

**INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA  
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**Potencial Reprodutivo e Regenerativo de Espécies Arbóreas em Florestas  
Secundárias na Amazônia Central**

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**Manaus, Amazonas  
Fevereiro, 2013**

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**Orientador: Dr. Henrique E. M. Nascimento**  
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**Sinopse:**

Verificou-se a importância das características reprodutivas e condições de micro-sítio sobre o recrutamento e estabelecimentos de espécies arbóreas em floresta secundária na Amazônia Central. Aspectos sobre a relação das características de frutos e sementes, remoção de serapilheira, revolvimento do solo e posição topográfica com o potencial regenerativo do banco de sementes no solo foram avaliados.

**Palavras chave:** Banco de sementes, clareiras artificiais, fenologia reprodutiva, número e peso de frutos, número e peso de sementes, pastagem abandonada, remoção de serapilheira, revolvimento do solo, recrutamento de plântulas.

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## RESUMO GERAL

Este estudo teve como objetivos principais: (1) Avaliar a relação entre peso de sementes, número de sementes, peso de frutos, número de frutos e número de sementes por fruto baseando-se na premissa de um modelo conceitual denominado de “seed packaging”; (2) Avaliar as relações das variáveis de sementes e frutos (peso e número), duração da frutificação e porcentagem de germinação com a densidade de plântulas e indivíduos adultos; e (3) Avaliar os efeitos da topografia e das condições de micro-sítio sobre o banco de semente e o sucesso no estabelecimento de espécies arbóreas. O local de estudo é a área experimental do Projeto Dinâmica Biológica de Fragmento de Florestais, localizado a 80 km ao norte da cidade de Manaus, Amazonas. Para os objetivos 1 e 2, durante cerca de três anos, o acompanhamento fenológico foi realizado para 12 espécies pioneiras, para as quais a floração e frutificação foram monitoradas mensalmente. O peso de sementes e frutos, número de sementes e frutos e a taxa de germinação foram determinados para essas 12 espécies pioneiras. Foi estabelecida uma amostragem baseada em parcelas para estimar a densidade de plântulas e adultos destas espécies se estabelecendo naturalmente. Para o objetivo 3, 21 clareiras criadas artificialmente em áreas de florestas secundárias com 20 anos de idade foram estabelecidas em três posições topográficas (platô, vertente e baixio), onde tratamentos de serrapilheira (com e sem remoção de serrapilheira) e solo (com e sem revolvimento do solo) foram alocados em quatro sub-parcelas no centro de cada clareira. Mesmo fazendo parte de uma mesma guilda ecológica, as 12 espécies estudadas mostraram alta variação tanto nos padrões fenológicos, variando de padrão contínuo até supra-anual, quanto nas características reprodutivas, em que o peso e número de sementes e frutos variaram amplamente entre as espécies. O número de sementes foi relacionado parcialmente com o peso de sementes, porém quando se incorpora no mesmo modelo o peso e o número de frutos, o número de sementes foi quase completamente explicado por estas variáveis. O número de sementes por fruto foi correlacionado positivamente com o peso de frutos e número de sementes e negativamente relacionado com o peso de sementes e o número de frutos. A densidade de plântulas e adultos das 12 espécies pioneiras objetos deste estudo foi melhor explicada pelo peso e número de frutos. Após 20 anos de regeneração natural em áreas de pastagem abandonada, o banco de sementes ainda é dominado por poucas espécies arbóreas típicas de sucessão inicial. Houve um forte efeito positivo da remoção de serrapilheira e um menor efeito positivo do revolvimento de solo sobre o recrutamento de plântulas. O recrutamento e crescimento inicial



também foram favorecidos em áreas de baixio, provavelmente devido à maior disponibilidade de água e maior disponibilidade de alguns nutrientes limitantes ao crescimento das plantas, como é o caso do fosforo. Os resultados deste estudo fornecem importantes ferramentas para o manejo de florestas secundárias, em que, apesar da baixa diversidade de espécies, o manejo do banco de sementes através da remoção de serrapilheira acoplado com o revolvimento do solo são ferramentas indispensáveis para ativar o banco de semente e acelerar a emergência de plântulas no estágio inicial de vida das plantas arbóreas.

## **Reproductive and Regenerative Potential of Tree Species in Central Amazonia Secondary Forests**

### **GENERAL ABSTRACT**

The main objectives of this study were to: (1) evaluate the relationship between seed weight, seed number, fruit weight, fruit number, and seed number per fruit using a conceptual model termed "seed packaging"; (2) evaluate the relationship of seed and fruit variables (weight and number), duration of fruiting and germination with seedling and adult tree density; and (3) evaluate the effects of topography and micro-site conditions on the seed bank and establishment of tree species. The study was conducted in the experimental area of the Biological Dynamics of Forest Fragment Project, located 80 km North of Manaus, Amazonas. For objectives 1 and 2, flowering and fruiting phenology were monitored monthly among 12 pioneer species over three years. The weight of seeds and fruits, number of fruits and seeds and germination rate were determined for each species. The density of seedlings and adult individuals was estimated using sampling plots. For objective 3, 21 artificially-created gaps in 20-year old secondary forests were established in three topographic levels (plateau, slope and bottomland), where litter (with and without litter removal) and soil treatments (soil turned and soil unturned) were allocated in four sub-plots at the center of each gap. Although the 12 pioneer species belonged to the same ecological guild, there was high variation in both phenological patterns (ranging from continuous to supra-annual) and reproductive traits, for which the weight and number of seeds and fruits varied widely among species. The number of seeds was partly related to the weight of seeds, but when incorporating number and weight of fruit into the same model, seed number was almost completely explained by these variables. The number of seeds per fruit was positively correlated with fruit weight and seed number and negatively correlated with seed weight and fruit number. The density of seedlings and adults of the 12 pioneer species were best explained by fruit weight and number. After 20 years of natural regeneration in abandoned pastures, the seed bank was still dominated by a few tree species typical of early succession. There was a strong positive effect of litter removal and a moderate positive effect of soil turning on seedling recruitment. Moreover, recruitment and initial growth were also favored in the bottomlands, probably due to the greater availability of water and fertile soils. The results of this study provide important tools for the management of secondary forests, for which the management of seed bank by removing litter coupled with soil turning are useful tools for activating the seed bank and accelerate seedling emergence.

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## INTRODUÇÃO GERAL

A implantação de grandes projetos agropecuários, que buscam em primeira instância o desenvolvimento econômico da região amazônica foi responsável pela redução significativa de grandes extensões de floresta tropical nas três últimas décadas (Fearnside *et al.* 2007; Malhi *et al.* 2008). Por volta do ano de 2008, a maior parte (52,5%) da área desmatada da Amazônia Legal brasileira destinava-se às atividades agropecuárias comerciais de grande escala, ao passo que uma pequena porção (3,4%) encontrava-se ocupada por atividades relacionadas à agricultura e à criação tradicional de gado por pequenos produtores rurais (Embrapa & INPE 2011). Essas duas diferentes categorias retratam padrões distintos de uso e ocupação da terra não apenas pela extensão de área que cada uma ocupa como também pelas consequências sobre a biota o que, em última análise, exercem papel determinante no potencial regenerativo da floresta após o abandono da área. Nas regiões tropicais, vários estudos são unânimes em revelar que o processo de sucessão secundária em áreas anteriormente utilizadas para atividades agropecuárias diferencia-se de acordo com a intensidade e tempo de uso da terra (p.ex., Purata 1986; Saldarriaga *et al.* 1988; Uhl *et al.*, 1988; Mesquita *et al.* 2001; Gehring *et al.* 2004; Norden *et al.* 2010; Williamson *et al.* in press). Embora ainda pouco exploradas, as florestas secundárias tropicais vêm sendo alvo de interesse do ponto de vista da importância econômica e de conservação, aliada ao papel de potencial mitigador das mudanças climáticas globais (Chazdon *et al.*, 2009).

Apesar dos múltiplos esforços, muito ainda precisa ser entendido no que diz respeito aos processos de sucessão secundária em áreas tropicais, de modo que tais processos possam ser adequadamente considerados dentro de um modelo de manejo das florestas secundárias. Dessa forma, informações relacionadas à fenologia reprodutiva, características biométricas e produção de sementes e frutos, e o potencial germinativo e de estabelecimento das espécies colonizando áreas abandonadas são informações cruciais que podem ser aplicadas na recuperação de áreas degradadas. Além disso, estudos experimentais que manipulam fatores ambientais, tais como disponibilidade de luz e umidade, ainda precisam ser melhor explorados no contexto das florestas secundárias.

Em florestas tropicais, o banco de sementes é dominado principalmente por espécies que apresentam sementes relativamente pequenas e que iniciam o processo de sucessão secundária em áreas abandonadas após o uso do solo (Guevara Sada e Gómez-Pompa 1972; Lawton e Putz 1988; Dalling *et al.* 1998). No entanto, a disponibilidade de sementes, dentre outros

fatores, é afetada pela forma e tempo de uso da terra. No caso das áreas que foram intensamente utilizadas para a pecuária, onde houve pisoteio constante e queimadas anuais para o controle de ervas daninhas, sementes de poucas espécies são encontradas (Uhl *et al.* 1988; Mônaco *et al.* 2003). A germinação de sementes de espécies pioneiras depende, em primeira instância, da disponibilidade de luz; assim, em florestas secundárias já estabelecidas e com dossel fechado, a germinação das sementes pode ser limitada pela falta deste recurso. Sabe-se que em florestas tropicais maduras, a formação de clareiras pela queda de uma ou mais árvores é considerado um dos mecanismos que determinam a manutenção da diversidade de espécies arbóreas tropicais, pois as espécies presentes no banco de sementes e de plântulas encontram condições abióticas (luz, umidade, etc.) favoráveis para a germinação e crescimento devido à partição de nichos (Orians 1982; Denslow 1986). As diferentes condições de micro-sítios em termos de variação na quantidade e profundidade da serrapilheira e reviramento da camada superficial do solo, presentes na zona de raiz das árvores caídas, também influenciam positivamente o sucesso do recrutamento (Orians 1982). No entanto, clareiras formadas em florestas secundárias são infrequentes e relativamente pequenas para a germinação de sementes (Saldarriaga *et al.* 1988; Yavitt *et al.* 1995; Nicotra *et al.* 1999; Montgomery e Chazdon 2001; Bebbler *et al.* 2002; Dupuy & Chazdon 2006). Desta forma, ações de manejo que visem criar condições favoráveis para a germinação e estabelecimento de plântulas de determinadas espécies se fazem necessárias em florestas secundárias.

Numa escala local, a topografia é considerada uma importante variável que influencia a distribuição de espécies e a estrutura das florestas tropicais, pois comumente está correlacionada às mudanças nas propriedades do solo, particularmente no regime de água e na fertilidade (Toumisto e Poulsen 2000; Webb e Peart 2000; Costa *et al.* 2005)). As variações topográficas podem gerar micro-ambientes responsáveis pela captura de matéria orgânica e sementes, determinar a intensidade de ocorrência de micro-organismos e influenciar a germinação, o estabelecimento e a mortalidade de plântulas (Eldridge *et al.* 1991; Vivian-Smith 1997). No entanto, desconhecemos estudos que avaliaram o sucesso no recrutamento de plantas pioneiras em relação à variação topográfica em floresta secundária.

Evidências mostram que as sementes produzidas em florestas secundárias são dispersas localmente (Wieland *et al.* 2011) e que também há uma relação entre a abundância do banco de semente e a composição florística do entorno (Mônaco *et al.* 2003). No entanto, diferentes estratégias na sazonalidade e intensidade da frutificação das espécies podem ser importantes



mecanismos para entender o porquê de algumas espécies serem abundantes no banco de sementes (Mooney *et al.* 1980; Camacho e Orozco 1998). Uma relação negativa é esperada entre massa de sementes e número de sementes por árvore (Jakobsson and Eriksson 2000; Aarssen and Jordan 2001; Henry and Westoby 2001). O equilíbrio entre massa de sementes e número de sementes por árvore significa que a energia alocada para a reprodução pode produzir poucas sementes grandes ou muitas sementes pequenas (Stearns 1992, Henry and Westoby 2001) Portanto, o equilíbrio entre o peso e o número de sementes está incorporado nos processos ecológicos, principalmente o equilíbrio entre o estabelecimento e a dispersão (Moles and Westoby 2004). A probabilidade de estabelecimento aumenta com o peso da semente, ao passo que a probabilidade de dispersão a locais adequados declina com o peso e aumenta com o número de sementes por árvore (Leishman and Murray 2001; Dalling *et al.* 2002; Dalling and Hubbell 2002; Westoby *et al.* 2002).

## **ORGANIZAÇÃO DA TESE**

Esta tese está organizada em dois capítulos. O capítulo 1 avalia a relação entre variáveis relacionadas às sementes, peso e número de sementes, com variáveis relacionadas a frutos, peso e número de frutos, de 12 espécies pioneiras abundantes em áreas de floresta secundária na Amazônia Central. Além disso, baseado em um modelo conceitual (conhecido como “seed packaging”), no qual o número de sementes por fruto é a variável fundamental, foram testadas correlações entre esta variável com as variáveis relacionadas à semente e variáveis relacionadas a frutos. Este modelo tem como premissa a alocação de biomassa, não apenas entre o peso de sementes e número de sementes por planta, mas também entre peso de frutos e número de frutos por planta. Por último, foram avaliadas as relações das variáveis sementes e frutos, duração de frutificação e porcentagem de germinação de semente com a densidade de plântulas e indivíduos adultos. No capítulo 2, com o intuito de aumentar o entendimento sobre o potencial regenerativo das florestas secundárias estabelecidas em áreas nas quais houve uso intenso do solo antes do abandono (pastagens), foi proposto examinar experimentalmente os efeitos da topografia, remoção de serrapilheira e revolvimento do solo sobre a densidade do banco de sementes e o sucesso no estabelecimento de espécies de árvores em áreas de florestas secundárias relativamente jovens (20 anos). Neste estudo, foram criadas clareiras artificiais com o intuito de fornecer as mesmas condições de luminosidade para testar os efeitos isolados de topografia, manipulação do solo e de serrapilheira.

## Capítulo 1

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Tony V. Bentos, Rita C. G. Mesquita, José L. C. Camargo and G. Bruce Williamson. **Seed and fruit tradeoffs – the economics of seed packaging in Amazon pioneers.** *Plant Ecology & Diversity* (in press.).

1 **Seed and fruit tradeoffs – the economics of seed packaging in Amazon pioneers**

2

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13 **Keywords:** Amazon; fruit mass; fruit number; pioneers; seed mass; seed number; seeds per  
14 fruit; tradeoffs; tropical trees.

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20 **Background:** The tradeoff between seed mass and seed number per plant is widely  
21 established for different taxa, guilds, and communities. Relative to primary forest species,  
22 pioneer species generally produce large numbers of small seeds.

23 **Aims:** We tested if the relationship between seed mass and seed number was connected to the  
24 fruit variables – namely, fruit mass and fruit number per tree – in order to evaluate tradeoffs  
25 in seed packaging.

26 **Methods:** Seed mass and seed number per tree as well as fruit mass and fruit number per tree  
27 were measured for 12 pioneer species common to secondary forests in the central Amazon.

28 **Results:** Seed mass, seed number, fruit mass, and fruit number varied by several orders of  
29 magnitude among species. Seed number was explained only partially by seed mass alone ( $R^2$   
30 = 0.55), but nearly completely by the combination of seed mass, fruit mass and fruit number  
31 ( $R^2 = 0.94$ ). The number of seeds per fruit was positively correlated with fruit mass and total  
32 seed number per tree and negatively with seed mass and fruit number. Seedling and adult  
33 abundances were most dependent on fruit number and fruit mass, not seed number and seed  
34 mass.

35 **Conclusions:** Biomass tradeoffs between seed mass and seed number are partially dependent  
36 on seed packaging, specifically seeds per fruit, fruit mass and fruit number per tree for pioneer  
37 trees in the central Amazon.

38 **Introduction**

39 A negative relationship between seed mass and seed number per tree has been established  
40 independently for different plant communities (Jakobsson and Eriksson 2000; Aarssen and  
41 Jordan 2001; Henery and Westoby 2001), for species in common taxa (Janzen 1969; Davies  
42 and Ashton 1999), and across plants globally (Moles et al. 2004, 2005). At its simplest, the  
43 tradeoff between seed mass and seed number per tree means that energy allocated to sexual  
44 reproduction can produce fewer, larger seeds or more, smaller seeds (Stearns 1992; Henery  
45 and Westoby 2001). The physical tradeoff between mass and number is embedded in  
46 ecological processes, most notably the tradeoff between establishment and dispersal (Moles  
47 and Westoby 2004a). The probability of establishment increases with seed mass, whereas the  
48 probability of dispersal to a suitable site declines with seed mass and increases with seed  
49 number per tree (Leishman and Murray 2001; Dalling and Hubbell 2002; Dalling et al. 2002;  
50 Westoby et al. 2002). Selection via dispersal and establishment varies in different  
51 communities, as establishment encompasses tolerance of abiotic stress and biotic hazards  
52 (predation and competition), while dispersal includes distance travelled and suitable  
53 microsites located (Coomes and Grubb 2003). The tradeoff between seed mass and seed  
54 number per tree also characterises early and late successional species, wherein the seed  
55 masses of mature forest or persistent species are demonstrably larger than the seed masses of  
56 pioneer species, and high fecundity or seed number per tree characterises pioneers (Salisbury  
57 1942; Foster and Janzen 1985; Ibarra-Manríquez and Oyama 1992; Grubb and Metcalfe 1996;  
58 Hewitt 1998; Davies and Ashton 1999).

59 Here, we analysed the allocation of fruit mass and fruit number per tree with seed mass  
60 and seed number – an application known as ‘seed packaging’ in intraspecific studies (Willson  
61 et al. 1990; Mehlman 1993), but here developed for interspecific comparisons. The economics  
62 of seed packaging in the title of our paper refers to how biomass is allocated, not just between  
63 seed mass and seed number per tree, but also between fruit mass and fruit number per tree,  
64 and how seed and fruit variables are related through the number of seeds per fruit. We had  
65 three main objectives: to determine (1) variability in seed and fruit variables across species  
66 and if fruit variables help explain variation in seed traits; (2) the seed packaging relationships;  
67 and (3) if seed and fruit variables explain seedling and adult densities.

68

69

70

71 *Variation in seed and fruit variables*

72 Utilising a dataset of 12 pioneer tree species from the Amazon rain forest, our first objective  
73 was to answer three questions in regard to mass and number of seeds and fruits among  
74 species: (a) given that pioneers generally share a set of characteristics different from mature  
75 forest or persistent species (Swaine and Whitmore 1988; Martínez-Ramos et al. 1989), is there  
76 significant interspecific variation in seed mass, seed number, fruit mass and fruit number in  
77 the 12 pioneer species? (b) How strong is the relationship between seed number and seed  
78 mass? (c) Can fruit variables – fruit mass and fruit number per tree – account for some of the  
79 unexplained variation in the relationship between seed mass and seed number per tree?

80

81 *Seed packaging relationships*

82 We determined the strength of the six predicted relationships (Figure 1) across the pioneer  
83 species in a simple conceptual model of mass and number of seeds and fruits. In the model,  
84 seeds per fruit is the pivotal variable relating seed traits to fruit traits (Figure 1). For example,  
85 more seeds per fruit implies a lower seed mass and a greater seed number per tree for any  
86 given fruit mass and fruit number per tree (Figure 1). Likewise, for any given seed mass and  
87 seed number per tree, more seeds per fruit should yield greater fruit mass and fewer fruits per  
88 tree (Figure 1). The relationships among the three seed variables (mass, number, and seeds per  
89 fruit) while holding fruit variables constant presume some limited energy level available to all  
90 species. Likewise, the relationships among the three fruit variables (mass, fruits per tree and  
91 seeds per fruit) while holding seed variables constant presume energy limitation. The  
92 uncertainty in the relationships increases when both fruit and seed traits vary across plant  
93 species because the level of resources devoted to reproduction is unlikely to be constant, and  
94 the allometric relationship between seed mass and fruit mass is likely to vary.

95 Besides the six predicted pair-wise relationships represented in Figure 1, there are four  
96 other pairs of variables that could be related indirectly through seeds per fruit. For example,  
97 seed mass and fruit mass could be associated, as both are related to seeds per fruit (Figure 1).  
98 However, such indirect relationships across species are less likely, especially as evolution has  
99 produced tremendous variation in seed packaging options. Therefore, we do not expect  
100 significant pairwise relationships among these four variables. Comparison of the six predicted  
101 relationships in Figure 1 with the four non-hypothesised ones provides an added measure of  
102 robustness to test the model.

103

104 *Seedling and adult tree densities*

105 We tested if seedling densities in light gaps and adult densities in our secondary forests were  
106 dependent on any of the five seed and fruit variables (Figure 1) of the 12 pioneer species.  
107 Given that our study area was young secondary forest undergoing colonisation and  
108 succession, we hypothesised that dispersal might be driving local pioneer abundances such  
109 that the number of diaspores (fruits in this case) might be as important as the number of seeds  
110 in determining seedling and adult densities. Traditionally, seed number is regarded as the  
111 critical variable in pioneer dispersal to suitable germination sites (Dalling et al. 2002). Where  
112 the landscape is patchy and dynamic, reaching germination sites may depend on the number  
113 of dispersal units more than the number of seeds (Howe 1989). We also tested for the effects  
114 of three additional variables known from other studies to affect plant abundances: fruiting  
115 duration, percent seed germination and maximum tree size per species (Grubb 1998; Davies  
116 and Ashton 1999; Leishman et al. 2000; Daws et al. 2007; Norden et al. 2009). Our first two  
117 objectives, focused on relationships of seed and fruit traits, differ from our third objective to  
118 relate plant species' abundances to those seed and fruit traits.

119

120 **Materials and methods**

121 *Study site*

122 The study was conducted in the secondary forest matrix surrounding the primary forest  
123 fragments of the Biological Dynamics of Forest Fragments Project (BDFFP), ca. 80 km north  
124 of Manaus, Amazonas State, Brazil. The climate of the region according to the Köppen (1936)  
125 system is *Am*, tropical humid with excessive rain in some months and only 1–2 months of less  
126 than 60 mm (Lovejoy and Bierregaard 1990; Nee 1995). Soils of the region are clays  
127 classified as yellow latosols (Oxisol) and red-yellow podzols (Ultisol) (Ranzani 1980).

128 Within the BDFFP, forest succession exhibits two distinct trajectories: a natural pathway  
129 characterised initially by *Cecropia* dominance, and an arrested pathway by *Vismia* dominance  
130 (Mesquita et al. 2001; Norden et al. 2010). Our study was conducted entirely in areas  
131 dominated by *Cecropia* species, the pathway that characterises natural regeneration for the  
132 region (Williamson et al. 2012). Primary forest at the study sites was cleared between 1984  
133 and 1988 and the sites subsequently abandoned without conversion to pastures and without  
134 prescribed burning.

135

136

137 *Study species*

138 Twelve pioneer species that were sufficiently abundant and widespread to accommodate  
139 sampling were selected from the secondary forests at the BDFFP. These species dominate  
140 secondary forests for 15–20 years following forest clearing, and they are well represented in  
141 canopy gaps in the adjacent old growth forests (Nee 1995; Oliveira and Mori 1999), although  
142 a number of less common secondary species were not included in the study. The 12 species,  
143 representing eight families, are widespread and generally characteristic of Neotropical  
144 successions (Joly 1993; Nee 1995; Appendix 1). Fruits of these pioneers are all dispersed by  
145 small birds and bats that swallow fruits and defecate seeds (Wieland et al. 2011), although  
146 dispersal mode was not a criterion for selecting species.

147

148 *Sampling*

149 To ensure representative sampling of the region, we stratified data collection across three  
150 sites: Florestal and Cidade Powell at the Esteio ranch and the Porto Alegre ranch (Figure 2).  
151 Initially, 30 trees of each species (10 per site at the three sites) in young (< 20-year-old)  
152 secondary stands were visited monthly over three consecutive years from June 2002 to May  
153 2005 to determine the fruiting duration. None of the species exhibited fruiting by all trees in  
154 all months of the year, so fruiting duration was defined as the sum of the proportion of trees  
155 fruiting each month through the year; then the 12-month sum was averaged over three  
156 consecutive years to yield fruiting duration per year. The *Cecropia* species (Appendix 1) were  
157 dioecious, so only female trees were used to determine fruiting duration and other  
158 reproductive traits. Further details on fruiting duration are available in Bentos et al. (2008).

159 In 2005, the number of fruits per tree was counted on seven trees of each species spread  
160 across the three farms, early in each species' fruiting season before ripe fruits had fallen or  
161 been dispersed. Complete canopy counts were possible for five species: *Vismia japurensis*,  
162 *Bellucia grossularioides*, *Bellucia dichotoma*, *Cecropia sciadophylla* and *Cecropia*  
163 *purpurascens*. Morphologically, *Cecropia* has single-seeded fruits but they are aggregated on  
164 an infructescence of separate rachises that are removed in whole or in part by bats and birds  
165 (Estrada et al. 1984; Lobova et al. 2003), so we counted rachises as the ecological equivalent  
166 of fruits in other species. Complete canopy counts were impossible for the seven other  
167 species, so we harvested 25% of the crown to count the fruits of *Goupia glabra*, *Vismia*  
168 *cayennensis*, *Croton matourensis*, *Laetia procera* and *Byrsonima duckeana*, or the  
169 infructescences and the number of fruits per infructescence for 30 infructescences of *Miconia*



170 *burchelli*, or the number of fruitlets (subunits) of 30 multiple fruits of *Guatteria olivacea*.  
171 Seed number per fruit was determined by counting the number of seeds in a fruit or fruitlet for  
172 each of the 30 fruits from each of the seven trees per species. In each fruit, *Byrsonima*  
173 *duckeana* has one pyrene that contains several seeds (Camargo et al. 2008), but the pyrene is  
174 the diaspore and its hard structure retains the seeds even after dispersal (Santamaría 2004).  
175 Henceforth, we refer to the fruitlets (*Guatteria olivacea*) and the pyrenes (*Byrsonima*  
176 *duckeana*) as fruit and seed, respectively, and we refer to *Cecropia* rachises as fruits, as they  
177 are broken off by dispersal agents. A fruit in this context is a unit of removal for consumption  
178 by a bat or a bird.

179 Seed mass and fruit mass (with seeds included) were determined on fresh samples to  
180 allow comparisons based on what local dispersal agents encounter, consume and disperse. To  
181 determine seed mass, 30 individual seeds were weighed for species with seeds larger than 2  
182 mg (*Byrsonima duckeana*, *Goupia glabra*, *Guatteria olivacea*, *Laetia procera* and *Croton*  
183 *matourensis*). For small seeded species (< 2 mg), seven lots of 100 seeds were weighed for  
184 each species (*Miconia burchelli*, *Bellucia grossularioides*, *Bellucia dichotoma*, *Vismia*  
185 *cayennensis*, *Vismia japurensis*, *Cecropia sciadophylla* and *Cecropia purpurascens*).

186 Percent germination was determined for cleaned seeds of each species in four replicates  
187 of 50 seeds each, randomly selected from the seeds obtained from the fruit samples described  
188 above. Germination tests were conducted in the INPA Tropical Silviculture plant nursery for  
189 two species, *Byrsonima duckeana* and *Guatteria olivacea*, and in the INPA Tropical  
190 Silviculture Seed Laboratory for the other 10 species. In the plant nursery, seeds from the two  
191 large-seeded species were spread into vermiculate over a substrate of fine sand in plastic  
192 trays. In the germination chamber the small seeds of the remaining 10 species were placed on  
193 moist filter paper and maintained at 25 °C on a 12:12 h photoperiod at a PAR of 70  $\mu\text{mol s}^{-1}$   
194  $\text{m}^{-2}$ . Germination was recorded weekly until 1 month passed without a new germination.

195 Given that trees in our study were relatively young, we determined the maximum  
196 diameter (dbh) of each species from the BDFFP Pioneers Project's database (Williamson et  
197 al. 2012). Maximum tree size, as a functional trait related to fecundity, usually refers to  
198 maximum height (Wright et al. 2007), a variable not available to us, so we used the maximum  
199 diameter for each species.

200 The density of adults (defined as stems  $\geq 3$  cm dbh) was determined in 20 belt transects,  
201 3 m  $\times$  100 m, in secondary forests at the BDFFP. Transects were parallel to one another,  
202 separated by at least 200 m, seven each in Cidade Powell and Porto Alegre and six in

203 Florestal (Figure 2). The density of seedlings ( $\geq 15$  cm tall) in recent light gaps of the same  
204 secondary forests were identified and counted in 10  $3\text{ m} \times 3\text{ m}$  quadrats, each quadrat located  
205 in a different canopy gap in each of the three sites, for a total of 30 quadrats (Figure 2). The  
206 canopy gaps were created by tree falls from natural thinning in the secondary vegetation and  
207 judged to be 1–3 years old based on regeneration which was less than 3 m tall. Nearly all the  
208 seedlings were less than 1 m tall, with a few that reached 2–3 m. The gaps sampled had areas  
209 of 39–250  $\text{m}^2$ , most of them (27 of 30) being small ( $< 150\text{ m}^2$ ) as they were in secondary  
210 forest. Gaps chosen were separated by at least 200 m to ensure independent seedling  
211 establishment. The quadrat and transect surveys provided estimates of the density of seedlings  
212 and adults, respectively.

213

#### 214 *Analyses*

215 We conducted three analyses to answer each of the three questions regarding mass and  
216 number of seeds and fruits. To determine variation in seed mass and number, fruit mass and  
217 number, as well as fruiting duration and germination rate, we calculated the magnitude of the  
218 variation in the means for the 12 pioneer species. Then, we performed linear regression of  
219 seed number on seed mass to determine the strength of the relationship across our pioneers.  
220 Finally, we implemented linear regressions of seed number on seed mass, fruit mass and fruit  
221 number to determine if fruiting traits could explain some of the variation in seed number by  
222 running stepwise forward models where independent variables were allowed to enter the  
223 model only when they significantly ( $P \leq 0.05$ ) improved fit. Then, we compared the chosen  
224 stepwise model with all other models with a ‘best subsets’ procedure that showed regressions  
225 and AIC values for each combination of 1–3 independent variables (Statistix 9, 2008). The  
226 linear regressions were repeated with seed mass as the dependent variable and with seed  
227 number, fruit mass, and fruit number as independent variables. Prior to testing, all variables  
228 were log<sub>10</sub>-transformed to produce approximately normal distributions.

229 The hypothesised relationships between the log<sub>10</sub>-transformed seed and fruit variables  
230 (Figure 1) were tested for significant Pearson correlations in six tests. For comparison, we  
231 also ran correlation tests for the four pairs of indirect relationships for which we had not  
232 hypothesized significance. These tests are usually adjusted by canopy volume or tree size;  
233 however, no adjustments by tree size were made because species diameter means were not  
234 significantly correlated with any of the seed and fruit variables in the study; thus, mass and  
235 number of seeds and fruits were independent of species’ mean tree size in our sample.

236 The seedling and adult densities were expected to be dependent to some degree on the  
237 five seed packaging variables in Figure 1, and based on other studies, possibly on three other  
238 variables – germination rate and fruiting duration (Bentos 2006) – and maximum tree  
239 diameter measured from the BDFFP Pioneers databases (Williamson et al. 2012). Because  
240 nine is a large number of dependent variables and many of them co-varied, we employed  
241 stepwise forward regression to determine which variables contributed the most to explain  
242 adult or seedling densities. Independent variables were allowed to enter the model at  $P \leq 0.05$ .  
243 To avoid some of the pitfalls of stepwise regression (Whittingham et al. 2006), we compared  
244 the chosen stepwise model with all other possible models of 1–9 independent variables  
245 through a best subsets regression procedure (Statistix 9, 2008). Models were compared  
246 through Mallows'  $C_p$ , AIC and the adjusted  $R^2$  values; models were improved when  $C_p$  was  
247 close to the number of estimated parameters ( $p$ ), when AIC is low, and when adjusted  $R^2$  is  
248 high (Statistix 9, 2008).

249 We also ran the stepwise forward regression of adult and seedling densities as a function  
250 of only seed variables (seed number, seed mass, and seeds per fruit) and of only fruit variables  
251 (fruits per tree, fruit mass, and seeds per fruit) to determine what conclusions we might have  
252 drawn had we measured just seed variables or just fruit variables, as many studies have  
253 measured only seed variables. We did not include adult density in the regression of seedling  
254 density or vice versa because we wanted to ascertain the importance of the reproductive  
255 variables apart from any effect of adults on seedlings or seedlings on adults. However, we  
256 separately determined the correlation of seedling and adult densities, as they potentially drive  
257 one another.

258 All statistical analyses were implemented with SYSTAT 9.0 or Statistix 9.0.

259

## 260 **Results**

### 261 *Variation in seed and fruit variables*

262 Variation in reproductive traits among the pioneers was notably high for a sample of 12  
263 species. Seed number per tree varied more than 5000 fold, from 7000 seeds year<sup>-1</sup> for *Croton*  
264 *matourensis* to 47,000,000 for *Miconia burchelli* (Figure 3, Appendix 2). Generally, species  
265 had very small seeds, < 15 mg for 10 of the 12 species (Figure 3, Appendix 1). Individual  
266 seed mass also varied about 5000 fold, from 0.07 mg for *Bellucia dichotoma* to 398.6 mg for  
267 *Byrsonima duckeana*.

268 Fruits per tree varied from 100 for *Bellucia grossularioides* to 500,000 for *Miconia*  
269 *burchelli*, both species of Melastomataceae, again a 5000-fold variation (Figure 3, Appendix  
270 2). The number of seeds per fruit also varied 5000 fold, from one in *Byrsonima duckeana* and  
271 *Guatteria olivacea* to over 5000 in *Cecropia sciadophylla* and *Bellucia dichotoma* (Figure 3,  
272 Appendix 2). In contrast, fruit mass varied only 1500 fold, from 0.019 g in *Miconia burchelli*  
273 to 29.4 g in *Cecropia sciadophylla* (Figure 3, Appendix 1).

274 Fruiting duration (sum of the proportion of adults fruiting monthly for 12 months) varied  
275 about 10 fold, from 0.55 for *Croton matourensis* to 6.26 for *Bellucia grossularioides*  
276 (Appendix 2). Eleven of the 12 species fruited annually, three of them (*Bellucia*  
277 *grossularioides*, *Goupia glabra*, and *Bellucia dichotoma*) nearly continuously throughout the  
278 year, although not all individuals fruited every month. One species, *Croton matourensis*,  
279 produced fruits biennially and then only for a month. Seed germination was much less  
280 variable, ranging from a low of 30% in *Byrsonima* to a high of 100% in *Vismia japurensis*.  
281 Eight species exhibited germination rates greater than 50% (Appendix 1).

282 About half the variation in seed number per tree was explained by seed mass in a highly  
283 significant regression ( $R^2 = 0.55$ ,  $P = 0.005$ ,  $N = 12$ ). In stepwise regression, the proportion of  
284 variance explained improved from 0.55 with only seed mass, to  $R^2 = 0.72$  with seed mass and  
285 fruit number, and again to  $R^2 = 0.94$  with seed mass, fruit number and fruit mass. Fruit traits  
286 entered the regressions significantly ( $P < 0.05$  in both cases) and co-linearity among the  
287 independent variables remained low as the variance inflation factor (VIF) remained below 5  
288 and the adjusted  $R^2 = 0.92$  remained close to the unadjusted value of 0.94. Stepwise forward  
289 and backward regressions produced the same model, as all three independent variables  
290 entered significantly. The best subsets regressions provided additional support for the same  
291 model over all other models, based on comparison of the AIC values. Switching the position  
292 of the two seed variables to regress seed mass on seed number, fruit mass and fruit number  
293 produced nearly identical results.

294

#### 295 *Seed packaging relationships*

296 The six hypothesised relationships between seed packaging variables were all statistically  
297 significant as predicted, at  $P \leq 0.01$  in three cases and at  $P \leq 0.05$  in the other three cases  
298 (Figure 4). A Bonferroni adjustment for multiple (six) tests would roughly double the  
299 resulting  $P$ -values, but employing one-tailed hypotheses would halve the resulting  $P$ -values,  
300 overall leaving them as indicated. In contrast, none of the four indirect relationships exhibited

301 statistical significance: seed number and fruit mass ( $R = 0.01$ ), seed number and fruits per tree  
302 ( $R = 0.11$ ), seed mass and fruits per tree ( $R = 0.35$ ), and seed mass and fruit mass ( $R = -0.15$ ).

303

#### 304 *Seedling and adult densities*

305 A total of 380 seedlings were encountered in the 30 quadrats, or a density of 1.41 seedlings  
306 per  $m^2$  (Appendix 2). There were 1–5 species per quadrat and 1–27 individuals per quadrat.  
307 The most abundant seedlings were *Miconia burchelli* (145) and *Guatteria olivacea* (144),  
308 together constituting 76% of the total seedlings encountered. The three next most common  
309 species, *Vismia cayennensis* (25), *Cecropia sciadophylla* (24), and *Croton matourensis* (16),  
310 comprised 17% of the seedlings. The remaining 7% of the total seedling count was divided  
311 among seven species, each of which had only 1–7 seedlings in all 30 quadrats.

312 A total of 556 adults of 12 species counted in the 20 belt transects produced a density of  
313 0.093 adults per  $m^2$  (Appendix 2). The number of species per plot was 2–11, and the number  
314 of individuals was 1–16. Seven species (*Miconia burchelli*, *Vismia cayennensis*, *Guatteria*  
315 *olivacea*, *Laetia procera*, *Cecropia sciadophylla*, *Croton matourensis* and *Byrsonima*  
316 *duckeana*) represented 88% of the trees counted ( $N = 104, 82, 70, 64, 62, 56$  and  $53$ ,  
317 respectively). The remaining five species were *Vismia japurensis*, *Goupia glabra*, *Byrsonima*  
318 *dichotoma*, *Croton purpurascens* and *Bellucia grossularioides*) which accounted for 12% of  
319 the trees ( $N = 20, 16, 12, 11$  and  $6$ , respectively). Across the 12 species, seedling and adult  
320 densities were positively correlated with one another ( $R = 0.66, P = 0.02$ ).

321 Stepwise regression models explaining seedling and adult densities selected independent  
322 variables from the pool of seven variables – four seed packaging variables, fruiting duration,  
323 percent germination, and maximum tree diameter; one other variable, seeds per fruit, was  
324 excluded by regression as it was too strongly correlated with other seed packaging variables.  
325 Seedling density was a positive function of only one variable, fruits per tree, according the  
326 significance criterion of  $P \leq 0.05$  for variables to enter, and it explained 45% of seedling  
327 density (Table 1). However, according to the AIC criterion, seedling density was best  
328 described as a function of fruits per tree, germination rate and fruit mass (adjusted  $R^2 = 0.76$ ,  
329 Table 1). Mallow's  $C_p$  indicated a model with more independent variables, including the  
330 same fruit and germination variables as well as dbh. Seeds per tree entered only when the  
331 model allowed for five independent variables, a model not chosen by Mallow's  $C_p$ , AIC or  
332 adjusted  $R^2$  (Table 1).

333 Adult density was a positive function of fruits per tree and fruit mass according to the  
334 stepwise regression and the AIC criterion (adjusted  $R^2 = 0.69$ , Table 1). Mallows'  $C_p$  suggests  
335 a model with five independent variables – fruits per tree, fruit mass, seed mass, fruiting  
336 duration and dbh.

337 When the pool of independent variables was limited to the three seed variables, stepwise  
338 regressions did not choose any of the seed variables, even under a liberal adjustment to the  
339 model of  $P \leq 0.15$  to enter. When the pool was limited to the three fruit variables, adult  
340 density was a function of fruits per tree and fruit mass (adjusted  $R^2 = 0.69$ ), whereas seedling  
341 density was a function of fruits per tree ( $R^2 = 0.45$ ).

342

### 343 **Discussion**

344 Variation in seed and fruit traits among the 12 Amazonian pioneer species was substantial,  
345 5000-fold in many variables, despite their representing a single ecological guild (Kroon and  
346 Olff 1995). Although pioneers generally share a set of characteristics different from mature  
347 forest or persistent species (Swaine and Whitmore 1988; Martínez-Ramos et al. 1989), the  
348 seed mass of pioneer tree species in tropical wet forests commonly varies by 3–5 orders of  
349 magnitude (Foster and Janzen 1985; Ibarra-Manríquez and Oyama 1992; Grubb 1998; Dalling  
350 and Hubbell 2002; Dalling et al. 2002; Daws et al. 2007). As Coomes and Grubb (2003) have  
351 noted, “in tropical lowland rainforests, the mean seed dry mass of shade-tolerant tree species  
352 is 10–100 times greater than that of light-demanding tree species, whilst the smallest and  
353 largest mean values within both these groups differ by  $10^5$ – $10^6$ .” It is perhaps surprising that  
354 our dataset for 12 species, limited to bat and bird-dispersed pioneers at a single site, was as  
355 variable as much larger datasets – for example, 139 species in Ibarra-Manríquez and Oyama  
356 (1992) and 2134 species in Wright et al. (2007).

357

#### 358 *Why Fruit Variables?*

359 Seed mass explained only 55% of the variation in seed number, whereas fruit mass and fruit  
360 number explained an additional 40%. As the majority of prior studies have also demonstrated  
361 incomplete correlations between seed mass and seed number, additional factors, such as  
362 climate, latitude, phylogeny, and maximum tree size, have been postulated as important  
363 determinants of seed number (Foster and Janzen 1985; Moles et al. 2004a, 2005; Moles and  
364 Westoby 2006; Moles et al. 2007; Wright et al. 2007). While these other factors are often  
365 significant, fruit mass and fruit number are adjoining factors that merit direct consideration

366 alongside seed mass and seed number. Fruits house and protect seeds against herbivores,  
367 pathogens and environmental stress, and fruits contribute to dispersal, so tradeoffs in  
368 allocation to seeds should be integrated with allocation to fruits.

369 The seed packaging concept utilizes seeds per fruit as the pivotal variable linking seed  
370 mass and seeds per tree to fruit mass and fruits per tree. This is the only variable among the  
371 five (Fig. 4) which had statistically significant correlations with all four other variables. Each  
372 of the other four had significant correlations with only two of the four other variables. Seeds  
373 per fruit was negatively related to fruits per tree and to seed mass but positively related to fruit  
374 mass and seed number—all relationships suggesting that production of many-seeded fruits  
375 results in fewer, larger fruits with more, smaller seeds. Fruits are often omitted from seed  
376 mass-seed number studies, although Ibarra-Manríquez and Oyama (1992) found seeds per  
377 fruit was positively related to fruit mass and negatively related to seed mass in a tropical wet  
378 forest at Los Tuxtlas; however, they did not quantify seed number per tree nor fruit number  
379 per tree. In fact, fruit number per tree (or fruits per volume of canopy) is rarely quantified in  
380 seed studies.

381 While the relationships between seeds per fruit and seed mass and number and fruit mass  
382 and number are statistically significant, alone they do support strong conclusions as our  
383 results are strictly correlative and cannot exclude alternative explanations. Nevertheless,  
384 nearly all studies of seed mass and seed number per tree, as well as other reproductive  
385 variables, are based on association, not experimentation, because these relationships are a  
386 result of long-term selection for seed and fruit traits. Further confounding interpretation of the  
387 results is the fact that some of the species are congeners whose seed and fruit traits are not  
388 necessarily independent of one another. While trait conservatism is not always the case  
389 among related species (Losos 2008), each of the three species pairs of congeners (*Vismia*,  
390 *Bellucia*, *Cecropia*) in our study did share some seed and fruit mass and numbers. However,  
391 at higher levels, there was little evidence for phylogenetic conservatism among our twelve  
392 species; for example, *Miconia* and *Bellucia* share similar seed mass but have fruit mass, fruit  
393 number per tree and seed number per tree that differ by several orders of magnitude  
394 (Appendices 1 and 2). Five of the eight families are scattered through the order Malpighiales,  
395 and the other three, the Melastomataceae (Myrtales), Urticaceae (Rosales) and Annonaceae  
396 (Magnoliales), have seed and fruit traits that do not separate well from those species in  
397 Malpighiales (Appendix 1 and 2). Our limited sample size precludes quantifying the

398 phylogenetic component of seed and fruit traits of the 12 pioneer species, but expansions of  
399 the economics of seed packaging could incorporate the phylogenetic signal.

400 In addition, our dataset is limited to species that share the same mode of dispersal,  
401 ingestion by small bats and birds—a fact that controls for some sources of variation in seed  
402 and fruit traits, but it also limits inferences beyond our study. Broader boundaries that include  
403 other dispersal modes, especially wind and terrestrial mammal, would certainly broaden the  
404 range of seed and fruit, mass and number, as well as offer options for phylogenetic analyses.

405

#### 406 *Boundary Limits of the Amazon Pioneer Dataset*

407 The pioneers in our study are dependent on small bats and birds for seed dispersal, a  
408 dependence which imposes limits on both seed mass and fruit mass. To visualize, suppose  
409 that in single-seeded fruits, there is some constant power relationship between seed mass and  
410 fruit mass; then the log of seed mass would exhibit a linear relation with the log of fruit mass  
411 (Fig. 5). For a given fruit mass, the mass of an individual seed in multi-seeded fruits would lie  
412 below the mass of the single seed in a single-seed fruits. In fact, points below the diagonal  
413 line of single-seed fruits (Fig. 5) would include combinations of multiple-seeded fruits. In  
414 general, across all possible multiple and single-seeded fruits, there might be a positive  
415 relationship between seed mass and fruit mass. However, second growth bats and birds  
416 impose other limits: seeds must be small enough to swallow, and fruits must be large enough  
417 to attract dispersers but not so large that they preclude handling (Howe 1989). These limits  
418 leave a potential subset of seed mass/fruit mass values that are unlikely to show a positive  
419 correlation between seed mass and fruit mass (Fig. 5). In contrast, surveys that cover all forest  
420 species may include very small single-seeded fruits that are dispersed abiotically and larger  
421 fruits and seeds dispersed by non-volant mammals, both of which would contribute to a  
422 positive seed mass-fruit mass relationship. Therefore, different datasets will impose their own  
423 boundary limits, determined by the subset of species studied. One task in studying  
424 evolutionary tradeoffs is to determine which relationships are universal and which are  
425 boundary limited and by what factors. Given that seed mass-seed number tradeoffs have been  
426 studied for communities, guilds and taxa, boundary limits are likely to be imposed by  
427 incongruous factors—phylogeny, dispersal mode, successional status, latitude—to name a  
428 few. For example, there are no wind-dispersed pioneer species in the rain forest at the BDFFP  
429 site studied here, although wind-dispersal is a common mode among pioneer species in  
430 seasonal tropical forests.



431 Two prior studies have shown a positive relationship between seed mass and fruit mass in  
432 tropical communities (Ibarra-Manríquez and Oyama 1992; Wright et al. 2007). These studies  
433 included early and late successional species (pioneers and persistents), whereas our dataset  
434 included only pioneer species. Pioneers generally have smaller seeds than later successional  
435 species, so the absence of a seed mass-fruit mass relationship could be regarded as  
436 characteristic of pioneers of wet forests, as dispersal is usually by birds and bats (Howe 1989).  
437 However, this limit is unrepresentative of wet forest trees generally where datasets include  
438 persistents as well as pioneers (Uhl and Clark 1983; Howe 1989; Rodrigues et al. 1990).

439

#### 440 *Drivers of Seedling and Adult Densities*

441 Fruits per tree explained over half the variation in adult and seedling densities, an interesting  
442 result, given that seed number is the variable most often associated with pioneer success  
443 (Table 1). It's possible that fruits per tree is a better predictor of success than seed number  
444 because the unit of dispersal of the pioneer species in our study was the fruit, consumed, more  
445 or less, whole, by birds and bats (Howe 1989). Fruit-removal events are closely tied to seed  
446 deposition regardless of how many seeds are in a fruit because handling and passage time in  
447 the gut are extremely fast. Dispersal of a multiple-seeded fruit may simply result in a pile of  
448 aggregated seeds, perhaps spread only over a microsite.

449 Fruit mass was also a significant factor in explaining seedling and adult densities (Table  
450 1). Logically, larger fruits could be more attractive to dispersal agents if rewards were  
451 greater, but fruit mass was negatively correlated with fruits per tree (Table 1), suggesting that  
452 larger fruits are produced at a cost of fruit number per tree. However, the stepwise regressions  
453 included a positive effect of fruit mass after including a positive effect of fruits per tree,  
454 implying an effect of mass on plant density, despite fruit mass' negative correlation with fruits  
455 per tree. Thus, sustaining higher fruit mass even while increasing fruits per tree provided  
456 added success as measured by seedling and adult densities.

457 Germination rate was the only other variable explaining seedling densities in the  
458 regressions. It also varied less among species (30-100%) than the seed packaging variables  
459 (Appendix 1). All pioneers would be expected to exhibit high germination rates when given  
460 adequate light or heat (Hewitt, 1998; Pearson et al., 2002). Germination rate did enter as a  
461 significant positive factor into the stepwise regressions, helping to explain seedling density in  
462 the recent light gaps, but it did not explain any variation in adults in secondary forest. This  
463 result is consistent with Dalling and Hubbell's (2002) finding that seed mass-seed number

464 differences, evident in seedling density, are largely eradicated 19 months after germination.  
465 Apparently, any differential effect in germination on seedlings may be overridden by other  
466 factors during growth to adulthood.

467 While there remain open questions in regard to interpretations of the stepwise  
468 regressions, the overall importance of fruit characteristics relative to seed traits is a novel  
469 finding of our study. Among plant reproductive traits, the tradeoff between seed mass and  
470 seed number is usually the focus of investigations (Janzen 1969; Westoby et al. 1992;  
471 Thompson et al. 1993). While our results showed such a tradeoff, the failure of seed variables,  
472 both seed mass and seed number, to enter into the regressions explaining seedling and adult  
473 densities suggests that fruit variables may have been overlooked in studies of plant  
474 reproductive strategies, especially for pioneers.

475 Other studies have revealed mixed results in use of seed size to explain plant abundances  
476 (Guo et al. 2000; Jakobsson and Eriksson 2000; Leishman and Murray 2001). However, none  
477 of these studies have offered fruit variables, along with seed variables, into their regressions.  
478 Perhaps some of the earlier studies would have drawn different conclusions if they had  
479 included the complete suite of seed-packaging variables in their analyses of plant abundances.  
480 When we included only seed traits among our independent variables, there was no significant  
481 relationship with seedling or adult abundance.

482 There are, of course, caveats to the interpretation of the seedling and adult regressions.  
483 First, the seed packaging variables were measured at the same time as the seedling and adult  
484 densities, whereas the latter are actually a function of the seed and fruit variables sometime in  
485 the past. In essence, our seed packaging variables are likely to determine future densities, not  
486 present ones. Still, the seed packaging variables are unlikely to change over short periods of  
487 time. Furthermore, the light gaps and second growth stands are representative of disturbance  
488 patches in the larger landscape, and these patches constantly turn over, offering some stability  
489 to the landscape mosaic. Current reproduction is most likely replenishing the seed bank where  
490 seeds await more favorable conditions to germinate (Thompson et al. 1993; M<sup>o</sup>naco et al.  
491 2003). Local disturbance regimes and successional patterns operate in conjunction with  
492 reproductive strategies to determine success. In our case, recent clearings over the last two  
493 decades have greatly increased the area available to pioneer species, so dispersal may be  
494 driving pioneer success.

495 Although we did include seedling and adult densities in the natural environment  
496 alongside functional traits of seed packaging, we did not monitor various components of

497 success, such as seed dispersal, seed bank composition and survivorship, seed and seedling  
498 predation, and seedling to sapling growth rates. Measuring these components is usually done  
499 experimentally and can reveal the underlying processes leading to success as seedlings in gaps  
500 and adults in secondary forests (Gross 1984; Dalling and Hubbell 2002; Moles and Westoby  
501 2004a, 2004b, 2006) and is a natural complement to comparing the functional traits to actual  
502 seedling and plant densities in the field. Future studies of seed packaging would benefit from  
503 such experiments.

504

#### 505 *Selection for Seed and Fruit, Mass and Number*

506 Tradeoffs in the production of seeds and fruits have been treated here mainly in the context of  
507 a plant's allocation of resources, mass or energy. While not explicitly stated, it is assumed that  
508 the pioneer species considered were equally capable of garnering resources to reproduce and  
509 equally efficient at converting resources into seeds and fruits. Thus, the economy of seed  
510 packaging is simply the differential allocation of an approximately equal biomass into seeds  
511 and fruits. As tradeoffs are evaluated beyond the limits here—for example, to mature forest  
512 tree species, other biomes, growth forms, photosynthetic pathways, the tradeoffs may no  
513 longer invoke an approximately equal reproductive effort. Therefore, selection may alter the  
514 relationships among fruit and seed variables, so global comparisons of seed and fruit tradeoffs  
515 present new challenges and may produce new relationships (e. g., Molles et al. 2005).

516 In addition, selection on seed and fruit variables may include a “familial” component.  
517 Differential contributions of parents to seed tissues in Angiosperms may result in parent  
518 conflicts in development of endosperm, thereby influencing seed size (Spielman et al. 2001;  
519 Sundaesan 2005). Similarly, parent-offspring conflicts may influence ovule receptivity (Uma  
520 Shaanker 1988; Sengupta and Tandon 2010). These forces clearly effect seed and fruit  
521 variables, especially seeds per fruit or “brood size” in plants. How these “familial” selective  
522 forces interact with traditional ecological tradeoffs remains to be unfolded. In any case, they  
523 do demonstrate that seed number per fruit is under selection even where ovule number per  
524 fruit may be phylogenetically constrained.

525

#### 526 **Conclusions**

527 Incorporating fruit mass and fruit number per tree into analysis of the seed mass and seed  
528 number per tree explained most of the unexplained variance in the seed mass-seed number  
529 relationship. The pivotal variable, seeds per fruit, links the seed mass and number with fruit

530 mass and number for analysis of seed packaging. The economics of seed packaging predicts  
531 that an increase in seeds per fruit will be associated with a lower seed mass and a greater seed  
532 number and with a greater fruit mass and a lower fruit number. These relationships were  
533 confirmed for 12 pioneer tree species from the Amazon Basin. Tree seedling and adult  
534 densities were best explained by fruit variables, mass and number, not by seed mass and  
535 number, highlighting dispersal as the critical component of success in this pioneer community  
536 subject to high perturbation. Seed germination rate also contributed to seedling success but  
537 the effect did not carry over to adults. Boundary limits of the seed packaging relationships  
538 may be imposed by dispersal agents or other factors for any plant community, guild or taxon  
539 analyzed. Our conclusions are all based on a limited set of 12 pioneer species, some of which  
540 are congeners, so extension of the conclusions beyond this dataset may be tenuous.  
541 Additional datasets as well as macrogeographic comparisons would be welcome where data  
542 for fruit mass and number accompany seed mass and number.

543

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557

#### 558 **Notes on contributors**

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560 establishment success of pioneer tree species in the Amazon.

561

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565

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569

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572 effects of El Niños, fires, floods and fragmentation; (3) adaptive strategies of trees in wood  
573 deposition and biomass allocation.

574

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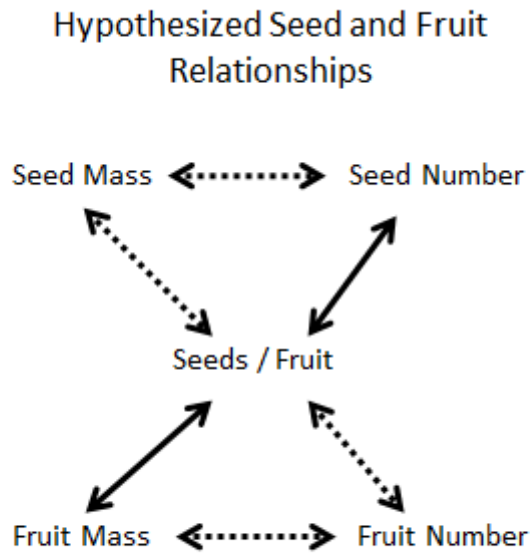
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724

725 **Table 1.** Results of linear regressions of seedling and adult densities on the five seed  
 726 packaging variables, percent seed germination, fruiting duration, and maximum tree diameter  
 727 from the BDFFP Pioneers database. Criteria for best model are Mallows'  $C_p$ , adjusted  $R$  and  
 728 AICc of the model minus the minimum AICc. AICc is a small-sample version of Akaike's  
 729 Information Criterion (Statistix 9.0).

730

731	Parameters	$C_p$	Adj $R^2$	AICc -Min.	Model's Independent Variables
733	Seedling Density				
734	<b>2</b>	<b>36</b>	<b>0.45</b>	<b>1.63</b>	<b>Fruits/Tree</b>
735	3	24	0.59	1.70	Fruits/Tree, % Germination
736	4	11	0.76	0.00	Fruits/Tree, % Germination, Fruit Mass
737	5	6	0.86	0.41	Fruits/Tree, % Germination, Fruit Mass, DBH
738	6	4	0.91	6.89	Fruits/Tree, % Germination, Fruit Mass, DBH, Seeds/Tree
739	Adult Density				
740	2	50	0.54	1.44	Fruits/Tree
741	<b>3</b>	<b>29</b>	<b>0.69</b>	<b>0.00</b>	<b>Fruits/Tree, Fruit Mass</b>
742	4	21	0.75	2.27	Fruits/Tree, Fruit Mass, Fruiting Duration,
743	5	13	0.83	5.19	Fruits/Tree, Seeds/Tree, Fruiting Duration, DBH
744	6	7	0.90	9.67	Fruits/Tree, Fruit Mass, Seed Mass, Fruiting Duration, DBH

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748 **Figure 1.** Hypothesised relationships among seed packaging variables: seed mass and seed  
749 number per tree, fruit mass and fruit number per tree and seeds per fruit. Solid lines are  
750 positive relationships and dotted lines are negative relationships.

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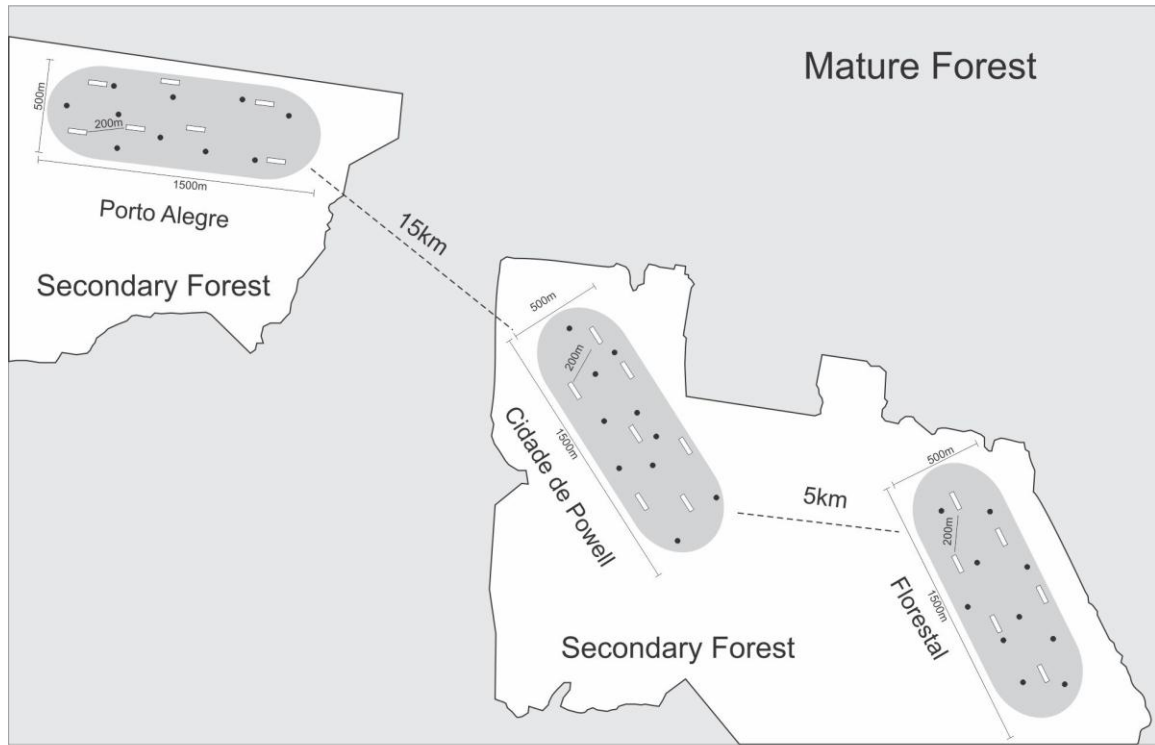
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100m  
 100m 3m Quadrats      3m 3m Quadrats in lightgaps

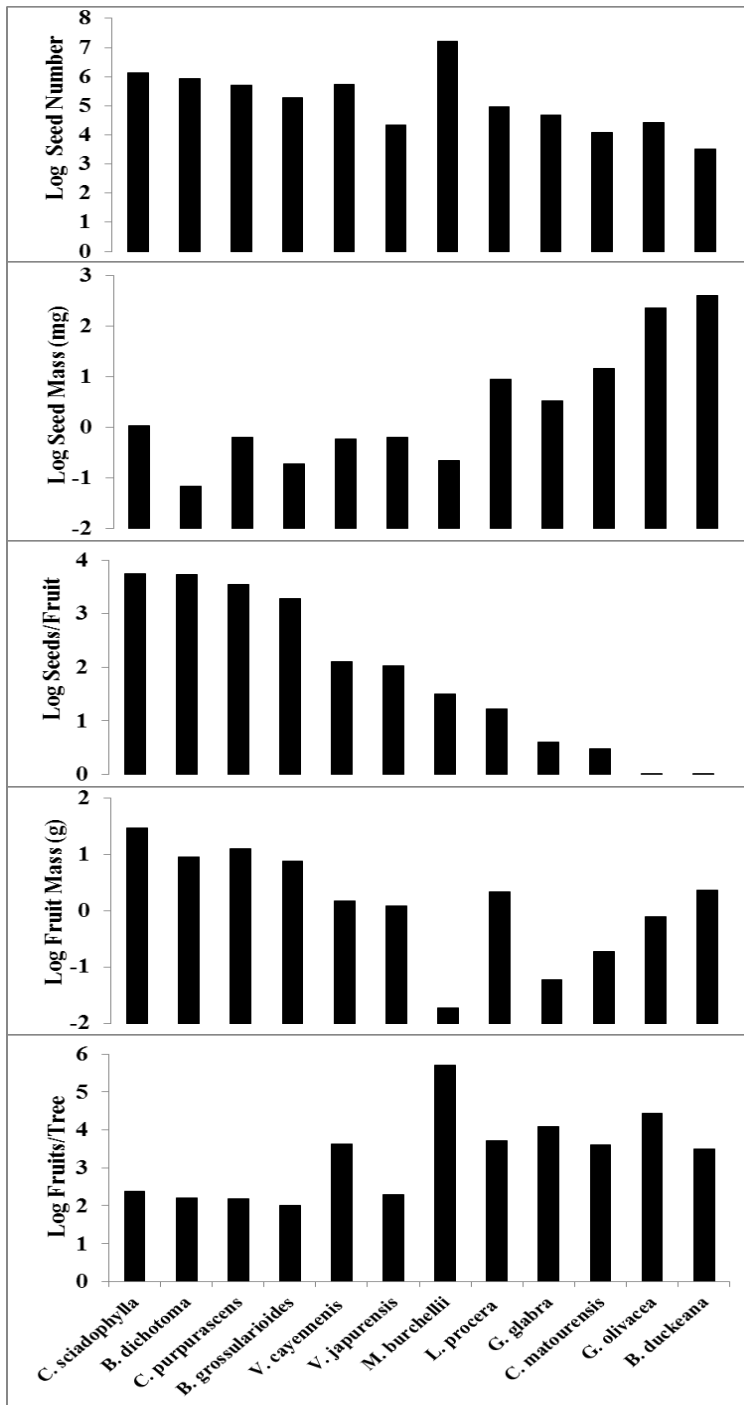
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760 **Figure 2.** Sampling design showing quadrats in light gaps and belt transects in secondary  
 761 forests, respectively, to determine seedling densities (black dots) and adult densities (open  
 762 rectangles) in secondary forest at the three sites.

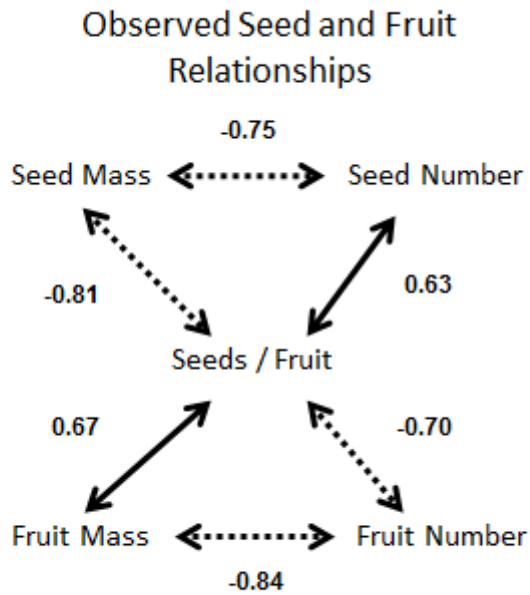
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**Figure 3.** Log<sub>10</sub> of seed number per tree, seed mass, seeds per fruit, fruit mass, and fruits per tree for 12 common pioneers tree species in Central Amazon. Species are ordered by seeds per fruit from greatest to least.

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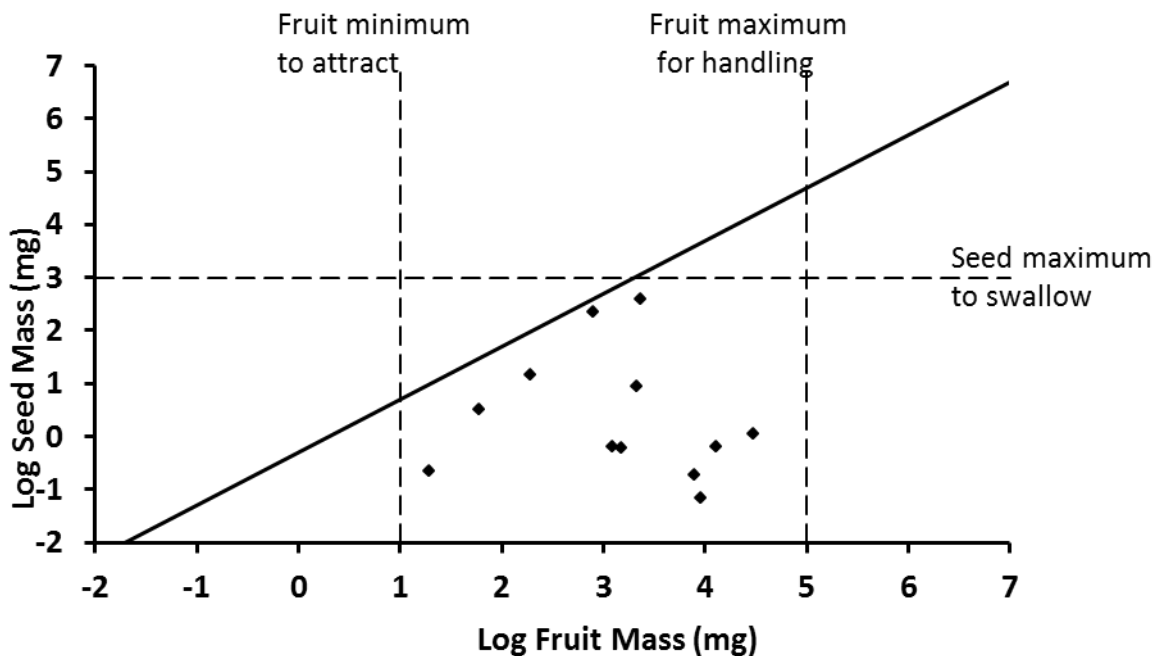


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**Figure 4.** Observed relationships among seed packaging variables for Amazon pioneer tree species. All Pearson correlation coefficients ( $R$ ) between the variable pairs are statistically significant, as critical values were  $|R| \geq 0.58$  for  $P \leq 0.05$  and  $|R| \geq 0.71$  for  $P \leq 0.01$  with  $N = 12$ .

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811 **Figure 5.** Hypothetical relationship between seed mass and fruit mass for tropical pioneer  
812 species. Solid diagonal represents one seed per fruit where seed mass equals one-half of fruit  
813 mass. All possible multi-seeded fruits would occupy space below the solid diagonal, i.e. lower  
814 seed mass for a given fruit mass. For pioneer species that are bird and bat dispersed, there are  
815 three additional limits: seed maximum to swallow is 1000 mg, fruit minimum to attract  
816 dispersers is 1.0 mg and fruit maximum for handling is 100,000 mg. Thus, the area bounded  
817 by the middle pentagon contains all possible pioneer relationships of seed mass and fruit mass  
818 for bird and bat dispersal fruits at our study site. The actual values for the 12 Amazon pioneer  
819 species from our study are the points inside the pentagon.

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824 **Appendix 1: Seed and fruit mass and germination rates.**

825 Pioneer tree species, their families, seed mass, fruit mass, percent germination, and day  
 826 number of the first and last recorded germinations. Species are ordered by seed mass,  
 827 smallest to largest.

828

Species	Mass		Germination		
	Seed (mg)	Fruit (g)	Percent	First day	Last day
<b>Melastomataceae</b>					
<i>Bellucia dichotoma</i> Cogn.	0.07	8.95	69.00	21	106
<i>Bellucia grossularioides</i> (L.) Triana	0.19	7.73	97.00	21	99
<i>Miconia burchelli</i> Triana	0.22	0.02	60.00	36	161
<b>Hypericaceae</b>					
<i>Vismia cayennensis</i> (Jacq.) Pers.	0.59	1.50	47.00	9	56
<i>Vismia japurensis</i> Reich.	0.63	1.23	100.00	14	42
<b>Urticaceae</b>					
<i>Cecropia purpurascens</i> C.C. Berg	0.65	12.91	96.00	7	34
<i>Cecropia sciadophylla</i> Mart.	1.09	29.44	46.00	7	34
<b>Goupiaceae</b>					
<i>Goupia glabra</i> Aubl.	3.30	0.06	44.00	21	56
<b>Salicaceae</b>					
<i>Laetia procera</i> (Poepp.) Eichler	9.00	2.15	50.00	14	41
<b>Euphorbiaceae</b>					
<i>Croton matourensis</i> Aubl.	14.40	0.19	70.00	22	106
<b>Annonaceae</b>					
<i>Guatteria olivacea</i> R.E. Fr.	224.00	0.78	80.00	50	120
<b>Malpighiaceae</b>					
<i>Byrsonima duckeana</i> . W.R. Anderson	398.60	2.30	30.00	103	183

829



830 **Appendix 2: Seed and fruit numbers per tree and densities.**

831 Fruiting duration, fruit number, seeds per fruit, and seed number, for the 12 pioneer  
 832 tree species, followed by seedling and adult densities (m<sup>-2</sup>). Species are ordered by  
 833 seed number per tree.

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Species	Fruiting duration	Fruit number	Seeds per fruit	Seed number	Seedling density	Adult density
<i>Miconia burchellii</i>	2.93	500,000	32	1.60 x10 <sup>7</sup>	0.5370	0.0173
<i>Cecropia sciadophylla</i>	3.33	240	5,600	1.34 x10 <sup>6</sup>	0.0890	0.0103
<i>Bellucia dichotoma</i>	5.58	160	5,300	8.48 x10 <sup>5</sup>	0.0260	0.0093
<i>Vismia cayennensis</i>	2.68	4,300	128	5.50 x10 <sup>5</sup>	0.0930	0.0137
<i>Cecropia purpurascens</i>	2.13	150	3,500	5.25 x10 <sup>5</sup>	0.0220	0.0018
<i>Bellucia grossularioides</i>	6.26	100	1,900	1.90 x10 <sup>5</sup>	0.0220	0.0010
<i>Laetia procera</i>	2.70	5,300	17	9.01 x10 <sup>4</sup>	0.0070	0.0107
<i>Goupia glabra</i>	5.21	12,000	4	4.80 x10 <sup>4</sup>	0.0040	0.0088
<i>Guatteria olivacea</i>	3.74	27,000	1	2.70 x10 <sup>4</sup>	0.5330	0.0117
<i>Vismia japurensis</i>	2.69	200	107	2.14 x10 <sup>4</sup>	0.0110	0.0033
<i>Croton matourensis</i>	0.55	4,000	3	1.20 x10 <sup>4</sup>	0.0590	0.0093
<i>Byrsonima duckeana</i>	3.15	3,200	1	3.20 x10 <sup>3</sup>	0.0040	0.0027

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## Capítulo 2

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Tony V. Bentos, Henrique E. M. Nascimento and G. Bruce Williamson. **Tree seedling recruitment in Amazon secondary forest: Importance of topography and gap micro-site conditions.** *Forest Ecology and Management* 287 (2013) 140-146.

1 **Tree seedling recruitment in Amazon secondary forest: Importance of topography and**  
2 **gap micro-site conditions**

3  
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31 ABSTRACT

32 Deforested lands in Amazonia are usually converted into pastures and maintained through  
33 annual prescribed burning which depletes the soil seed bank. Here, we assess the effect of  
34 topography and micro-site conditions on the seed bank and recruitment success of tree species  
35 in 20-year old secondary forests developing on abandoned pastures in Central Amazonia,  
36 Brazil. Seedling emergence, mortality, and growth were monitored in four 1x1-m sub-plots  
37 located systematically in the center of 21 10x10-m artificial canopy gaps, seven each on three  
38 different topographic positions - plateau, slope, and bottomland. The 84 seedling sub-plots  
39 were assigned to four different treatments generated by the combination of two litter  
40 treatments, litter intact and litter removed, and two soil treatments, soil turned and soil  
41 unturned. Sixteen soil samples were collected from the four corners of each sub-plot for  
42 analysis of seed bank. There was no significant effect of topography on the number of seed,  
43 although on the average, densities on the plateaus and the bottomlands were more than double  
44 that on the slopes. Seedling emergence increased 200% with litter removal and 50% with soil  
45 turning relative to respective controls. Seedling emergence was significantly higher in  
46 bottomlands than in slopes, and seedling growth was significantly higher in bottomlands and  
47 slopes than in plateaus, indicating that water availability may be the limiting factor for the  
48 recruitment success on the higher parts of relief. There were no effects of topography and  
49 litter removal on seedling mortality. Management tools that can accelerate succession on  
50 intensively used land offer options for fostering reforestation. Based on this study,  
51 manipulating litter and soil micro-environment provide viable methodological tools.

52

53 *Keywords:*

54 Artificial gaps

55 Seed bank

56 Litter removal

57 Soil disturbance

58 *Vismia* spp.

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## 63 1. Introduction

64 In the Brazilian Amazon, as in other tropical regions, extensive areas of primary forest,  
65 initially converted to pastures and agricultural lands, have been abandoned, leaving the  
66 vegetation in various stages of secondary succession (Aide and Grau, 2004). These secondary  
67 forests, although poorly explored, offer great potential for economic use and for conservation  
68 of anthropogenically modified landscapes (Guariguata and Ostertag, 2001; Chazdon et al.,  
69 2009). By 2006, approximately 20% of the deforested area of the Brazilian Amazon had  
70 returned to some stage of secondary succession (INPE, 2008). There is a great need to deepen  
71 and broaden our understanding of the potential for recuperating areas that have been subjected  
72 to high intensity of land use. In this regard, experimental manipulative research may provide  
73 the information necessary to develop management methodologies to facilitate the process of  
74 succession.

75 Compared to areas not subjected to annual prescribed fires, secondary forests from  
76 abandoned pastures exhibit low floristic richness (Uhl et al., 1988; Mesquita et al., 2001;  
77 Chazdon et al., 2007; Williamson et al., in press). For the Central Amazon, Norden et al.  
78 (2010) showed that during eight years of secondary succession on *Vismia*-dominated pastures,  
79 species turnover was lower than in secondary forests dominated by *Cecropia* species  
80 established on abandoned clearcuts not subjected to annual, prescribed fires. The slow  
81 succession in secondary forests originating as abandoned pastures summons the development  
82 of management practices that can accelerate succession on previously intensively used land.  
83 The seed bank, traditionally loaded with pioneer species, offers great potential for recovery of  
84 tropical degraded areas (Garwood, 1989; Aide and Cavelier, 1994). However, the diversity of  
85 species in the bank diminishes with the intensity of land use prior to abandonment. Although  
86 a majority of the pioneer species, dispersed by wind or animals, can reach abandoned areas  
87 via seed rain from adults in nearby forests, they are unlikely to germinate once secondary  
88 succession is underway. The factor that is commonly limiting to the emergence of seedlings is  
89 the availability of light, as seeds of pioneer species require radiation in the red and infrared  
90 bands in order to germinate (Vásquez-Yanes, 1980). Thus, in secondary forests just a few  
91 years old, the closing of the canopy can inhibit the emergence of seedlings as a result of low  
92 light penetration to the soil surface. For *Vismia* dominated pastures, diversity of pioneers from  
93 seed rain remains locked in the seed bank. The formation of canopy gaps from treefalls is an  
94 important mechanism maintaining the diversity of tree species, as seeds in the soil are  
95 exposed to abiotic conditions of light and humidity that are favorable to germination and

96 establishment (Orians, 1982; Denslow, 1987). Furthermore, different microsite conditions,  
97 such as the quantity and depth of litter and superficial soil disturbance that occurs in the root  
98 zone of fallen trees, tend to promote successful seedling recruitment (Orians 1982). Even so,  
99 canopy gaps from single or even multiple treefalls in secondary forests are relatively small  
100 and offer limited light and soil disturbance for successful germination as single or multiple  
101 treefalls may not turn the soil sufficiently (Saldarriaga et al., 1988; Yavitt et al., 1995;  
102 Montgomery and Chazdon, 2001; Bebber et al., 2002; Dupuy and Chazdon, 2006). Dalling  
103 and Hubbell (2002) have shown that removal of litter, instead of soil turning, has a strong  
104 effect on the emergence of seedlings in 70-year old secondary forests in Panama. Other  
105 experimental studies have also demonstrated the effect of litter removal on the germination  
106 potential of tropical tree species (e.g., Dupuy and Chazdon, 2008; Dias et al., 2011). The  
107 interaction between the quantity of litter and the quantity of light on successful recruitment of  
108 seedlings in secondary forests results both from facilitation and inhibition (*sensu* Connell and  
109 Slatyer, 1977), but the result of these two mechanisms depends on the life history  
110 characteristics of the species involved (Ganade and Brown, 2002; Dupuy and Chazdon, 2008,  
111 Shiels et al. 2010).

112 In tropical forests of central Amazonia, topography can exert a strong influence on the  
113 distribution of plant species and vegetation structure as a result of variation in the chemical  
114 and physical properties of soils. Soils on high ground, such as hilltops and plateaus, generally  
115 have a high clay content and low nutrient levels, whereas soils in bottomlands near  
116 watercourses have a high sand content, high soil humidity, and high nutrient levels, partly as a  
117 result of the accumulation of organic matter (Luizão et al., 2004; Toledo et al., 2011).  
118 Although topography has been shown to influence the angle of penetration of light such that  
119 inclined areas receive more light than bottomlands, the effects of topography on the  
120 composition of the soil seed bank and recruitment success have generally been ignored.

121 Overall, studies relating the effects of topographic position and microsite conditions such  
122 as litter and soil disturbance on seedling recruitment in young tropical forests could augment  
123 our understanding of the regeneration potential of secondary forests (Shiels et al. 2010). Thus,  
124 our study proposes to experimentally examine the effects of topography, soil litter and soil  
125 disturbance on the seed bank and on recruitment success of tree species in young secondary  
126 forests (20 years old) developing on abandoned pastures in central Amazonia. The study  
127 specifically addresses the following questions: (1) Does seed density in the soil seed bank  
128 vary with topographic position? (2) Does seedling recruitment (germination, growth and

129 mortality) in canopy gaps vary with topographic position, with presence or absence of litter,  
130 and with soil disturbance?

131

## 132 **2. Material and methods**

### 133 *2.1. Study site*

134 This study was carried out at the Biological Dynamics of Forest Fragments Project  
135 (BDFFP). The BDFFP reserves are located on *terra firme* in tropical moist forest, about 80  
136 km north of Manaus in the state of Amazonas, Brazil (2°30'S, 60°W) [Fig. 1A]. Mean annual  
137 temperature is 27° C, with a mean monthly minimum of 19° C and a monthly maximum of  
138 36° C; mean annual precipitation is about 2500 mm, with two well defined seasons - a rainy  
139 season from November through June when precipitation can exceed 300 mm/month and a dry  
140 season from July through October when precipitation occasionally drops below 100  
141 mm/month (Lovejoy and Bierregaard, 1990).

142 Soils of the region are classified as yellow latosols (Oxisol) and red-yellow podzols  
143 (Ultisol) [Ranzani, 1980]. In general, the soils are acidic and poor in nutrients, especially  
144 phosphorous, calcium, magnesium, sodium and potassium (Chauvel et al., 1987; Toledo et al.,  
145 2011). The topography in the region shows rolling hills interrupted by plateaus and  
146 bottomlands, with elevations between 40 and 140 m msl. Soils are related to topography with  
147 higher clay content on plateaus and greater sand content in the bottomlands (Chauvel et al.,  
148 1987; Toledo et al., 2011). Oxisols dominate on the plateaus, Ultisols are more common on  
149 the slopes, and Spodosols dominate the bottomlands.

150 The PDBFF reserves are composed of replicated fragments of 1, 10 and 100 ha  
151 distributed across three ranches (Dimona, Porto Alegre and Esteio) that were clearcut of  
152 primary forest in the early 1980s and abandoned or converted to pastures (Lovejoy and  
153 Bierregaard, 1990). After 4-6 years of prescribed fires for management of grasses,  
154 productivity declined in the pastures, so they were abandoned and plant succession began.  
155 These abandoned pastures are dominated by species of the genus, *Vismia*, mainly *V.*  
156 *guianensis* (Aubl.) Choisy, *V. japurensis* Reichardt e *V. cayennensis* (Jacq.) Pers. Other areas  
157 that were clearcut were never burned or burned only once and never converted to pastures;  
158 secondary vegetation on these unburned clearcuts is dominated initially by the genus  
159 *Cecropia*, mainly *C. sciadophylla* Mart. and *C. purpurascens* C.C. Berg. The two types of  
160 secondary vegetation differ substantially in structure, diversity and species composition  
161 (Mesquita et al., 2001; Williamson et al., in press). For the current study, sites were chosen in

162 the secondary forests dominated by *Vismia* at the Esteio ranch (Figure 1A) where in 2009 the  
163 secondary forests were approximately 20 years old following abandonment. In the study  
164 region, the canopy of the 20-year old secondary forests are about 15 m tall and form a  
165 relatively dense layer that impede full sunlight from reaching the understory, although the  
166 understory is less shaded than that of the primary forests. In nearby *Vismia*-dominated  
167 secondary forests, PAR (photosynthetically active radiation) level averaged  $14.7\% \pm 18.3$   
168 (mean  $\pm$  standard deviation) of full sunlight (Jakovac et al., in press). Stand basal area is  $20.4$   
169  $\pm 6.9$  m<sup>2</sup>/ha and stem density is  $2009.5 \pm 709.8$  individuals/ha for trees with DBH  $\geq 5$  cm.  
170 Species richness is relatively low with only 51 espécies (DBH  $\geq 5$  cm) found in a 0.21 ha  
171 sample area. Only four species (*Vismia cayennensis*, *Bellucia dichotoma*, *Bellucia*  
172 *grossularioides* and *Vismia japurensis*) constitute 53% of the individuals (T.V. Bentos,  
173 unpublished data).

174

## 175 2.2. Experimental design

### 176 2.2.1. Canopy gaps and topographic position

177 In the first week of May of 2009, at the end of the rainy season, 21 plots of approximately  
178 100 m<sup>2</sup> (10 x 10 m) were located under closed canopy in the secondary forests distributed  
179 throughout an 8-km<sup>2</sup> study area at the BDFFP. Distance between nearest neighbor plots was  
180 at least 200 m from each other and more than 350 m for most of them, (Figure 1B). The  
181 200m criterion was intended to ensure independence of the plots. The plots were distributed  
182 across six different secondary forest stands spread throughout the study area, each stand  
183 representative of 20-year old secondary forest dominated by *Vismia* species. Our objective  
184 was to obtain plots representative of pastures that had been abandoned 20 years after high  
185 intensity use following clearcutting. This type of secondary forest is very common throughout  
186 the Central Amazon, although extrapolating outside our study area requires accommodating  
187 additional variation in soil, climate and seed sources. The plots were converted into artificial  
188 canopy gaps by cutting and removing all trees, including seedlings, vines and decomposing  
189 woody matter. Adult trees were cut at the trunk base with a chainsaw, while smaller  
190 individuals were uprooted manually and discarded. Care was taken to minimize disturbance to  
191 soil and litter throughout the 10 x10 plot, and trees were cut to fall outside the 3 x 3 m center  
192 of the canopy gap. When necessary, litter depths after creation of a canopy gap were corrected  
193 in small patches to return to levels measured prior to opening the canopy gap (data not  
194 shown). The 21 plots were spread evenly across three topographic positions - plateaus, slopes



195 and bottomlands (Figure 1B). Elevation varied significantly among topographic positions  
196 ( $F_{2,18} = 88.79$ ,  $P < 0.001$ ), averaging  $135.4 \pm 1.79$  m.s.n.m (mean  $\pm$  standard error),  $126.7 \pm$   
197  $0.52$  and  $113.3 \pm 0.84$  for plateaus, slopes bottomlands, respectively. Soil particle size also  
198 differed by topographic position ( $F_{2,18} = 7.31$ ,  $P = 0.005$ ), as there was less sand on plateaus  
199 ( $126.4 \pm 35.1$  g kg<sup>-1</sup>) than on slopes ( $225.4 \pm 40.2$ ) than on bottomlands ( $383.2 \pm 63.6$ ).

200

#### 201 2.2.2. *Litter and soil treatments*

202 In the middle of each artificial canopy gap plot, a 3 x 3 m quadrat was delineated along  
203 with four 1 x 1 m sub-plots at its corners (Fig. 1C) in the third week of May of 2009. The four  
204 sub-plots received the four litter and soil turning treatments (Figure 1C): litter removed or not  
205 and soil turned or not. Hereafter, we designate the treatments as “CC” for litter control, soil  
206 control; “LC” for litter removed, soil control; “CS” for litter control, soil turned; and “LS” for  
207 litter removed, soil turned. For the CS treatment, we first removed the litter and subsequently  
208 turned the soil and then litter was returned in place. To some degree, these treatments  
209 approximate part of the variation in microsite conditions in natural canopy gaps (Orians,  
210 1982). For example, litter removal and soil turning characterize the uprooting zones or trunk  
211 scrapes of treefalls. Besides initially removing litter, we removed freshly fallen litter monthly  
212 for seven months. Soil turning was concentrated in the upper 5 cm of soil, as the majority of  
213 viable seed is generally found in the surface soils (Garwood, 1989; Dalling et al., 1995).

214

#### 215 2.2.3. *Seed bank*

216 For each plot, 16 soil samples were collected from the four corners of each sub-plot for  
217 analysis of viable seeds (Figure 1C). Soil samples were extracted with a soil borer, 5 cm deep  
218 and 10 cm diameter, immediately after converting the plots into canopy gaps (third week of  
219 May, 2009). The 16 samples from each plot were thoroughly mixed and then spread in a layer  
220 1 cm deep over washed sand, in rectangular (55 x 35 cm) plastic trays 8 cm deep. Trays were  
221 exposed to natural light under 50% shade cloth in a greenhouse and monitored every two  
222 weeks for germinations over 258 days. Germinating seedlings were allowed to grow until they  
223 could be identified, at which time they were removed.

224

#### 225 2.2.4. *Monitoring seedlings*

226 After conversion of plots into canopy gaps, emerging seedlings were monitored monthly  
227 over a period of seven months from the end of the rainy season (May) to the end of the dry

228 season (December, 2009). Data recorded monthly were the heights of all living individuals  
229 between censuses, as well as new seedlings and mortality during the interval from the prior  
230 monitoring. Each new plant to emerge at the monthly census was marked with a plastic tag to  
231 distinguish it in future censuses. As the dry season is mild at this site, germinations normally  
232 are frequent when the soil is exposed to light. The experiment was concentrated in the dry  
233 season in order to determine seedling emergence from the seed bank, stocked during prior  
234 fruiting months and years, as fruiting is concentrated in the rainy season, December to April  
235 (Bentos et al., 2008). Our intent was to monitor seedling emergence from the seed bank,  
236 without undue influence of fresh seed rain.

237

### 238 2.3. *Data analysis*

239 Seedling mortality was calculated as the ratio of the number of seedling deaths divided  
240 by the total number of seedling emergences during the seven months. For all individuals alive  
241 after seven months, relative growth rate (RGR) was calculated as the logarithm of the final  
242 height, minus the logarithm of the initial height measurement, divided by the time over which  
243 the height difference was recorded. As seedlings emerged at different months, the time of  
244 growth varied among them. Three-way ANOVAs were used to test for the effects of  
245 topography, litter removal and soil turning on number of seedlings emerging, relative growth  
246 rate, and mortality of seedlings. Topography, litter removal and soil turning were fixed effects  
247 with three classes of topography (plateau, slope and bottomland), two classes of litter  
248 (C=litter control and L=litter removed), and two classes of soil turning (C=soil control and  
249 S=soil turned). Each combination of litter and soil treatments had 21 replicates, equal to the  
250 21 plots, and each topographic position had 7 replicates. For the soil collected, the effect of  
251 topographic position on number of seedlings emerging from the seed bank was evaluated with  
252 a one-way ANOVA.

253 Prior to the analyses, data were log-transformed where necessary to achieve normality  
254 and reduce heterocedasticity. Our data variables were extremely variable (variance  $\gg$  mean  
255 and correlated with it) indicative of a negative-binomial which is better analyzed by  
256 logarithmic transformation than by a GLM with Poisson errors. For mortality, no  
257 transformation was necessary as the rates were not near the extremes of one or zero. All  
258 analyses were performed with SYSTAT 12.0 (Wilkinson, 2007).

259

260

261 **3. Results**

262 *3.1. Soil seed bank*

263 In the greenhouse, a total of 3,439 seeds germinated in the soil trays over 258 days of  
264 observation. They represented 18 species from ten genera in eight families, all typical  
265 pioneers of the region. Melastomataceae was the richest family with seven species and the  
266 most abundant family with 82.3% of the individuals. The four most common species  
267 comprised 90% of the individuals: *Bellucia dichotoma* Cong. (Melastomataceae) was the  
268 most abundant with 54% of the individuals, followed by *Miconia poeppigii* Triana  
269 (Melastomataceae) com 19%, *Vismia cayennensis* (Hypericaceae) and *Miconia burchellii*  
270 Triana, each with 9%. At the other extreme, *Aparisthium cordatum* (A.Juss.) Baill.  
271 (Euphorbiaceae) and *Miconia phanerostila* Pilg. were represented by only one individual  
272 (Supplementary material Table S-1).

273 The density of seeds germinated in the trays was extremely variable within topographic  
274 classes, ranging from 427 to 4,312 seeds m<sup>-2</sup> on soil from plateaus, from 142 to 1,202 from  
275 slopes and from 554 to 3,267 from bottomlands. This extreme variability between replicate  
276 sites within topographic positions also characterized the four most abundant species (Fig. 2).  
277 The ANOVA of the total germination revealed no significant effect of topographic position  
278 ( $F_{2, 18} = 1.99, P = 0.17$ ), despite the average densities on the plateau and the bottomland being  
279 more than double that on the slopes. Species richness of the germinated species varied only  
280 slightly across topographic classes with 14 species in the plateaus and bottomlands and 13  
281 species on the slopes.

282

283 *3.2. Seedling emergence in canopy gaps*

284 A total of 906 seedlings, from 30 species in 22 genera and 14 families emerged in the 21  
285 plots during the 209 days of study. Hypericaceae, Melastomataceae and Euphorbiaceae were  
286 the richest families with five species each. The three most abundant families, Hypericaceae,  
287 Melastomataceae and Urticaceae constituted 81.4% of the plants germinated. *B. dichotoma*,  
288 *Cecropia sciadophylla* (Urticaceae) and *V. cayennensis* represented almost half (46.7%) of all  
289 recruits, followed by *Vismia japurensis*, *V. guianensis*, *C. purpurascens*, *M. poeppigii*, *Isertia*  
290 *hypoleuca* Benth. (Rubiaceae), *Trema micrantha* (L.) Blume (Cannabaceae) and *M.*  
291 *burchellii*. The 20 least common species accounted for only 7.8% of the individuals  
292 (Supplementary material Table S-1).

293 There were significant effects of topographic position ( $F_{2,63}=3.28$ ,  $P=0.044$ ) and litter  
294 removal ( $F_{1,63}= 22.9$ ,  $P<0.0001$ ) on the density of seedlings emerged. Soil turning had a  
295 modest, positive effect on seedling emergence, statistically significant for a one-tailed  
296 hypothesis ( $F_{1,63}=3.62$ ,  $P=0.031$ ). There was no interaction of the three main factors  
297 ( $F_{6,72}=0.5$ ,  $P=0.80$ ). The density of seedlings in the bottomlands ( $15.3 \pm 5.5$ , mean  $\pm$  SE) was  
298 significantly higher than on the slopes ( $6.63 \pm 1.6$ ) (Tukey's pairwise tests,  $P<0.05$ ); however,  
299 the density on the plateaus ( $12.7 \pm 4.8$ ) did not differ from the bottomlands or the slopes (Fig.  
300 3A). Litter removal and soil turning (LC and LS treatments, respectively) generated the  
301 highest recruitment, whereas litter control (CS) and soil control (CC) showed the fewest  
302 seedlings. Differences pairwise between LC and LS and between CC and CS were not  
303 significant (Tukey's pairwise tests,  $p < 0.05$ , Fig. 3A). On average, recruitment of seedlings  
304 with litter removal was about three times that with litter intact, and recruitment with soil  
305 turned was about one and a half times that with soil unturned, as shown by the treatment  
306 means of CS ( $6.3 \pm 1.6$  seedlings  $m^{-2}$ ), LC ( $14.8 \pm 5.2$ ), LS ( $20.7 \pm 7.6$ ), and CC ( $4.4 \pm 1.4$ ).

307 Among the most common species only *C. purpurascens* showed a significant effect of  
308 topographic position on recruitment ( $F_{2,9} = 4.53$ ;  $P=0.044$ ), where the density in the  
309 bottomlands was higher than on the plateaus (Tukey's pairwise test,  $P<0.05$ ). Comparisons  
310 among congeners showed no significant differences in seedling recruitment across  
311 topographic classes (*Cecropia sciadophylla* versus *C. purpurascens* and *Vismia cayennensis*,  
312 *V. guianensis* and *V. japurensis*). Comparisons between these genera, *Cecropia* and *Vismia*,  
313 also showed no significant differences in seedling density.

314

### 315 3.3. Seedling mortality and growth in canopy gaps

316 There were no significant effects of the main factors - topographic position ( $F_{2,63}=0.56$ ,  
317  $P=0.58$ ), litter presence ( $F_{1,63}=0.0004$ ,  $P=0.95$ ) and soil turning ( $F_{1,63}=0.04$ ,  $P=0.84$ ) on the  
318 proportion of seedlings dying during the monitoring (Fig. 3B).

319 There was a significant effect of topographic position on relative growth rate ( $F_{2,52}=6.9$ ,  
320  $P=0.002$ ). On average, relative growth in the bottomlands ( $0.22\pm 0.02$ ) and the slopes  
321 ( $0.23\pm 0.03$ ) was significantly greater than on the plateau ( $0.15\pm 0.02$ , Tukey's Test,  $P<0.05$ ),  
322 but growth in bottomlands was not different than on slopes (Fig. 3C). Relative growth rates  
323 were not affected significantly by litter removal ( $F_{1,52}=1.81$ ,  $P=0.18$ ), by soil turning  
324 ( $F_{1,52}=0.36$ ,  $P=0.55$ ) or their interactions.

325

## 326 4. Discussion

### 327 4.1. Seed bank

328 Mônaco et al. (2003) found only six species in the seed bank of an 8-year old *Vismia*  
329 secondary forest at the BDFFP, and here we encountered 18 species in a secondary forest that  
330 was 20 years old. Thus, the pioneer species are arriving to become part of the seed bank as  
331 time since abandonment increases. Species richness aside, the density of seeds in the seed  
332 bank was similar in the two studies, with a mean of 1.46 seeds m<sup>-2</sup> in Mônaco et al. (2003)  
333 and 1.30 in this study. The seeds in the soil were predominantly small (<15mg wet weight;  
334 Bentos et al., in press ), typical of pioneer species established in secondary forests dominated  
335 by *Vismia*, suggesting dispersal by small bats and small birds foraging in secondary forests,  
336 but not bringing primary forest seeds into the foraging area (Wieland et al., 2011). At a  
337 distance of 3 to 4 km from primary forest, dispersal agents from the primary forest apparently  
338 were not seeking food or shelter in the secondary forests, as there was little recruitment of  
339 primary forest tree species. In the BDFFP, Mesquita et al. (2001) showed a substantial decline  
340 of regenerating plants in adjoining second regrowths as the distance from primary forest  
341 increases.

342 The density of seeds in the soil was extremely variable spatially among plots across  
343 topographic positions. Dalling and Hubbell (2002) also found tremendous variation among  
344 plots, in their case plots separated by only 30 m and located on a single plateau of secondary  
345 forest. In our study two of the four most common species, *B. dichotoma* and *M. poeppigii*,  
346 were excessively abundant in two plots, suggesting that seed dispersal probably resulted from  
347 nearby reproductive trees because seeds and seedlings of these species tend to be concentrated  
348 around adults (Dalling et al., 1998). Dominance of a few pioneer species is characteristic of  
349 secondary forests derived from abandoned pastures in the central Amazon (e.g., Mesquita et  
350 al., 2001; Mônaco et al., 2003; Norden et al., 2010); furthermore, there is little differentiation  
351 among them across topographic position as seedlings (shown here) or as adults (T.V. Bentos,  
352 unpublished data). Several studies have reported the influence of topography on the  
353 composition of species in the soil seed bank of intact, mature forests (e.g. Bertiller, 1992;  
354 Ashton et al., 1998; Singhakumara et al., 2000), although the causal processes driving these  
355 patterns are rarely known. Additionally, studies conducted out in tropical forests, for both  
356 intact and perturbed stands, but without consideration of topography, have demonstrated that  
357 the abundance of species in the seed bank generally depends on seed rain and seed survival in  
358 the soil (Roberts, 1986; van Tooren, 1988; Simpson et al., 1989). Here, we uniquely

359 investigated seed bank composition across topography in secondary forests, but we were  
360 generally unable to establish a relationship between species composition or seed density, as  
361 there was tremendous variation among plots, as shown elsewhere in neotropical secondary  
362 forests (Van Bruegel 2006, 2007). Perhaps other factors such as proximity to fruiting trees are  
363 regulating the content of the seed bank and obscuring any effect of topography. However,  
364 other studies, conducted in Mediterranean vegetation (Cerdeira and García-Fayos, 2002) and in  
365 areas of restoration in the central Amazon (Nascimento, 2009), have confirmed that seed loss  
366 from the soil seed bank is accelerated on slopes. Such a mechanism may be driven by the  
367 small size of pioneer seeds and their location in the superficial layers of soil (Garwood, 1989;  
368 Dalling et al., 1995).

369

#### 370 4.2. *Recruitment success*

371 In the initial stage of plant life, germination and establishment appear to be enhanced  
372 greatly by litter removal and only moderately by soil turning. The multiple effects, direct and  
373 indirect, of litter on recruitment and growth of seedlings are widely known. Micro-conditions  
374 under leaf litter include physical pressure, high humidity, reduced light, altered light  
375 spectrum, presence of pathogens, and allelopathic compounds - all potentially inhibiting  
376 germination, emergence, and survival of seedlings (Vásquez-Yanes et al., 1990; Facelli and  
377 Pickett, 1991; Cintra, 1997; Dupuy and Chazdon, 2008; Dias et al., 2011). In this study, most  
378 of the species in the seed bank, as well as those that germinated in the field plots after litter  
379 removal, had small seeds. Therefore, the negative effect of the litter on seedlings probably  
380 resulted from the physical barrier and the lack of light. In Costa Rica, large canopy gaps (>  
381 270 m<sup>2</sup>) in secondary forest at La Selva exhibited substantially more recruitment than small  
382 gaps (Dupuy and Chazdon, 2006). In our study, variability in light was controlled by creating  
383 artificial canopy gaps, all of which were the same size (100 m<sup>2</sup>) and initiated simultaneously.  
384 In a separate study, near the artificial canopy gaps, but under closed canopy, only two  
385 seedlings emerged in 56 1 x 1m sub-plots over the seven months after litter removal and soil  
386 turning (T.V. Bentos, unpublished data), therein showing the importance of light for  
387 recruitment of tropical pioneers at the site.

388 The higher number of plants emerging and the greater growth of those plants in the  
389 topographic bottomlands indicate some factors other than light are limiting, as light levels are  
390 likely to be lowest in the bottomlands. One plausible explanation is higher soil fertility in the  
391 bottomlands as they exhibit higher concentrations of exchangeable bases and phosphorous

392 (Chauvel et al., 1987; Toledo et al., 2011). Phosphorous is one of the essential elements most  
393 limiting to plants especially in highly mineralized soils (Lambers et al., 2008). A second  
394 plausible explanation for more recruitment in bottomlands is the added soil moisture and  
395 humidity during the dry season. Daws et al. (2008) suggested that pioneer species with their  
396 small seeds need humid microsites to germinate and establish as the seeds germinate best at or  
397 near the soil surface where mortality from drying can occur rapidly (Bewley and Black, 1982;  
398 Ashton, 1992). In our study, seedling emergence was relatively uniform across topographic  
399 position for the first half of the study, but in the latter half, germinations in the plateau  
400 dropped off considerably (data not shown). In areas where soil nutrients have been leached or  
401 exhausted by agriculture, different responses by species may become pronounced for  
402 seedlings as this stage is critical in the plant life cycle (Harper, 1977). Thus, factors related to  
403 photosynthetic efficiency and absorption of water and nutrients are fundamental establishment  
404 characteristics differentiating pioneers from mature forest species (Santos et al., 2006; Silva et  
405 al., 2006).

406 Despite the existence of variation in the availability of soil water and nutrients, seedling  
407 mortality was not affected significantly across topographic positions. Although we did not  
408 attempt to determine the causes of mortality, many dying seedlings appeared to suffer from  
409 desiccation. Therefore, we assume that competition could be a factor responsible for the  
410 mortality especially during the second half of the study, which corresponded to the driest time  
411 of the year. Other studies also suggest that hydric stress in canopy gaps is responsible for  
412 mortality of seedlings in the dry season (Dalling and Hubbell, 2002; Daws et al., 2005).  
413 Timing of seed germination may be critical for survival, as emergence in the rainy season  
414 may permit sufficient root growth to weather the first dry season, whereas seedling  
415 emergences in the dry season avoid competition for resources that characterizes the start of  
416 the rainy season when most fruit is produced (Daubenmire, 1972; Bentos et al. 2008). Dupuy  
417 and Chazdon (2008) experimentally showed that removal of nearby competitors significantly  
418 reduced seedling mortality in canopy gaps.

419 Finally, one might question whether the seedlings emerging in the artificial gaps here  
420 would contribute to the secondary forests where they lay in the seed bank unable to germinate  
421 without a natural disturbance to permit penetration of light into the understory. Other studies  
422 in young *Vismia* stands near the study area have clearly demonstrated that pioneers continue  
423 recruitment as openings occur through self-thinning and disturbance (Mesquita et al., 2001;  
424 Williamson et al., in press). In fact, *Vismia* stands exhibit exceeding by slow species

425 turnover, despite mortality of adult stems, suggesting that pioneers are continuing to recruit  
426 during the early years, and perhaps decades, of succession (Norden et al., 2010). Similar  
427 pioneer recruitment has been documented in other Neotropical successions, even where  
428 turnover is more rapid (Van Bruegel et al., 2006, 2007).

429

## 430 **5. Conclusions**

431 This study provides some guidance on effects of factors that determine seedling  
432 recruitment success in natural regeneration in secondary forests. Based on these results and  
433 concordance with others studies, the following recommendations are offered here. The first  
434 step in making decisions about alternative management options, especially where natural  
435 restoration relies on the soil seed bank, is to understand the variation in potential regeneration  
436 across an area. The predominant form of land use in the Amazon Basin, conversion to pasture  
437 after deforestation, results in the total elimination of natural forest and depletion of much of  
438 the seed bank. Reforestation of these abandoned pastures requires available seed sources.  
439 Thus, managing the seed bank through manipulation such as litter removal and soil turning,  
440 may be effective in enriching the secondary community where it lacks breadth in biodiversity  
441 as is the case in abandoned pastures. The extremely strong effect of removing litter and the  
442 moderate effect of soil turning are useful tools to activate the seed bank and accelerate the  
443 emergence of seedlings.

444

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454

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614 **Figure Captions**

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616 Fig. 1. A) Map of the experimental area of the Biological Dynamics of Forest Fragments  
617 Project (BDFFP), showing three ranches (Dimona, Porto Alegre, and Esteio). Areas in gray  
618 and white are secondary and primary forests, respectively. B) Sketch showing the distribution  
619 of the plots of artificial clearings as a function of topographic position in the secondary  
620 vegetation at the Esteio ranch where the study was conducted. C) Sketch of the 1 x 1 m sub-  
621 plots which received the four treatments: CC = litter control, soil control; LC = litter  
622 removed, soil control; CS = litter control, soil turned; and LS = litter removed, soil turned.  
623 The points on the corners of each sub-plot indicate where soil was collected for the seed bank  
624 study.

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626 Fig. 2. Variation in the density of seeds in the soil seed bank (mean  $\pm$  maximum and  
627 minimum) that germinated during 258 days in the greenhouse for three topographic positions  
628 (plateau, slope and bottomland) for the four most abundant species germinating.

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630 Fig. 3. A) Density of seedlings that emerged (mean  $\pm$  standard error), B) proportion of  
631 seedlings that died (mean  $\pm$  standard error) and C) relative growth rate of seedlings (mean  $\pm$   
632 standard error) for the four combinations of litter and soil treatment (CC = litter control, soil  
633 control; LC = litter removed, soil control; CS = litter control, soil turned; and LS = litter  
634 removed, soil turned) after 209 days of monitoring (May to November of 2009) in the three  
635 topographic positions (plateau, slope and bottomland).

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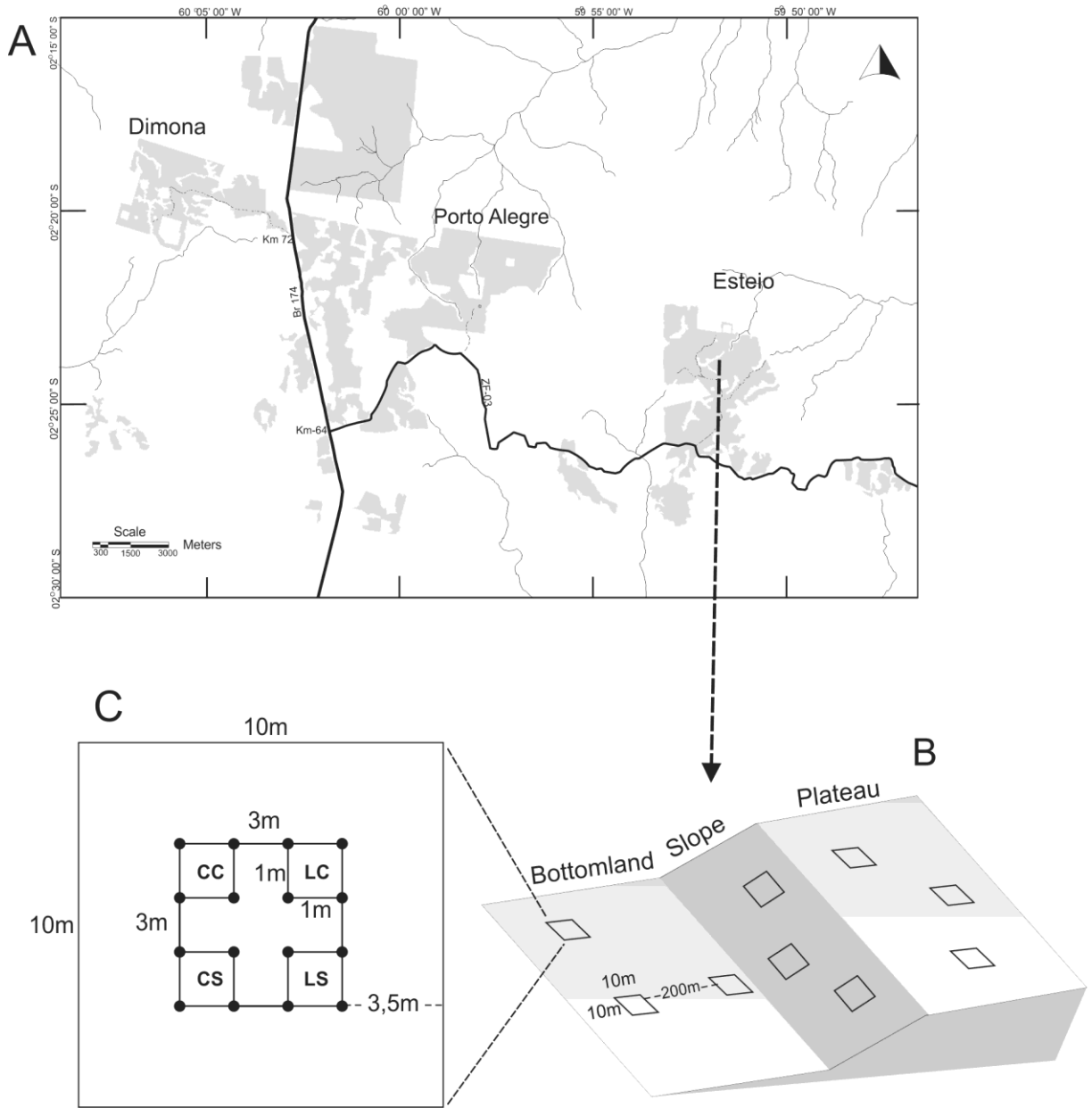
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645 **Fig. 1**

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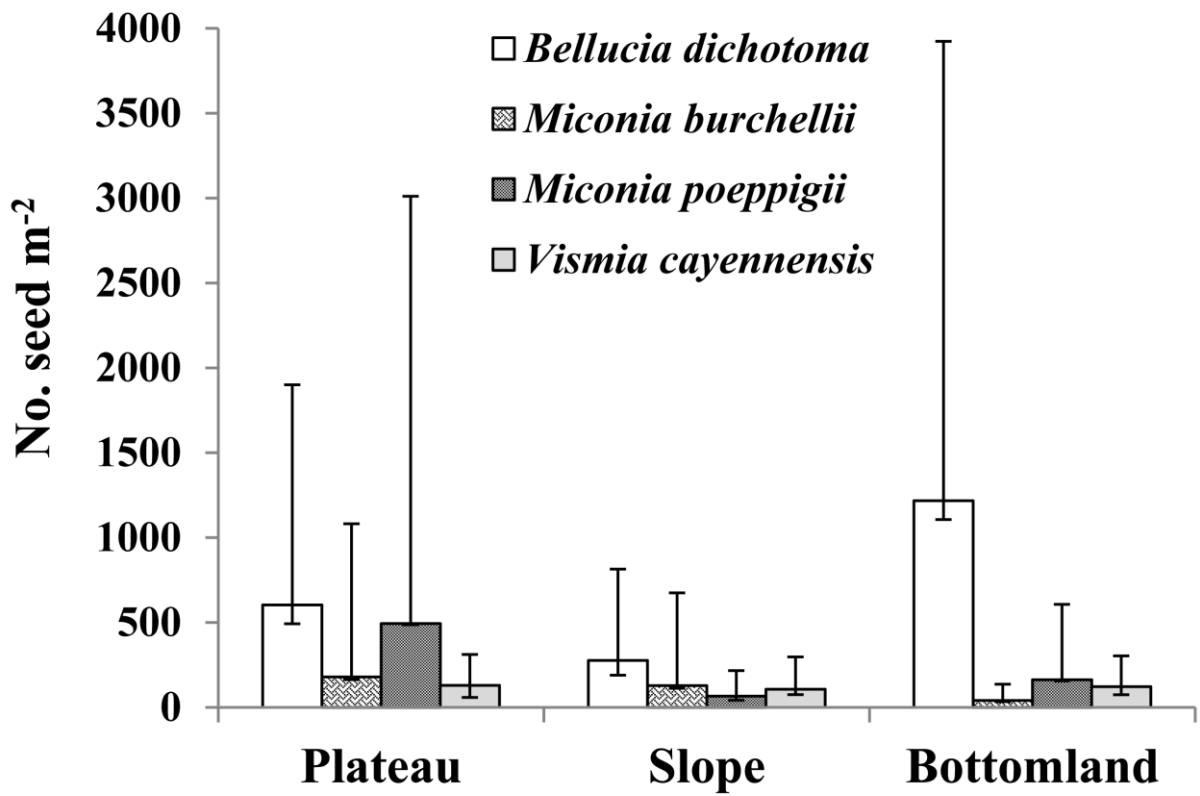
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654 Fig. 2



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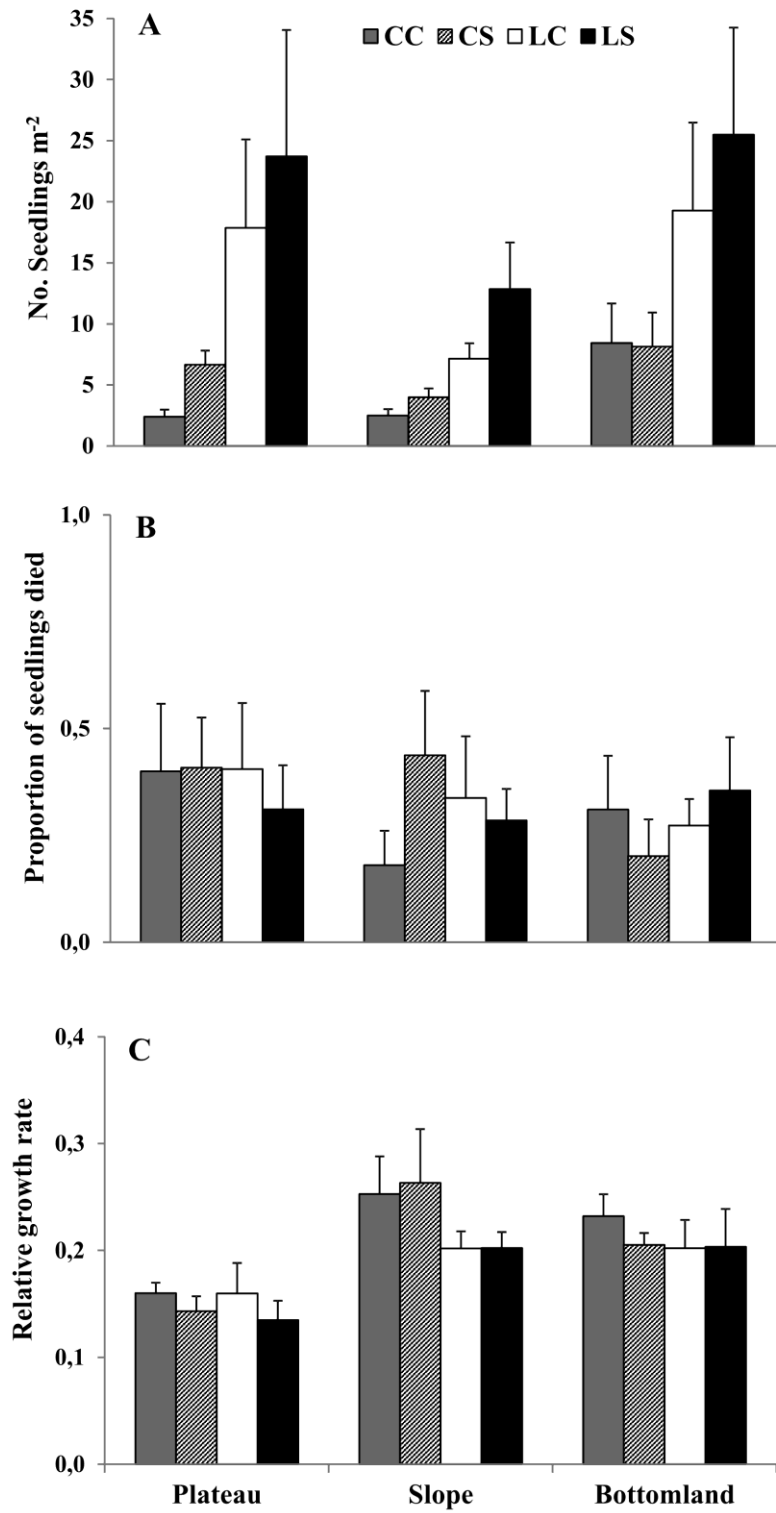
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668 Fig. 3



670 Table S-1. Number of seedling emergents in the soil seed bank study and in the artificial  
 671 canopy gaps. Values represent numbers individuals per m<sup>2</sup>.

Family/Species	Density (m <sup>2</sup> )	
	Soil Seed Bank	Canopy Gaps
<b>Annonaceae</b>		
<i>Bocageopsis multiflora</i> (Mart.) R.E.Fr.		0.01
<i>Guatteria scytophylla</i> Diels		0.04
<b>Bignoniaceae</b>		
<i>Jacaranda copaia</i> (Aubl.) D.Don		0.04
<b>Burseraceae</b>		
<i>Trattinnickia burserifolia</i> Mart.		0.08
<b>Cannabaceae</b>		
<i>Trema micrantha</i> (L.) Blume	7.53	0.61
<b>Euphorbiaceae</b>		
<i>Aparisthium cordatum</i> (A.Juss.) Baill.	0.38	0.07
<i>Alchornia discolor</i> Poepp.		0.04
<i>Croton matourensis</i> Aubl.		0.07
<i>Maprounea guianensis</i> Aubl.		0.04
<i>Sapium glandulosum</i> (L.) Morong		0.01
<b>Goupiaceae</b>		
<i>Goupia glabra</i> Aubl.		0.01
<b>Hypericaceae</b>		
<i>Vismia cayennensis</i> (Jacq.) Pers.	119.80	1.33
<i>Vismia guianensis</i> (Aubl.) Choisy	8.66	0.89
<i>Vismia japurensis</i> Reichardt	4.52	0.90
<i>Vismia gracilis</i> Hieron.		0.04
<i>Vismia sandwithii</i> Ewan		0.01
<b>Lacistemataceae</b>		
<i>Lacistema aggregatum</i> (P.J.Bergius) Rusby	3.77	0.05
<b>Malpighiaceae</b>		
<i>Byrsonima duckeana</i> W.R.Anderson		0.02

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679 Table S-1. Continuation

Family/Species	Density (m <sup>2</sup> )	
	Soil Seed Bank	Canopy Gaps
<b>Melastomataceae</b>		
<i>Bellucia dichotoma</i> Cogn.	699.22	1.93
<i>Bellucia grossularioides</i> (L.) Triana	3.77	0.02
<i>Miconia poeppigii</i> Triana	241.86	0.65
<i>Miconia burchellii</i> Triana	116.79	0.48
<i>Miconia dispar</i> Benth.	6.03	
<i>Miconia pyrifolia</i> Naudin	1.51	0.02
<i>Miconia phanerostila</i> Pilg.	0.38	
<b>Rubiaceae</b>		
<i>Isertia hypoleuca</i> Benth.	36.17	0.65
<i>Palicourea guianensis</i> Aubl.	1.13	0.10
<b>Salicaceae</b>		
<i>Casearia arborea</i> (Rich.) Urb.	5.65	0.12
<i>Laetia procera</i> (Poepp.) Eichler		0.05
<b>Siparunaceae</b>		
<i>Siparuna guianensis</i> Aubl.		0.01
<b>Urticaceae</b>		
<i>Cecropia sciadophylla</i> Mart.	31.65	1.77
<i>Cecropia purpurascens</i> C.C. Berg.	6.78	0.71

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## SÍNTESE

Neste estudo foi possível avaliar a importância das características reprodutivas, condições de micro-sítio e da posição topográfica sobre o recrutamento e estabelecimento de espécies arbóreas em áreas de florestas secundárias da Amazônia Central.

Apesar de espécies pioneiras fazerem parte de uma única guilda ecológica, a fenologia reprodutiva das 12 espécies variou de contínuo para supra-anual, sendo que a sazonalidade anual foi a mais comum para estas espécies. Com isso, a duração da frutificação não teve relação com o estabelecimento de plantas. No entanto, a variação do peso e número tanto de sementes como de frutos para as 12 espécies foi extremamente alta, quando comparada com outros estudos também realizados com espécies pioneiras e com espécies de floresta madura. Além disso, a maior importância das variáveis relacionadas a frutos, comparativamente às variáveis relacionadas às sementes, é um resultado inédito neste estudo, pois a variação no número de sementes não explicada pela variável peso de semente foi melhor explicada pela variável peso e número de frutos. O modelo “seed packaging” prediz que o incremento no número de sementes por fruto está associado com o menor peso de sementes e o maior número de sementes, e com um maior peso de frutos e menor número de frutos e estas relações foram confirmadas neste estudo. Além disso, a densidade de plântulas e adultos foi melhor explicada pelo peso e número de frutos e não pelo peso e número de sementes, mostrando a importância da dispersão de frutos como o componente mais importante no sucesso do recrutamento em comunidades pioneiras.

A variação do banco de sementes no solo foi também importante para se conhecer o potencial regenerativo de florestas secundárias estabelecidas após pastagem abandonada, nas quais a remoção de serrapilheira e o revolvimento da camada superficial tiveram um forte efeito sobre o estabelecimento de espécies arbóreas. Além disso, tanto a emergência como o crescimento de plântulas também foram influenciadas pela variação topográfica. Áreas mais baixas do relevo tiveram maior recrutamento de plântulas, indicando a importância da disponibilidade de água e de alguns nutrientes limitantes ao crescimento das plantas, tal como o fósforo, como fatores importantes no sucesso do recrutamento. Dessa forma, apesar de refinar o nosso conhecimento no que diz respeito à importância das características reprodutivas sobre o estabelecimento de plantas em florestas secundárias, nossos resultados também fornecem ferramentas práticas visando iniciar a recuperação de áreas degradadas, em que a remoção de serrapilheira juntamente com o revolvimento do solo é uma importante técnica de manejo para incrementar a emergência de plântulas a partir do banco de sementes presentes no solo.

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## **ANEXOS\***

\*Pareceres emitidos pelas bancas examinadoras da aula de qualificação, da versão escrita da tese e da defesa pública da tese, respectivamente.



Ministério da  
Ciência e Tecnologia



## AULA DE QUALIFICAÇÃO

### PARECER

Aluno(a): TONY VIZCARRA BENTOS  
 Curso: ECOLOGIA  
 Nível: DOUTORADO  
 Orientador(a): HENRIQUE E. M. NASCIMENTO  
 Co-Orientador(a): BRUCE G. WILLIAMSON

#### Título:

"A importância das características micro-ambientais e topográficas no recrutamento e estabelecimento de espécies pioneiras em clareiras artificiais dentro de uma área de floresta secundária dominada por *Vismia* spp."

#### BANCA JULGADORA:

##### TITULARES:

José Francisco Gonçalves (INPA)  
 Renato Cintra (INPA)  
 Antônio C. Webber (INPA)  
 Newton Leal (INPA)  
 Rita G. Mesquita (INPA)

##### SUPLENTES:

Alberto Vicentin (INPA)  
 João Ferraz (INPA)

EXAMINADORES	PARECER	ASSINATURA
José Francisco Gonçalves (INPA)	<input checked="" type="checkbox"/> Aprovado ( ) Reprovado	
Renato Cintra (INPA)	<input checked="" type="checkbox"/> Aprovado ( ) Reprovado	
Antônio C. Webber (INPA)	<input checked="" type="checkbox"/> Aprovado ( ) Reprovado	
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João Ferraz (INPA)	<input type="checkbox"/> Aprovado ( ) Reprovado	

Manaus(AM), 26 de junho de 2009

OBS: Os membros da banca julgadora estão de acordo que o aluno apresentou e respondeu satisfatoriamente os questionários que foram formulados. No sentido de contribuir com a formação do curso os membros sabem que o mesmo apresenta bons conhecimentos de áreas que se sua pesquisa

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### Avaliação de tese de doutorado

Título: **Potencial Reprodutivo e Regenerativo de Espécies Arbóreas em Florestas Secundárias na Amazônia Central**

Aluno: **Tony Viscarra**

Orientador: Henrique Nascimento

Co-orientador: Bruce Williamson

**Avaliador: Carolina Volkmer de Castilho**

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 )	( )	( )	( )
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### Avaliação de tese de doutorado

Título: **Potencial Reprodutivo e Regenerativo de Espécies Arbóreas em Florestas Secundárias na Amazônia Central**

Aluno: **Tony Vizcarra**

Orientador: **Henrique Nascimento**

Co-orientador: **Bruce Williamson**

**Avaliador: Bráulio Almeida Santos**

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Relevância do estudo	( X )	( )	( )	( )
Revisão bibliográfica	( )	( X )	( )	( )
Desenho amostral/experimental	( X )	( )	( )	( )
Metodologia	( X )	( )	( )	( )
Resultados	( X )	( )	( )	( )
Discussão e conclusões	( )	( X )	( )	( )
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João Pessoa, PB

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Literature review	( )	( X )	( )	( )	( )
Sampling design	( )	( X )	( )	( )	( )
Methods/procedures	( )	( X )	( )	( )	( )
Results	( )	( X )	( )	( )	( )
Discussion/conclusions	( )	( )	( X )	( )	( )
Writing style and composition	( )	( X )	( )	( )	( )
Potential for publication in peer reviewed journal(s)	( )	( X )	( )	( )	( )

<p><b>FINAL EVALUATION</b></p> <p><input checked="" type="checkbox"/> <b>Approved without or minimal changes</b></p> <p><input type="checkbox"/> <b>Approved with changes</b> (no need for re-evaluation by this reviewer)</p> <p><input type="checkbox"/> <b>Potentially acceptable, conditional upon review of a corrected version</b> (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)</p> <p><input type="checkbox"/> <b>Not acceptable</b> (This product is incompatible with the minimum requirements for this academic level)</p>
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ATA DA DEFESA PÚBLICA DA TESE DE  
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GRADUAÇÃO EM ECOLOGIA DO  
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DA AMAZÔNIA

Aos 15 dias do mês de janeiro do ano de 2013, às 09:00 horas, no auditório do Programa de Pós Graduação em Clima e Ambiente – PPG CLIAMB/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Flávio Jesus Luizão**, do Instituto Nacional de Pesquisas da Amazônia – INPA/CDAM, o(a) Prof(a). Dr(a). **Renato Cintra**, do Instituto Nacional de Pesquisas da Amazônia – INPA/CBio e o(a) Prof(a). Dr(a). **Charles Eugene Zartman**, do Instituto Nacional de Pesquisas da Amazônia – INPA/CBio, tendo como suplentes o(a) Prof(a). Dr(a). Niwton Leal Filho, do Instituto Nacional de Pesquisas da Amazônia – INPA/CDAM e o(a) Prof(a). Dr(a). José Francisco de Carvalho Gonçalves, do Instituto Nacional de Pesquisas da Amazônia – INPA/CDAM, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública do trabalho de **TESE DE DOUTORADO** de **TONY VIZCARRA BENTOS**, intitulado “Potencial Reprodutivo e Regenerativo de Espécies Arbóreas em Florestas Secundárias na Amazônia Central”, orientado pelo(a) Prof(a). Dr(a). Henrique Eduardo Mendonça Nascimento, do Instituto Brasileiro de Informação em Ciência e Tecnologia – IBICT/MCTI e co-orientado pelo(a) Prof(a). Dr(a). Bruce Williamson, da Louisiana State University – LSU/EUA.

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


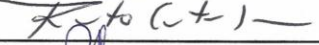

- APROVADO(A)                       REPROVADO(A)  
 POR UNANIMIDADE                       POR MAIORIA

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

Prof(a).Dr(a). Flávio Jesus Luizão

Prof(a).Dr(a). Renato Cintra

Prof(a).Dr(a). Charles Eugene Zartman

  
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