely explored. The understorey vegetation cover within forests varies in a scale of meters and this variability can influence the establishment of tree seedlings (Diwold, Dullinger & Dirnböck 2009). In this study we also hypothesized that, if herbivory significantly influences species survival or growth, higher cover of the neighboring understorey vegetation may provide better sites by sheltering seedlings against consumers in relation to locations with less cover (Hypothesis 3). We predict that biotic disturbances will be less intense where understorey vegetation cover is higher.

Methods

STUDY SPECIES

To test the effect of root competition on species with different functional traits we selected three tree species accordingly to their seed size and leaf morphology. According to the classification used by Camargo *et al*. 2008, *Handroanthus serratifolius* (Vahl) S. O. Grose (Bignoniaceae) has very small wind-dispersed seeds (mean = 0.071 g, range = 0.011-0.155 g) and has small leaves with low mass per area. *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg. (Euphorbiaceae) has medium seed mass (mean = 4.9 g, range = 2.0-6.2 g) that is primarily dispersed by explosion and secondarily dispersed by mammals, and it has a relatively higher leaf area. *Bertholletia excelsa* Bonpl. (Lechytidaceae) is the most characteristic of a stress-tolerant species, with larger seeds than the others species (mean = 10.4 g, range = 4.5-15.6 g) and higher leaf area per mass (LMA). All seedlings were grown and watered regularly at a plant nursery located at the Seed Laboratory of the National Institute for Amazon Research (INPA). After germination, seedlings were transplanted to plastic bags (3 cm diameter x 10 cm height) with a substrate compound equally (1:1) consisting of sand and organic soil.

Only *Handroanthus serratifolius* occurs in the forest of the studied region. The other two species were selected due to their economical value and potential to be considered in a management plan to economically rehabilitate the abandoned second growth forests. Other species of *Hevea* and *Handroanthus* and other species of the Lecythidaceae family occur in the region. Hereafter we will identify species by their generic name.

STUDY AREA

The study areas were located in secondary forests sites at the Biological Dynamics of Forest Fragments Project Conservation Unit complex, approximately 80 km North of Manaus, Brazil, in the Central Amazon Basin. The secondary forests sites were ~40 km apart at Esteio farm (2º24'S, 59º52'W) and Dimona farm (2º20'S, 60º07'W). The soils in the areas were classified as clay-rich yellow oxisols, and are very poor in nutrients (Fearnside & Leal-Filho 2001). The mean annual precipitation is about 2500 mm per year and in general, the driest months (<100 mm) last from July to November. In 2009, the rainy season lasted until May and there was an unexpectedly long dry season that began earlier and lasted until December.

Two distinct forest secondary succession trajectories result from differences in the land-use history of these farms. In places where the mature forest was clear-cut, but not burned, subsequent re-growth was usually dominated by species of the genus *Cecropia* and the recovery of species richness in the secondary forest was rapid (Mesquita *et al*. 2001). However, in places when the mature forest was slashed-and-burned, species of the genus *Vismia* dominated early stages of plant succession and regeneration was slower compared to only clear-cut (Mesquita *et al*. 2001). In this study, we selected secondary forests dominated by *Vismia* because the growth of such forests replaced most of the slashed-and-burned mature forests in the region. Additionally, these secondary forests may have a great potential for economic exploitation of forest products (such as fibers, timber, charcoal or biomass) or such forests allow the establishment of economically important species plantations (Mesquita 2000).

Experimental design

In each studied location at the farms mentioned above (Esteio and Dimona), we selected three secondary forests patches divided in the following classes: young (four years old since the last cut and burning), intermediate (eight to eleven years old) and old (28 years old). Ages for young and old classes were fairly precise, however, for the intermediate class it was difficult to obtain the precise year of the last burn and the estimations varied three years according to people that worked in these sites for many years. Nevertheless, the two areas classified as intermediate had similar forest structure.

Within each of the six second-growth forest areas, we randomly established five experimental blocks in a grid with 18 points spaced 25 m apart. Each of the five experimental blocks consisted of a 1 x 1 m control plot and a 1 x 1 m treatment plot also assigned at random and spaced 50 cm from each other. During the first two weeks of February 2009, we trenched 20 cm deep around each of the treatment plots and removed every plant located within. After trenching, we tried to remove all possible roots by hand, pulling them out of the trench walls and the plot itself in order to minimize the effects that larger, deeper roots could exert on soil structure, also in addition to possible nutrient contributions during the time of the study from decomposing roots. Although this procedure disturbed the soil surface, the disturbance occurred almost three months before the seedling's planting, which allowed time for soil processes to stabilize. Before trenching each treatment plot, all litter fall in the plot was temporarily removed, to be subsequently replaced after the procedures described above. The control plot was intentionally left untouched because we were specifically interested in measuring the understorey vegetation cover. Three months after planting, we visually estimated the vegetation cover of the understorey plants up to 1m above the ground in the treatment plots.

During the last week of April and the first week of May, we planted at random two three month-old seedlings of each focal species in each treatment and control plots within the blocks located at the described grid of 18 points, totaling six seedlings per plot. The seedlings' root systems were still protected by the substrate. Each seedling was spaced at least 20 cm apart and this distance was maintained from the edge of the plot. A total of 120 seedlings of each species were planted. After planting, we counted the number of leaves and measured the seedling's height. Every three months we reestablished the trenches to avoid invading roots.

Seedling monitoring and performances

Every three months we counted the number of leaves on all planted seedlings, monitored survival and measured plant damage. Causes of mortality were recorded whenever possible and biotic damage was visually assigned to one of the following categories: C0 = intact; C1 = 1–20%; C2 = 21–40%; C3 = 41–60%; C4=61–80%; C5=81–99% of leaf damage. When a seedling was completely defoliated or when the terminal apex was damaged (e.g. by mammal herbivory), it was assigned to category 5. The score for each leaf was used to define an index of damage (*ID*) per plant: $ID = \Sigma\, ni\, (Ci)/N$. Where i is the category of damage, ni is the number of leaves in the ith category of damage, Ci is the midpoint of each category (i.e. C1 =10%, C2 =30%, C3 =50%, C4 =70%, C5 =90%), and N is the total number of leaves of the plant. Values are expressed as a weighted average of the percentage of leaf area damaged per seedling (Benitez-Malvido *et al*. 2005).

Ten months after planting, we cut all seedlings at ground level and collected the last fully expanded leaf of each individual. The leaf area (A) of the last leaf was measured using a scanner and the images were processed with LAFORE software. Seedlings and leaves were oven-dried for three days at 60 ºC. Leaf area per mass (LMA) was calculated with leaves weighed to the nearest 0.001 g. Leaves and stems of the seedlings were weighed separately. With this data we calculated the total mass (leaf mass plus stem mass plus root mass), leaf mass fraction (LMF = leaf mass per total mass) and plant elongation (stem mass per height). Relative growth rate in height (R_H) was calculated as follows: $R_H = \ln(h_f - h_i)/t$. Where h_f and h_i are average final height and initial height of the live seedlings, respectively, and t is ten months, the total period of data collecting. Relative growth rate in leaf number (R_L) was calculated following the same manner.

Abiotic measuring

In September, a 20 cm^3 soil sample from the top 10 cm of the soil we collected between all control and treatment plots and, according to the protocols of the Soil Laboratory at the INPA, the samples were dried in shade for three months. Soil phosphorous and potassium content were obtained by inductively coupled plasma optical emission spectrometer. Nitrogen content in the soil was obtained In December and January we took hemispherical photographs at 75 cm above the ground in the space between control and treatment plots for all pairs of plots and under overcast sky conditions. The percentage canopy openness was obtained after processing the photographs using the software Gap Light Analyzer 2.0 (Frazer *et al*. 2001).

Competition indexes

The intensity and importance of competition indexes were calculated following Brooker and colleagues (2005), where intensity of competition (C_{int}) equals the difference between average mass of the seedlings without competition (P_{-c}) and average mass of the seedlings planted in the control plots (P_{+c}). This difference was divided by the higher value among P_{-c} or P_{+c} (X), as following: $C_{int} = (P_{-c} – P_{+c}) / X$. The importance of competition was measured as the difference between performances of treatment (P_{-c}) and control (P_{+c}) divided by the maximum value of performance in the absence of competition (P_{max-c}) minus the minimum value in all cases (y): $C_{imp} = (P_{-c} – P_{+c}) / (P_{max-c} – y)$. Both indexes varied between 1 and -1; negative values indicated competition and positive values indicated facilitation.

Site suitability index

The effects of multiple environmental constrains will be represented as a site-specific quality index (Berkowitz, Canham & Kelly 1995). Average mass of all individuals of the same species in the treatment plot (without competition) was divided by the maximum average biomass of all treatment plots. This index provides a measure that varies from zero (where both seedlings died) to one (where both individuals achieve its greater performances). The index is calculated using the average biomass of the two individuals of each species and if one individual died, its biomass will be set to zero, providing a measure of performance without root competition and the effect of understorey vegetation which integrates both survival and growth.

DATA ANALYSIS

All analysis were conducted using the statistical software R 2.9.2 (R Core Development Team 2009). To account for spatial clustering of the experimental design, we performed some of the analysis by means of linear and generalized linear mixed-effects models (LMMs e GLMMs; Bolker *et al*. 2009) using the lme4 package (Bates, Maechler & Dai 2008). The models included blocks nested within secondary forest age classes and secondary forest age class nested within farm as random variables.

We used generalized linear mixed-effects models (GLMMs) with binomial error structure and logit link function using the function *glmer* of the lme4 package and Laplace approximation method. Survival or death (1/0) of each seedling was used as the dependent variable and treatment was used as the fixed effect. The significance of the fixed parameters was assessed by the Wald *z* test (Bolker *et al*. 2009).

The linear mixed-effects models (LMMs) were used using the *lmer* function of the lme4 package assuming a normal distribution of the error and restricted maximum-likelihood estimation. R_H, R_L,final mass, leaf mass fraction, elongation and biotic disturbances (square-root arcsine transformed) were used as dependent variables, treatment was used as a fixed effect. Trenching effects on leaf area (A) and leaf mass per area (LMA) of each species were analyzed using log-transformed variables as the response, treatment as a fixed effects and only block was used as a random variable due unbalanced data. The model parameters were tested using Markov Chain Monte Carlo (MCMC) simulations with the *mcmcsamp* function from the lme4 package, and their 95% highest posterior density (HPD) intervals and probabilities were obtained using the *pvals.fnc* function from the *languageR* package (Baayen, Davidson & Bates 2008). We also ran all analysis with the *aov* function from stats package using block as a random variable, however, the MCMC estimates were more conservative.

The relation between C_{imp} and C_{int} and the relation between the suitability index of the species were tested with Pearson's correlation test and the influence of the vegetation cover on biotic disturbance intensity for each species was assessed with a simple regression. Differences between species in the mean C_{imp} and C_{int} were tested with *lmer* function using only species as a fixed factor and a random slope model with species depending on the secondary age class nested within farm. To test if there was a relationship between C_{imp} and the site suitability index, and if this relationship was different for each species, we included species as a fixed effect, specific site suitability index as a continuous variable, plus their interactions. A significant interaction was interpreted that the relationship of C_{imp} with specific site suitability index differs among species. The random-slope model was built with one slope per species per secondary forest age class nested within farm. Since *mcmcsamp* is not available for random-slope models, we tested the significance of the terms with a likelihood-ratio test using a parametric bootstrap (Faraway 2006).

The relationship between the site suitability index of each species and the environmental variables was assessed with multiple regressions using the *z*-scores of the variables. The relation between biotic disturbance intensity and understorey cover was assessed with a simple regression. The significance of all analysis were evaluated with $\alpha = 0.05$.

Results

SEEDLING SURVIVAL

Despite the atypical length of the drought season, mortality was low for all planted individuals (15%, 6% and 25% for *Hevea*, *Handroanthus*, *Bertholletia*, respectively). There were no differences in survivorship between plants in the control and treatment plots (GLMM fit for all species: $z < 0.9$, $P > 0.3$). A total of 74% of the mortality was caused by biotic disturbances, but the type of biotic disturbance differed among species (Table 1). The main cause of *Hevea* seedlings mortality was damage caused by mammal herbivory (possibly deer). These animals managed to eat all parts of the leaves of *Hevea* and sometimes even part of the stem, and the seedlings were unable to re-sprout due to the injuries incurred at the terminal apex. We were unable to detect a possible animal that uprooted *Handroanthus* seedlings, but such a disturbance can be caused by agoutis. *Bertholletia* seedlings were mostly killed by rodents that usually excavate the soil to reach the nutritious seeds that do not detach from newly established seedlings after germination; most of the species of Lecythidaceae have bi-polar germination and seeds became part of the root system or stem of the new plant. Surprisingly, only six seedlings of all species (see Table 1) were found completely desiccated, which was what we had expected to be the most common cause of death and a good indicator of water limitation.

TRENCHING EFFECTS ON GROWTH, FUNCTIONAL TRAITS AND BIOTIC DISTURBANCES

The seedling growth responses to treatment varied among species. *Hevea* seedlings did not grow in height (R_H), leaf number (R_L) or achieve a greater final biomass in comparison to control plants (Table 2). *Handroanthus* seedlings dropped its leaves in the dry season, a very typical pattern for this species, however, the R_L decreased 56.3% more for seedlings in the control plots and the final biomass was 44.5% higher for trenched seedlings (Table 2). *Bertholletia* seedlings height growth and leaf number did not increase under treatment conditions; however, final biomass was 54.7% higher for trenched seedlings (Table 2).

Root competition affected functional traits differently and was species-specific. Leaf area was smaller for *Hevea* and *Handroanthus* in control plots compared to treatment plots (Table 3). Leaf mass fraction (LMF) was higher only for *Handroanthus* seedlings in treatment plots (Table 3); Leaf mass per area (LMA) and stem mass per stem height were higher in treatment plots only for *Bertholletia.*

For all species there was no difference in the intensity of biotic disturbances between treatment and control plots ($t < -0.9$ for all comparisons) or between biotic disturbances in trenched plots and vegetation cover ($t < 1.7$ and $P > 0.9$ for all comparisons).

ROLE OF ROOT COMPETITION ALONG THE SUITABILITY OF THE SITES

Competition indexes varied from negative to positive for all species. Despite the fact that C_{imp} was ranked according to our expectation, there was no difference between the intensity (C_{int}) or the importance of competition (C_{imp}) among species (LRT for both analyses: $\chi^2 < 2.23$, $P >$ 0.3; Fig. 1). However, mean *Handroanthus* C_{imp} and C_{int} were both different from zero (C_{imp}: $t = -3.5$, C_{int}: $t = -2.4$; Fig. 1) and both indexes were correlated for all three species ($r = 0.9$; $P <$

0.0001), but there was greater variation at the extreme ends of the relationship. We do not report the analyses of the relationship of C_{int} with the site suitability indexes because they did not converge. However, it should be observed that the negative values of C_{int} are much more variable. C_{imp} was negatively correlated with the specific site suitability index for all species, demonstrating that the negative effects of root competition are higher when site conditions are favorable for survival and growth for all species (Fig. 2). When the analysis included all data, we found that the slopes of the relationship between C_{imp} and site-suitability index varied among species with *Bertholletia*, showing a less pronounced slope (LRT: $\chi^2 = 6.91$, $P = 0.03$; Fig. 2). However, when we removed five points which represented seedling death caused by mammals in both trenched and control plots, the difference was not sustained (LRT: $\chi^2 = 2.98$, $P = 0.23$).

The site-suitability indexes were not correlated when compared among species ($P > 0.1$ for all comparisons), showing that the favorable site for one species to develop may not be favorable for all species. Table 4 illustrates the mean and variance of the environmental variables measured. The fitted linear models with the environmental variables explaining site-suitability index of each species explained 52% of the variation of *Hevea*, 30% for *Handroanthus* and 55% for *Bertholletia* (Fig. 3). Biotic disturbance and canopy openness explained most of the variation observed for *Hevea* (biotic disturbance: $F_{1,24} = 17.05$, $P < 0.0001$, canopy openness: $F_{1,24} = 5.08$, $P = 0.034$). Interestingly, the productivity of the light-loving *Handroanthus* was only affected by potassium availability (Potassium: $\text{F}_{1,24} = 4.74$, $P = 0.039$). *Bertholletia* was most affected by biotic disturbances, a combination of intense herbivory caused by insects, and seed consumption by mammals (biotic disturbance: $\text{F}_{1,24} = 23.25$, $P < 0.0001$).

Discussion

The first of our hypothesis, that *Bertholletia* (the large-seeded specie) would experience less competition, was not confirmed. Despite the fact that the mean C_{imp} was ranked according to our expectation, there was no difference in the response to root competition with the resident vegetation. This pattern contrasts with previous studies that show that the most stress-tolerant species experience more competition than less tolerant species (Choler *et al.* 2001, Liancourt, Michalet & Callaway 2005). The second hypothesis that the relationship between site suitability and C_{imp} would differ among species was also not confirmed when we removed five points of *Bertholletia*'s data that pushed the intercept down. Our last hypothesis, that the intensity of biotic disturbances would be inversely related to the understorey cover, was also not confirmed.

Competition with the resident vegetation may be more important at sites where individual seedlings can perform better. The results gathered in this study corroborate the predictions of the stress-gradient hypothesis (SGH), in which competition in stressful or extreme conditions is considered less important; however, the pattern found in this study is not caused by a community-driven stress gradient because site suitability indexes were not correlated among species implying that species were affected by distinct factors. This pattern suggests that a site where one species can perform well is not necessarily a good site for other species because the main causes of mortality or reduced growth were distinct among species (Table 1, Fig. 3).

CONSEQUENCES OF ROOT COMPETITION

All species modified at least one functional trait in response to trenching in a way to maximize light capture. Higher total plant leaf area, reported by seedlings of *Hevea* and

Handroanthus, is associated with increased light capture area, while the higher LMA observed for *Bertholletia*'s seedlings is likely to increase leaf longevity, increasing total light capture per leaf (Valladares & Niinemets 2008). Higher LMA also improves protection against leaf consumers and the higher stem mass of *Bertholletia*'s seedlings in trenched plots is probably related to an increase in carbohydrate storage in the stem, implying an increase in the ability of the seedlings to survive in the shade or to re-sprout after damage (Myers & Katajima 2007).

Goldberg & Novoplansky (1997) hypothesized that lack of nutrients in a habitat mostly affects plant growth while a lack of water affects plant survival. If this hypothesis is correct and general, our results support reports that advocate that root competition in forests is caused by nutrient foraging and is not due to reduction in water availability (Coomes & Grubb 2000, Lewis & Tanner 2000, Kueffer *et al*. 2007, Tanner & Barberis 2007). The treatment did not increased mortality for any species in this study; in most of cases, mortality was associated with biotic disturbances (Table 1). However, seedlings of *Bertholletia* and *Handroanthus* achieved a higher final biomass in trenched plots (Table 2). In this study, these results were mostly attributed to leaf loss during the dry season by *Handroanthus* seedlings in trenched plots and increased stem mass and LMA of *Bertholletia* seedlings in trenched plots (Table 2 and Table 3). Although reduced leaf area or increased leaf abscission in control plots for *Hevea* and *Handroanthus* are evidence of possible competition for water, reduced nutrients may also cause such responses (Fredeen, Rao & Terry 1989).

INTERACTIONS ALONG THE ENVIRONMENTAL GRADIENT

We found that the three species similarly experienced the effects of root competition (based on C_{int} and C_{imp}). This similarity is likely related to the variation of the responses of all three species, which varied from facilitative to intense competition. In addition, facilitation caused by the understorey neighboring vegetation occurred only in locations where a site was more limiting to survival and growth, as the indicated by a low site suitability index. Site suitability for *Hevea* and *Bertholletia* was primarily affected by biotic damage (Fig. 3). The apparent lack of competition between understorey plants (Wright 2002, Svenning, Fabbro & Wright 2008) may contribute to increasing the benefit of a seedling can experience when co-occurring with other understorey plants from different species. Several studies reported facilitation from the neighboring vegetation through reduction of biotic damage in early successional communities (Zanini, Ganade & Hübel 2006, Brooker *et al*. 2006, Smit *et al*. 2007), but this type of interaction with understorey plants was not reported. When the probability of damage is high for a given species, understorey vegetation may provide better or safer sites by reducing seedling exposure, since individuals that are less conspicuous are less likely to be consumed. However, we did not find a difference in biotic damage among control and treatment plots or a reduction of damage when understorey cover increased for any species. Nevertheless, for *Hevea* and *Bertholletia* facilitation more commonly occurred when biotic damage was high in plants located in trenched plots (Fig. 4), which is an evidence that positive interactions may be related to a reduction in the herbivory experienced by seedlings. Under natural conditions with different herbivore species associated with different plant species, facilitation by the neighboring vegetation via herbivory reduction may not depend only on the role of understorey vegetation cover, but also, on the attractiveness (or palatability) of the neighboring vegetation to a specific herbivore. Svenning and collaborators (2008) found that heterogeneric seedlings that were planted together performed better than pairs of congeneric species. This result was attributed to a possible higher attractiveness to enemies by congeneric pairs, however, it could also reflect positive interactions among seedlings that are consumed by different herbivores.

Although herbivory was included in the original version of the SGH as a linear increase of facilitation at high herbivore pressures (Bertness & Callaway 1994), recent studies found a hump-shaped relation of herbivores pressure and facilitation (Smit *et al*. 2007). These authors suggested that in environments with high herbivore pressure, facilitation declines because the less palatable species (benefactors) were also damaged and facilitation was more common at intermediate herbivore pressure situation. We probably did not find such a relationship because under the natural conditions of the sites, the seedlings of the three study species were affected by different consumers. In the study of Smit and collaborators (2007), damage was made by one generalist herbivore and the intensity of herbivory in the high herbivore pressure treatment may be much higher than those observed in our secondary forests.

Hevea's seedlings were also affect by light availability; this was an expected result since it is considered a light-lover species. When light availability was higher and biotic damage low, the importance of competition increased (Figs 4a and 4b). This is in accordance with the results reported by Lewis and Tanner (2000), which showed that seedlings under high light conditions were more affected by trenching. We do not have a causal explanation for the positive effect on *Handroanthus* performance caused by the neighboring vegetation because the environmental variables that we measured explained a small fraction of *Handroanthus* site suitability index (Fig. 3). Nevertheless, potassium availability influenced *Handroanthus* performance when root competition was absent (Fig. 3), suggesting that this resource is limiting for *Handroanthus* seedlings. Such observation is in accordance with the already reported results that small seeded species is more responsive to increased availability of soil resource (Milberg, Perez-Fernandez & Lamont 1998). Actually, competition was more important for this species when potassium availability was higher (Fig. 4d). According to the resource supply and demand hypothesis, competition should be reduced when the supply of a limiting resource increases and the demand by the neighboring vegetation do not change (Davis, Wrage & Reich 1998). Despite the fact that potassium availability varied threefold among experimental blocks (Table 4), it is possible that this increase is far from exceeding the demand by the neighboring vegetation. Or it is quite probable that the potassium foraging is more intense in patches of soil where the availability of this resource is higher (Schenk 2006). If the availability of soil resources is inherently down to levels that do not exceed the demand of the neighboring vegetation, it is possible that competition intensity will be constant for any species and its importance will depend on the relative impact of all other factors. *Bertholletia*'s seedling mortality and growth were not affected by resource availability that we measured; this may be related to higher carbohydrate reserves. However, since the *Bertholletia*'s response to trenching was similarly to *Hevea* and *Handroanthus* responses, it is possible that root competition with the established vegetation also occurs for other mineral nutrients that we did not measured.

CAVEATS

We conducted the experiment in secondary forests with different ages to assess a high variation of light availability; however, there was little difference in light availability among secondary age classes (data not shown). A study conducted in a nearby secondary forest dominated by *Cecropia* spp. reported that intermediate levels of canopy removal had the greatest influence on growth of seedlings and saplings (Mesquita 2000). It is possible that light availability in an undisturbed forest would be closer to plants light compensation point and, and if we included undisturbed forests sites in our study, the role of light availability would be higher. Also, despite the fact that the seed masses of the study species varied 100-

fold, seed mass can vary from less than 0.01 g to more than 150 g in these forests and our experiment was restricted to only three species. Even if the benefits of a large seed are more prominent in the first year after germination (Coomes & Grubb 2003), some of the inconclusive results could be due to the short time frame of this study (10 months). Further studies with different species characteristic of the shaded environment are recommended to test if the same results found in this study are robust.

CONCLUSIONS

Our results highlight that the importance of root competition to seedling survival and growth in Central Amazonian terra firme forests depends on the suitability of a site for an individual seedling. Observing no differences in measured performance with and without competition does not mean absence of competition because the intensity and importance of competition may vary along environmental gradients. We found that for all three study species, root competition importance at the individual level is higher when seedlings can develop better, in accordance with the SGH (Bertness & Callaway 1994). *Handroanthus* performance was affected by potassium availability in the soil and in places where the availability of this resource is higher, the importance of competition increased. Facilitation occurred for all three species and is possibly driven by interaction with the understorey vegetation. For individuals of *Hevea* and *Bertholletia* the primary cause of reduced performance was biotic disturbances and when individuals in trenched plots experienced higher damage by animals, facilitation was more common. If species are consumed by selective herbivores, the attractiveness of the neighborhood should influence either herbivore attraction or reduction. The importance of this type of interaction between seedling performance and the understorey vegetation of tropical forests should be further investigated.

Table 1. Categories of the discernible causes of mortality of the seedlings in this study. Numbers in parentheses are the proportion of total seedling death for each species.

Causes of mortality	*Hevea*	*Handroanthus*	*Bertholletia*
Biotic disturbances	14 (0.78)	4 (0.57)	19 (0.76)
Cutted/Pulled	2 (0.11)	4 (0.57)	0
Apex's herbivory	12 (0.67)	0	0
Seed consumption	0	0	19 (0.76)
Desiccation	1 (0.06)	1 (0.14)	4 (0.16)
Unknown	3 (0.16)	2 (0.28)	2 (0.08)
Total	18 (0.15)	7 (0.06)	25 (0.21)

Table 2. Effect of trenching on the relative growth in height (R_H [$cm.cm^{-1}.month^{-1}$]), relative growth in leaf number (R_L [$number.number^{-1}.month^{-1}$]) and final biomass (g) of the living seedlings. Mean estimated values from linear mixed-effect model from trenched (T) and control (C) are shown. Significant effects are shown in bold.

	T	C	P_{MCMC}
Hevea			
R_H	0.04	0.03	0.2344
R_L	-0.02	0.01	0.4040
Mass	3.66	3.11	0.1764
Handroanthus			
R_H	0.03	0.02	0.2604
R_L	-0.02	-0.07	**0.0008**
Mass	0.09	0.06	**0.0122**
Bertholletia			
R_H	0.05	0.05	0.9314
R_L	0.06	0.05	0.3280
Mass	2.75	2.07	**0.0260**

Table 3. Trenching effect on leaf area (A [cm^2]), leaf mass per area (LMA [mg/cm^2]), leaf mass fraction (LMF [g/g]) and etiolation (g/cm) of the living seedlings. Mean estimated values of the linear mixed model for trenched (T) and control (C) are shown. Significant effects are in bold.

	T	C	P_{MCMC}
Hevea			
Log(A)	4.58	4.17	**0.0062**
Log(LMA)	3.25	3.30	0.5906
LMF	0.02	0.03	0.2390
Etiolation	0.46	0.44	0.7540
Handroanthus			
Log(A)	1.80	1.54	**0.0418**
Log(LMA)	3.13	3.14	0.9282
LMF	0.47	0.39	**0.0396**
Etiolation	0.06	0.05	0.5090
Bertholletia			
Log(A)	4.14	3.98	0.1370
Log(LMA)	4.13	4.07	**0.0290**
LMF	0.62	0.61	0.7052
Etiolation	0.42	0.33	**0.0308**

Table 4. Mean and range of the measured environmental variables on the experimental blocks.

Environmental variables	Mean	Range
Nitrogen (%)	0.15	0.08 - 0.24
Phosphorus (mg/kg)	0.78	0.12 - 1.40
Potassium (mg/kg)	26.85	13 - 40
pH	4.27	3.9 - 4.9
Canopy openess (%)	12.63	9.22 - 15.2
Biotic damage (%)		
Hevea	29.17	0.0 - 90.0
Handroanthus	11.27	0.0 - 52.1
Bertholletia	28.29	0.0 - 90.0

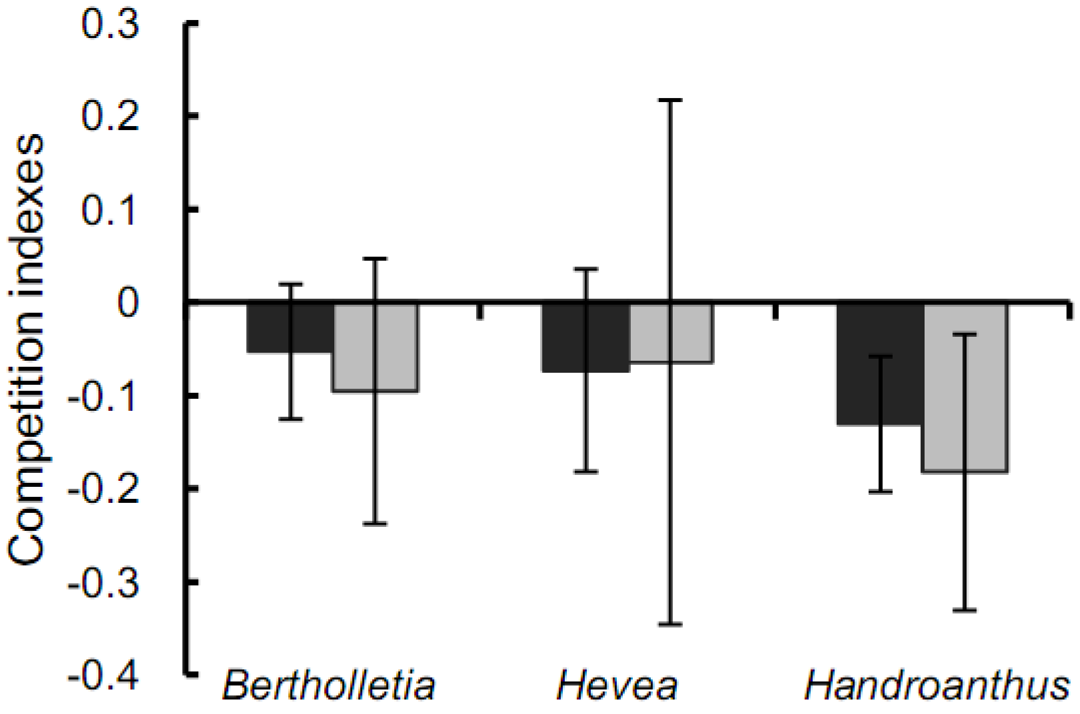

Fig. 1 Competition importance index (dark gray bars) and competition intensity index (light gray bars) for all species. Bars represents approximate 95% of confidence intervals (1.96*SE).

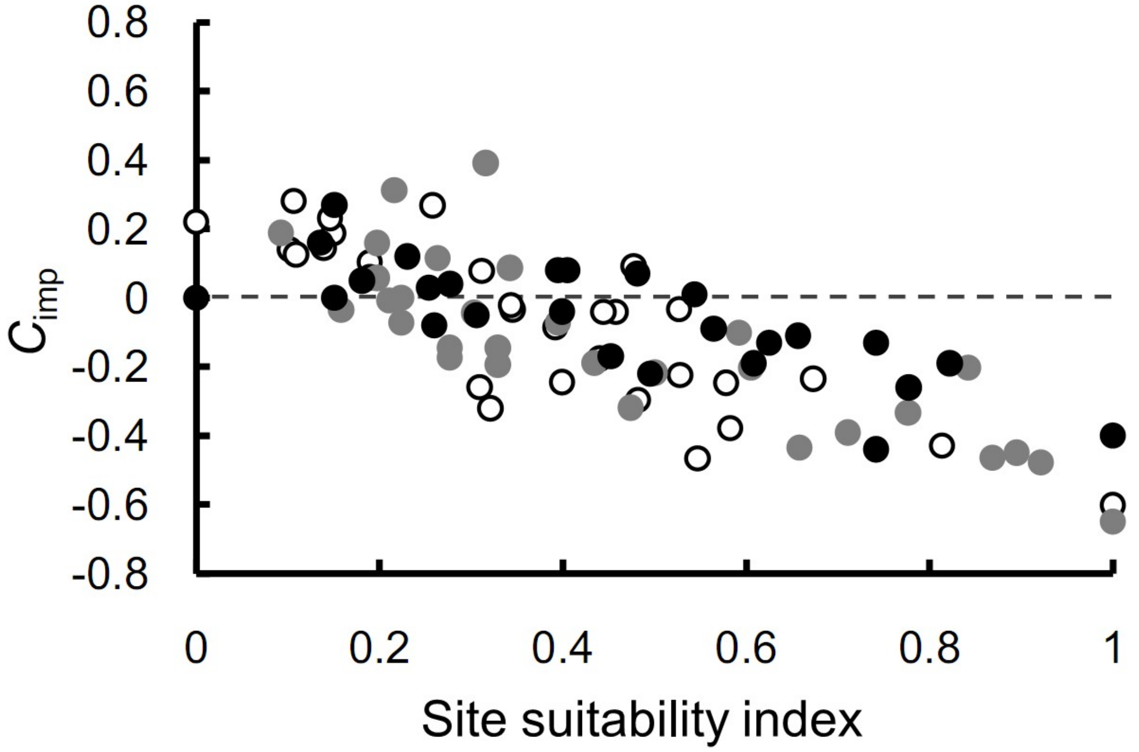

Fig. 2 Relationship of specifics site suitability indexes and competition importance. Open circles represent *Hevea*, gray circles represent *Handroanthus* and black circles and represent *Bertholletia*. The hatched line indicate neutral effect of the treatment.

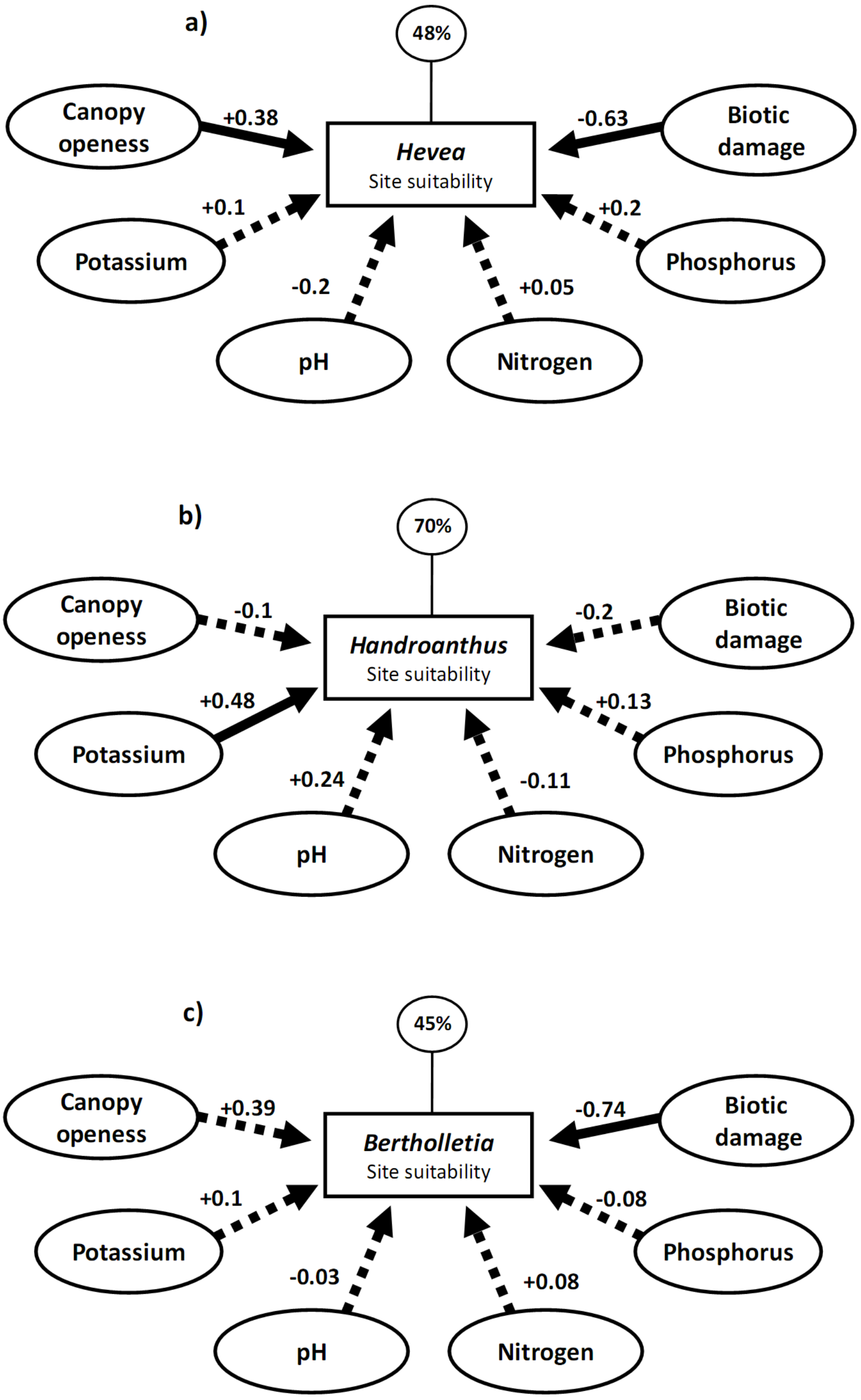

Fig. 3 Relationship of the environmental variables with site suitability index for (a) *Hevea*, (b) *Handroanthus* and (c) *Bertholletia*. Solid arrows indicate statistical significance of the relations and numbers indicate the slope of *z* transformed variables. Percentages inside the circle indicate the residual variance.

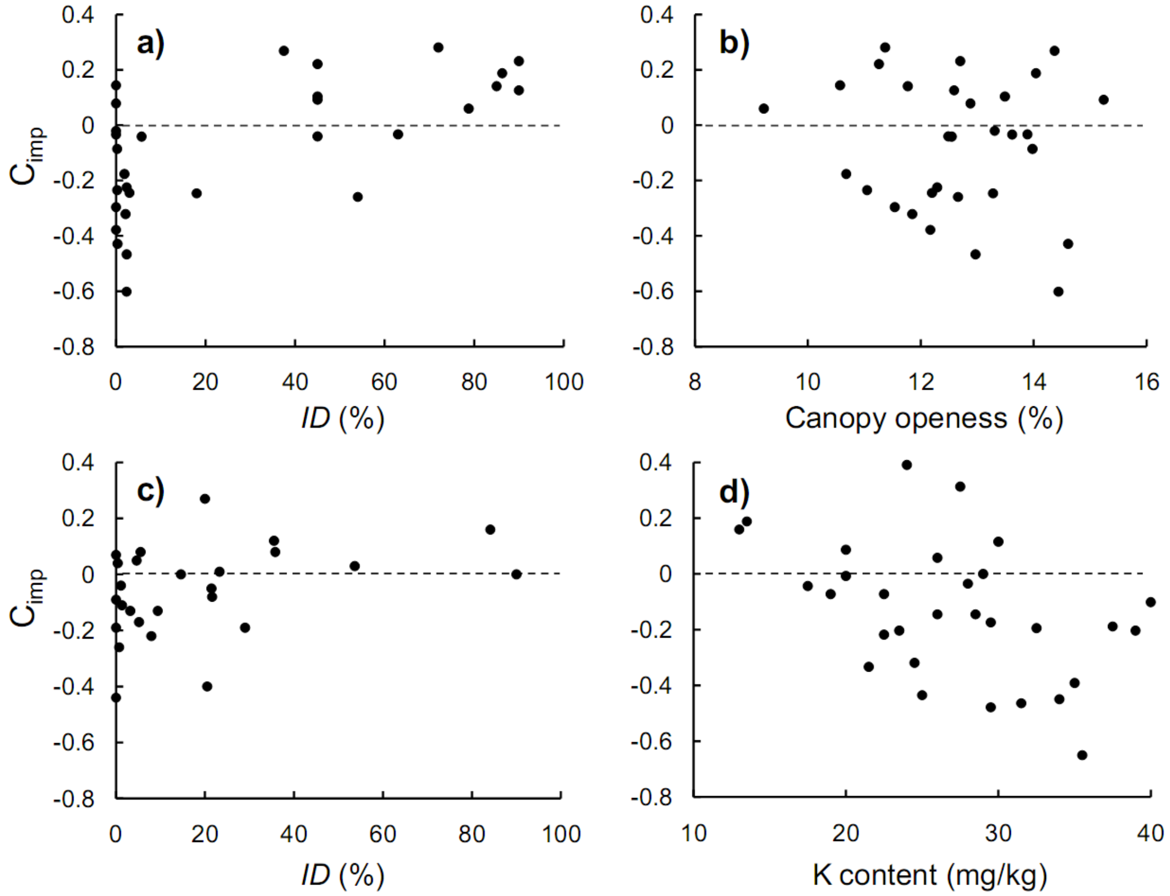

Fig. 4 Relationship between C_{imp} and the environmental variable that significantly affected species' site suitability indexes. (a) *Hevea* and index of damage (*ID*) by animals; (b) *Hevea* and canopy openness; (c) *Bertholletia* and *ID*; and (d) *Handroanthus* and potassium (K) content in the soil. The hatched line indicate neutral effect of the treatment.

CONCLUSÃO GERAL

Nossos resultados demonstraram que em florestas de terra firme na Amazônia Central, a importância da competição de raízes na mortalidade e crescimento depende da intensidade de estresse experimentada por uma determinada plântula. Não encontrar diferença em alguma medida de performance com e sem competição não significa ausência de competição porque a intensidade e a importância da competição variam ao longo de gradientes ambientais. Nós encontramos que para todas as espécies estudadas, a competição com a vegetação residente foi maior onde as plântulas conseguiam se desenvolver melhor, corroborando a hipótese do gradiente de estresse. Para plântulas de *Handroanthus*, a disponibilidade de Potássio no solo foi a única variável que influenciou seu desempenho na ausência de competição e onde a disponibilidade desse recurso era maior, a importância da competição também aumentou. Facilitação ocorreu para as três espécies somente nas partes mais severas do gradiente e é possivelmente causada por uma interação com a vegetação do sub-bosque. Para plântulas de *Hevea* e *Bertholletia*, a principal causa de desempenho reduzido foi dano causado por herbívoros e quando indivíduos nas parcelas sem competição sofreram danos acentuados, a facilitação foi mais evidente. Como as espécies foram consumidas por diferentes herbívoros, a palatabilidade das plantas circundantes pode influenciar a atração ou redução de herbívoros específicos. A importância desde tipo de interação entre plântulas e a vegetação circundante do sub-bosque devem ser investigadas em futuros estudos.

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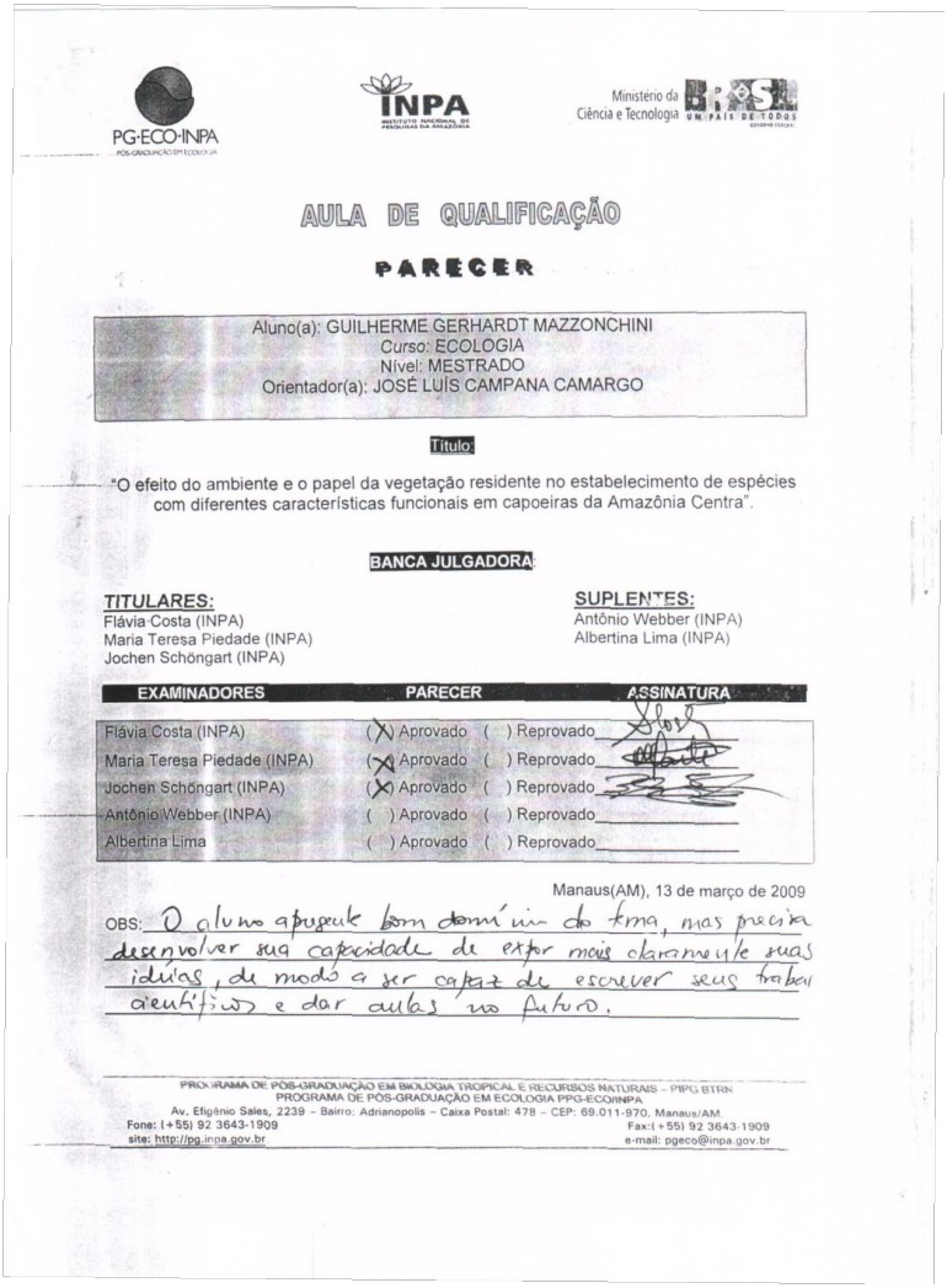
APÊNDICE 1. Parecer da aula de qualificação.



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AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): GUILHERME GERHARDT MAZZONCHINI
Curso: ECOLOGIA
Nível: MESTRADO
Orientador(a): JOSÉ LUÍS CAMPANA CAMARGO

Título:

"O efeito do ambiente e o papel da vegetação residente no estabelecimento de espécies com diferentes características funcionais em capoeiras da Amazônia Centra".

BANCA JULGADORA:

TITULARES:
Flávia Costa (INPA)
Maria Teresa Piedade (INPA)
Jochen Schöngart (INPA)

SUPLENTES:
Antônio Webber (INPA)
Albertina Lima (INPA)

EXAMINADORES	PARECER		ASSINATURA
Flávia Costa (INPA)	(X) Aprovado	( ) Reprovado	
Maria Teresa Piedade (INPA)	(X) Aprovado	( ) Reprovado	
Jochen Schöngart (INPA)	(X) Aprovado	( ) Reprovado	
Antônio Webber (INPA)	( ) Aprovado	( ) Reprovado	
Albertina Lima	( ) Aprovado	( ) Reprovado	

Manaus(AM), 13 de março de 2009

OBS: O aluno apresenta bom domínio do tema, mas precisa desenvolver sua capacidade de expor mais claramente suas idéias, de modo a ser capaz de escrever seus trabal científicos e dar aulas no futuro.

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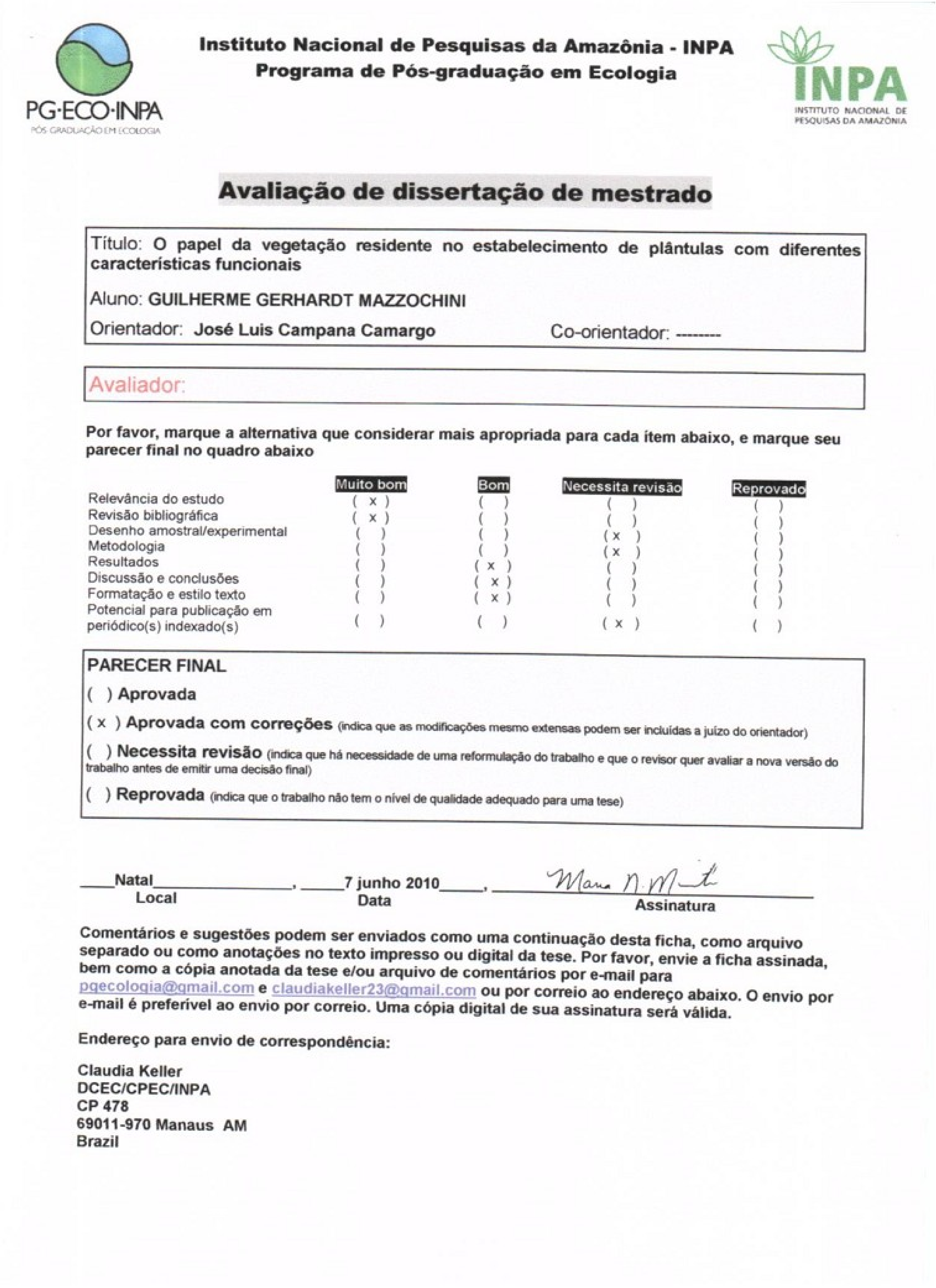
Fone: (+55) 92 3643-1909 Fax:(+55) 92 3643-1909
site: http://pg.inpa.gov.br e-mail: pgeco@inpa.gov.br

APÊNDICE 2. Avaliação da dissertação por Maria Miriti.



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Programa de Pós-graduação em Ecologia

Avaliação de dissertação de mestrado

Título: **O papel da vegetação residente no estabelecimento de plântulas com diferentes características funcionais**

Aluno: **GUILHERME GERHARDT MAZZOCHINI**

Orientador: **José Luis Campana Camargo** Co-orientador: --------

Avaliador:

Por favor, marque a alternativa que considerar mais apropriada para cada ítem abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(x)	( )	( )	( )
Revisão bibliográfica	(x)	( )	( )	( )
Desenho amostral/experimental	( )	( )	(x)	( )
Metodologia	( )	( )	(x)	( )
Resultados	( )	(x)	( )	( )
Discussão e conclusões	( )	(x)	( )	( )
Formatação e estilo texto	( )	(x)	( )	( )
Potencial para publicação em periódico(s) indexado(s)	( )	( )	(x)	( )

PARECER FINAL

( ) **Aprovada**

(x) **Aprovada com correções** (indica que as modificações mesmo extensas podem ser incluídas a juízo do orientador)

( ) **Necessita revisão** (indica que há necessidade de uma reformulação do trabalho e que o revisor quer avaliar a nova versão do trabalho antes de emitir uma decisão final)

( ) **Reprovada** (indica que o trabalho não tem o nível de qualidade adequado para uma tese)

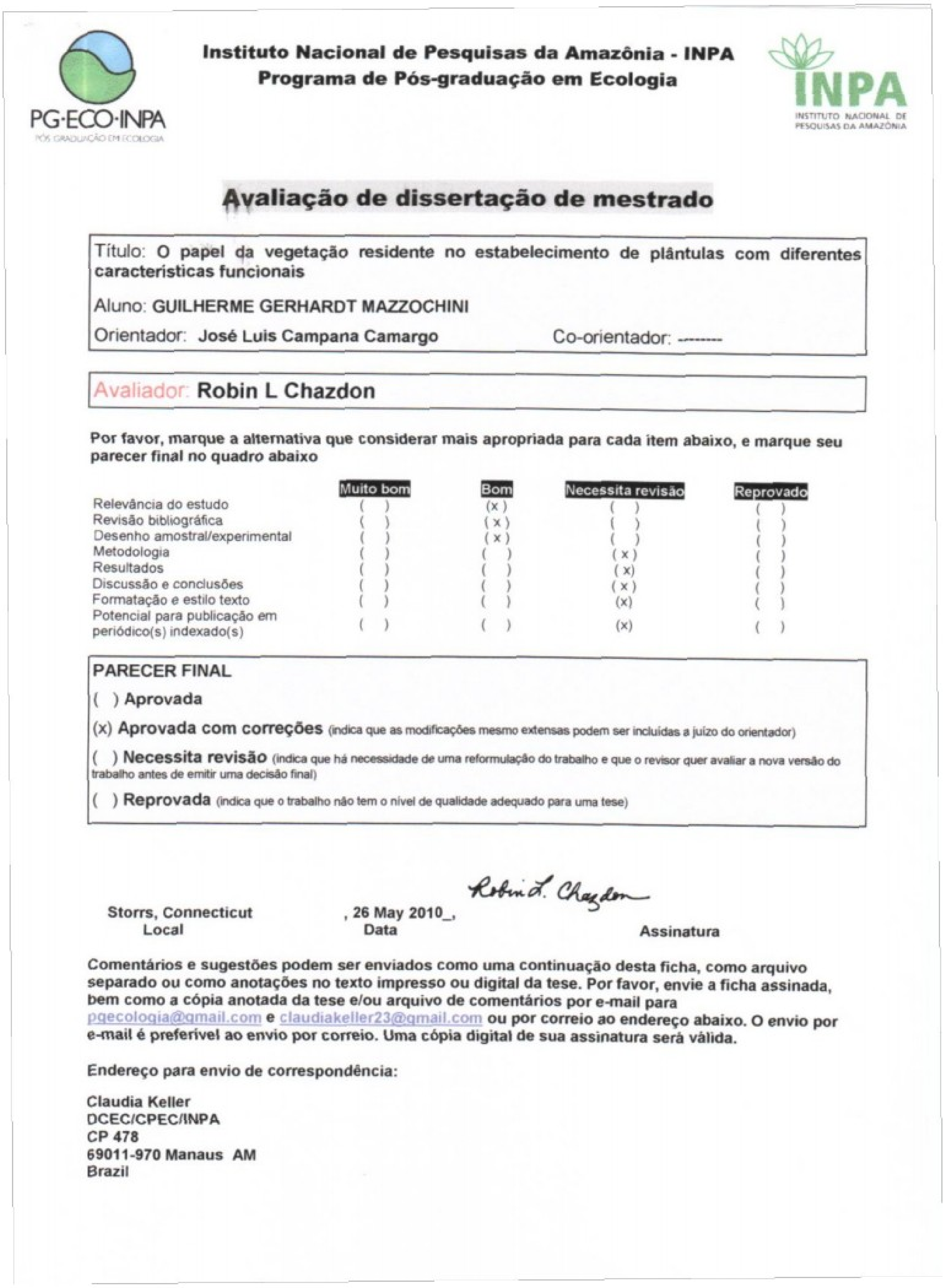
____Natal________________, _____7 junho 2010_____, ______Maria M. M______
Local Data Assinatura

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

Endereço para envio de correspondência:

Claudia Keller
DCEC/CPEC/INPA
CP 478
69011-970 Manaus AM
Brazil

APÊNDICE 3. Avaliação da dissertação por Robin Chazdon.



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Avaliação de dissertação de mestrado

Título: **O papel da vegetação residente no estabelecimento de plântulas com diferentes características funcionais**

Aluno: **GUILHERME GERHARDT MAZZOCHINI**

Orientador: **José Luis Campana Camargo** Co-orientador: --------

Avaliador: **Robin L Chazdon**

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	( )	(x)	( )	( )
Revisão bibliográfica	( )	(x)	( )	( )
Desenho amostral/experimental	( )	(x)	( )	( )
Metodologia	( )	( )	(x)	( )
Resultados	( )	( )	(x)	( )
Discussão e conclusões	( )	( )	(x)	( )
Formatação e estilo texto	( )	( )	(x)	( )
Potencial para publicação em periódico(s) indexado(s)	( )	( )	(x)	( )

PARECER FINAL

( ) **Aprovada**

(x) **Aprovada com correções** (indica que as modificações mesmo extensas podem ser incluídas a juízo do orientador)

( ) **Necessita revisão** (indica que há necessidade de uma reformulação do trabalho e que o revisor quer avaliar a nova versão do trabalho antes de emitir uma decisão final)

( ) **Reprovada** (indica que o trabalho não tem o nível de qualidade adequado para uma tese)

Robin L. Chazdon

Storrs, Connecticut **, 26 May 2010_,**
Local **Data** **Assinatura**

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

Endereço para envio de correspondência:

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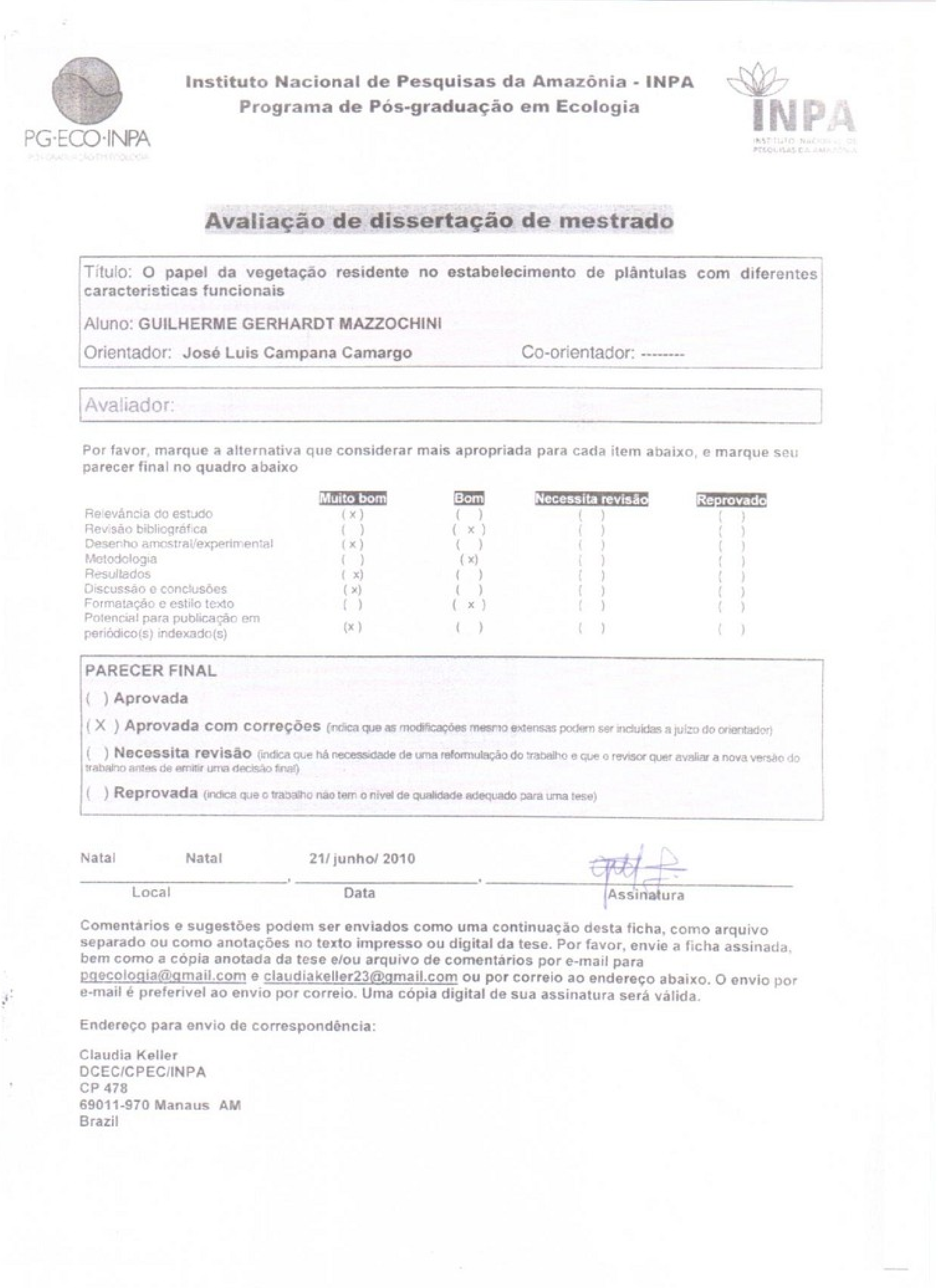
APÊNDICE 4. Avaliação da dissertação por Gislene Ganade.



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Avaliação de dissertação de mestrado

Título: **O papel da vegetação residente no estabelecimento de plântulas com diferentes caracteristicas funcionais**

Aluno: **GUILHERME GERHARDT MAZZOCHINI**

Orientador: **José Luis Campana Camargo** Co-orientador: --------

Avaliador:

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	**Bom**	**Necessita revisão**	**Reprovado**
Relevância do estudo	(x)	( )	( )	( )
Revisão bibliográfica	( )	(x)	( )	( )
Desenho amostral/experimental	(x)	( )	( )	( )
Metodologia	( )	(x)	( )	( )
Resultados	(x)	( )	( )	( )
Discussão e conclusões	(x)	( )	( )	( )
Formatação e estilo texto	( )	(x)	( )	( )
Potencial para publicação em periódico(s) indexado(s)	(x)	( )	( )	( )

PARECER FINAL

( ) **Aprovada**

(X) **Aprovada com correções** (indica que as modificações mesmo extensas podem ser incluidas a juízo do orientador)

( ) **Necessita revisão** (indica que há necessidade de uma reformulação do trabalho e que o revisor quer avaliar a nova versão do trabalho antes de emitir uma decisão final)

( ) **Reprovada** (indica que o trabalho não tem o nível de qualidade adequado para uma tese)

Natal Natal, 21/ junho/ 2010,
Local Data Assinatura

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

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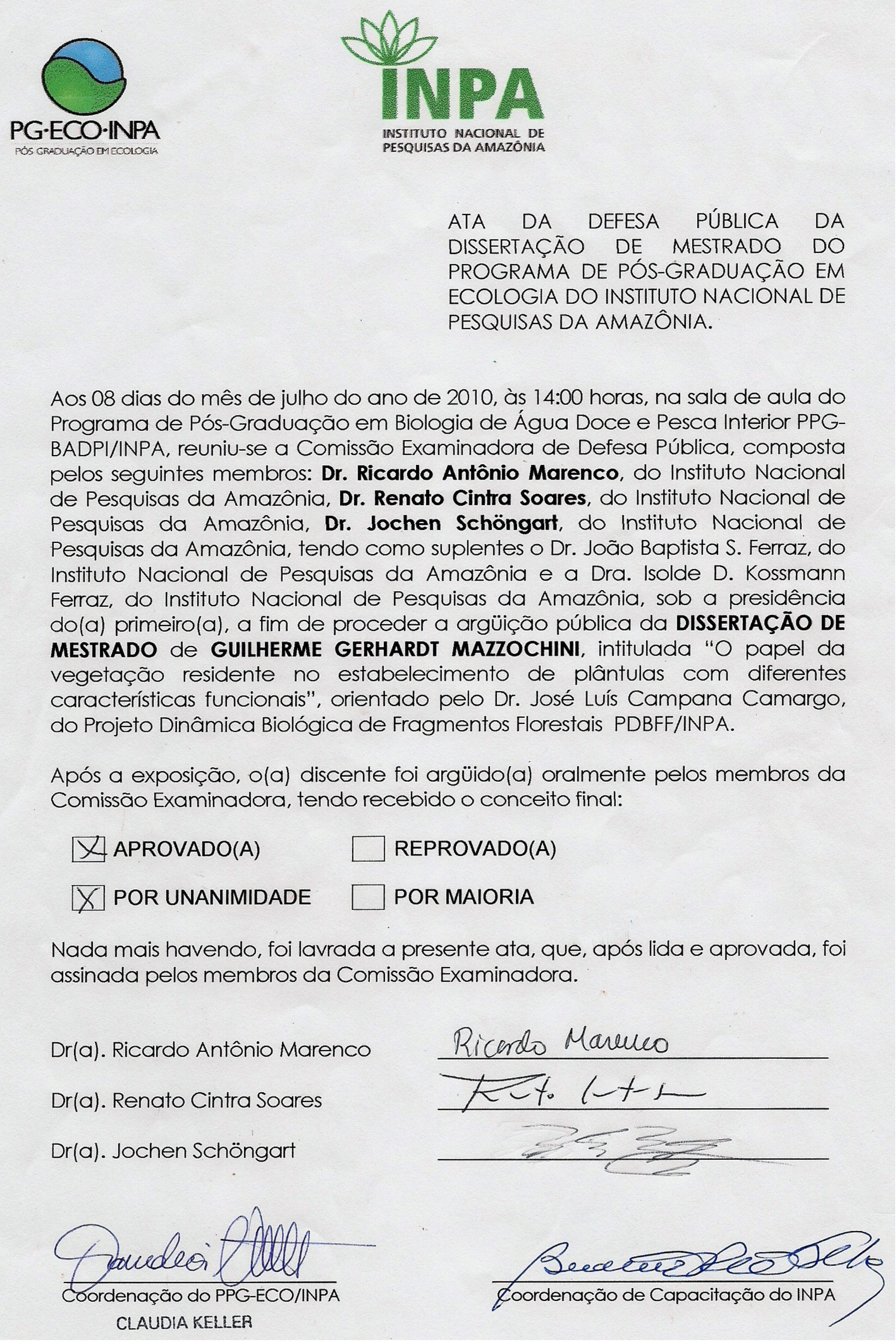
APÊNDICE 5. Ata da defesa de mestrado.



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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 08 dias do mês de julho do ano de 2010, às 14:00 horas, na sala de aula do Programa de Pós-Graduação em Biologia de Água Doce e Pesca Interior PPG-BADPI/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: **Dr. Ricardo Antônio Marenco**, do Instituto Nacional de Pesquisas da Amazônia, **Dr. Renato Cintra Soares**, do Instituto Nacional de Pesquisas da Amazônia, **Dr. Jochen Schöngart**, do Instituto Nacional de Pesquisas da Amazônia, tendo como suplentes o Dr. João Baptista S. Ferraz, do Instituto Nacional de Pesquisas da Amazônia e a Dra. Isolde D. Kossmann Ferraz, do Instituto Nacional de Pesquisas da Amazônia, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública da **DISSERTAÇÃO DE MESTRADO** de **GUILHERME GERHARDT MAZZOCHINI**, intitulada "O papel da vegetação residente no estabelecimento de plântulas com diferentes características funcionais", orientado pelo Dr. José Luís Campana Camargo, do Projeto Dinâmica Biológica de Fragmentos Florestais PDBFF/INPA.

Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADO(A) ☐ REPROVADO(A)

☒ POR UNANIMIDADE ☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Dr(a). Ricardo Antônio Marenco Ricardo Marenco
Dr(a). Renato Cintra Soares
Dr(a). Jochen Schöngart

Coordenação do PPG-ECO/INPA
CLAUDIA KELLER

Coordenação de Capacitação do INPA