ANDRÉ ARAÚJO DA PAZ

SIMULAÇÃO DE ALAGAMENTO COMO FILTRO AMBIENTAL PARA O RECRUTAMENTO DE ESPÉCIES ÁRBÓREAS

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Ecologia, para obtenção do título de *Magister Scientiae*.

VIÇOSA
MINAS GERAIS - BRASIL
2016

Ficha catalográfica preparada pela Biblioteca Central da Universidade Federal de Viçosa - Câmpus Viçosa

T
P348s
2016

Paz, André Araújo da, 1990-
Simulação de alagamento como filtro ambiental para o recrutamento de espécies arbóreas / André Araújo da Paz. – Viçosa, MG, 2016.
19f. : il. (algumas color.) ; 29 cm.

Orientador: Aristéa Alves Azevedo.
Dissertação (mestrado) - Universidade Federal de Viçosa.
Inclui bibliografia.

1. Ecologia vegetal. 2. Matas ripárias. 3. Comunidades vegetais. 4. Plantas e solo. 5. Plantas - Efeito das inudanções. I. Universidade Federal de Viçosa. Departamento de Biologia Vegetal. Programa de Pós-graduação em Ecologia. II. Título.

CDD 22. ed. 577.82

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APROVADA: 08 de Abril de 2016

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O caminho que o rio segue não é o mais curto, o mais direto. Com modéstia e sabedoria, sem se impor, o rio apenas segue a linha de menor resistência. Demora, mas chega ao mar. Seu segredo é a persistência. Sua força é a humildade.

(Professor Hermógenes)

Agradecimentos

Agradeço às minhas famílias. Meus parentes que me deram apoio para continuar os estudos, e luz nos momentos de desespero que, infelizmente, parecem comuns na Pós-graduação. Aos amigos e colegas que me acompanharam nesses anos de trabalho e durante todo o processo de aprendizado e construção de um "cientista". Agradeço à Professora Flávia Maria, minha amiga, pela oportunidade de trabalhar no projeto Floresta Escola, onde surgiram as primeiras perguntas que guiaram minha monografia, e em sequência, meu mestrado. Seu jeito irreverente e amigável contribuiu significativamente para a minha formação, principalmente como pessoa. À HidroEx, aqui representando todos que conheci na etapa anterior ao mestrado e que me permitiu ver com meus próprios olhos aquilo que seria minha linha de pesquisa pelos anos vindouros e que me estimulou a pensar mais alto do que eu achava que poderia chegar. Ao professor Ricardo Campos, pela formação durante os cursos de campo e o apoio e incentivo em dar continuidade às questões não respondidas na minha Monografia. Agradeço também aos meus Co-orientadores pela ajuda durante a discussão do projeto e durante o decorrer dos experimentos.

Agradeço a todos que conheci durante as disciplinas, principalmente aos amigos que fiz na Ecologia e na Botânica, minhas casas na UFV. Aos professores, que junto com os alunos, me ensinaram durante as saídas de campo, nas salas de aula, durante os treinamentos em escrita científica, e que me passaram todo o conhecimento que foi necessário para formular e responder as perguntas que surgiram durante esta etapa.

Durante a coleta de dados, foi essencial a ajuda de vários amigos. Agradeço em especial ao Caio Victor pelo apoio antes, durante e depois das coletas, sem contar os cafezinhos diários e seu humor único. Ao meu irmão Samu Fernandes, que deu apoio em várias fases, principalmente no projeto e treinamento em técnicas de laboratório. Agradeço à Lizandra, que chegou enquanto estávamos em uma parte complicada do trabalho, mas que ainda assim permaneceu para que chegássemos até o final. Ao Ricardo Mundinho, Luan Calegari, Tércia Vargas, Kyle Larson, e todos que ajudaram a trocar a água e lavar os potes semanalmente durante a fase da inundação das sementes. Ao João Paulo e ao Camilo Guzmán pelas contribuições durante a manutenção do experimento quando me ausentei. Agradeço ao Luiz Ladeira e ao Fábio Loatti pela ajuda durante o final do experimento na casa de vegetação. Durante a análise de dados foi essencial a ajuda do Bob Solar, que me mostrou a melhor forma de analisar os dados e me permitiu seguir com as demais análises por mim mesmo, além de ajudar com o forte incentivo na comunicação científica. Agradeço ao pessoal do Laboratório de Anatomia, em nome da Aurora, Luana e Isabel, por me ajudarem durante todo o processo, pouco conhecido por mim.

Agradeço ao pessoal do curso de Ecologia da Floresta Amazônica, que me mostrou como escrever um artigo científico e divulgar meu trabalho. Além das experiências no "coração da Amazônia", onde pude ver ambientes naturalmente sujeitos ao alagamento. Agradeço à Profª Astrid por me receber na UFAM e compartilhar várias idéias e artigos, essenciais para minha formação.

Aos meus amigos da Trem Folk, pela válvula de escape musical que me permitiu aprofundar mais em uma parte importante de mim e relaxar durante os momentos de tensão: "Life is a long song". À Zoë Fahy por toda a paciência e carinho, e pela ajuda durante parte da coleta de dados, escrita e revisão de alguns termos.

Por fim agradeço ao Laboratório de Ecologia, onde por tanto tempo fiquei. Um obrigado especial à Sílvia, nossa técnica que fazia sempre mantinha tudo a nosso alcance. Ao “English day”, ao cafezinho e ao chopp pós-laboral! Sentirei saudades.

RESUMO

PAZ, André Araújo da, M.Sc., Universidade Federal de Viçosa, abril de 2016. **Simulação de alagamento como filtro ambiental para o recrutamento de espécies árbóreas**. Orientadora: Aristéa Alves Azevedo. Coorientadores: Flávia Maria da Silva Carmo e Cleberson Ribeiro.

Em áreas ciliares o alagamento nas planícies de inundação pode ocorrer em diferentes frequências e intensidades, dependendo das condições locais. Habitats às margens dos rios são mais propensos a inundações do que os mais elevados na paisagem. Este gradiente hídrico seleciona diferentes grupos de plantas de acordo com sua tolerância à inundação. No entanto, quando os rios são barrados por ações antrópicas pode ocorrer o alagamento de áreas até então nunca inundadas. As condições hídricas geradas afetarão as comunidades e determinadas espécies poderão ter sua distribuição comprometida, uma vez que suas sementes ou plantas jovens podem não suportar o alagamento. Consequentemente, pode haver perda de espécies e serviços ecossistêmicos em decorrência das novas condições impostas. Na recuperação dessas áreas ciliares há espécies indicadas para recuperar hábitats alagáveis (HA) e não-alagáveis (HA). Para testar a hipótese de que sementes e plântulas de espécies de HN não resistem a inundações prolongadas, escolhemos espécies de ambos hábitats e realizamos um experimento de inundação prolongada em sementes e plântulas por 90 dias. O alagamento afetou de forma distinta a germinação das sementes das diferentes espécies, havendo respostas semelhantes em ambos os grupos. A germinação sob alagamento foi acelerada, mas ocorreu em menor número. Ao contrário do esperado, duas espécies de HA não germinaram enquanto submersas. As plantas jovens também tiveram seu desenvolvimento comprometido pelo alagamento, diminuindo o crescimento em altura, o investimento em folhas e a taxa fotossintética. Plantas das espécies de HN foram mais prejudicadas e praticamente perderam suas raízes. A restauração ecológica de reservatórios e áreas submetidas ao alagamento temporário deve ser criteriosa e levar em conta as características das diferentes fases de vida das plantas a serem utilizadas.

ABSTRACT

PAZ, André Araújo da, M.Sc., Universidade Federal de Viçosa, April, 2016. **Flooding simulation as an environmental filtering for recruitment of tree species**. Adviser: Aristéa Alves Azevedo. Co-advisers: Flávia Maria da Silva Carmo and Cleberson Ribeiro

In riparian areas the waterlogging of floodplains can occur at different frequencies and intensities, depending on the conditions of each site. Habitats near river banks are more prone to flooding than the ones higher in the landscape. This gradient of water conditions between habitats select different groups of plants according to their tolerance to flooding. However, when rivers are barred by human actions, it can occur the waterlogging of areas never flooded before. The water conditions generated in these new margins affect plant communities. Certain species may have its spatial distribution compromised, since their seeds or young plants can not withstand flooding. Consequently, these communities could lose ecosystem services and biodiversity as a result of the saturated conditions. In the restoration of these ecosystems different species are indicated according to the flood susceptibility of the area, so being species for restoration of flooded (FH) and non-flooded habitats (NH). To test the hypothesis that seeds and seedlings of NH species do not withstand prolonged flooding, we submitted seeds and seedlings of eight species of both groups to 90 days of flooding. The induced flooding affect differently the germination of seeds of different species. Germination under flooding was accelerated, but in a small number. Contrary to expectations, two species of FH did not germinate while submerged. Young plants also have their development compromised by flooding, with lower growth, less investment in new leaves and lower photosynthetic rate. Plants of NH species were more affected and almost lost their roots. The ecological restoration of reservoirs and areas subject to temporary flooding needs to be cautiousness and take into account the characteristics of the different stages of plant life to be used.

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Introdução Geral

As matas ciliares, ou matas ripárias são aquelas que ocorrem ao redor de rios e corpos d'água. Dessa forma estão sujeitas a condições hídricas do solo variáveis, dependendo da distância em relação ao canal principal do rio. Os pulsos de inundação ocorrem naturalmente nestas áreas, de acordo com a vazão e a precipitação das chuvas principalmente. Dessa forma, a comunidade vegetal ao redor de cursos d'água é estruturada de modo que nas margens alagáveis há espécies tolerantes a certo nível de inundação enquanto que distante dess1a borda as espécies tendem a ser mais sensíveis. Ao construir uma barragem, quer seja para o armazenamento de água ou para produção de energia elétrica, a água atinge áreas nunca antes alagadas, e que antes faziam parte do interior da mata ciliar. Além disso, ao longo do ano ocorrem pulsos de inundação que variam conforme as necessidades antrópicas, e que ocorrem em diferentes intensidades e frequências. Durante os pulsos de inundação muitos propágulos são dispersos pela água, e portanto, novas sementes irão compor o banco de sementes local, além daquelas já trazidas pela chuva de sementes. Porém, a mesma água que traz as sementes pode ser responsável pela sua morte, funcionando como um filtro ambiental nesses hábitats. Os filtros ambientais são condições ou processos abióticos que permitem ou não o estabelecimento de indivíduos em determinado local, e que precede os processos bióticos. Se as sementes e plântulas das margens alagáveis não resistem ao distúrbio da inundação, elas não farão parte da comunidade regenerante e não terão chances de participar da sucessão ecológica em processo. Os indivíduos arbóreos na margem formada podem morrer devido ao alagamento, abrindo espaço para que novos indivíduos regenerantes os substituam. Dessa forma a sucessão e o processo de recrutamento de espécies arbóreas será alterado pelo alagamento induzido. Uma vez que há plantas com diferentes níveis de tolerância a esse distúrbio, e que sua distribuição é dependente das condições locais, é importante compreender como sementes e plântulas de espécies ocorrentes em hábitats naturalmente alagáveis ou não-alagáveis respondem ao alagamento induzido. Compreender a dinâmica de comunidades vegetais atingidas por barragens e auxiliar na tomada de decisões frente a restauração ecológica dessas áreas se faz importante em um país rico em recursos hídricos e que possui diversos barramentos de água e que vem construindo cada vez mais represas hidroelétricas para suprir a crescente demanda energética do país.

INDUCED FLOODING AS AN ENVIRONMENTAL FILTERING FOR RIPARIAN TREE SPECIES

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Abstract

The waterlogging of commonly non-flooded soils acts as a filtering for plant communities. Rivers impoundment can flood a large area never flooded before, changing the local conditions and affecting seeds and growing plants. Therefore, the recruitment process in the regenerating community on these new formed margins may be inhibited. We hypothesize that tree species indicated to restore flooded habitas (FH) are more tolerant then species indicated to the restoration of non-flooded habitats (NH), by having a higher seed germination and better seedling development. Seeds of species from (FH) and (NH) were submitted to treatments of flooding (F) and non-flooding (N) for 90 days, and germination was daily registered. Also individuals of *P. guajava* and *H. serratifolius* were submmited to the same treatments and morphophysiological parameters were measured. Species from both groups had similar patterns of germination, and for most species flooding led to a faster germination. Contrary to the expected, two species from FH had no germination under flood, what was not seen in the NH group. The number of germinated seeds was smaller in F, except for two species, one of each group. The only difference in *P. guajava* plants was a decreased in growth and photosynthesis under flooding. For *H. serratifolius* there were chlorosis, foliar abscission, a negative net photosynthetic rate and root-rotting. Flooding was harmful for plants of both groups, but were worst for seeds and seedlings NH species. The outcomes show that the indication of species to restoration must take into account the different life stages, since the responses must be different among them. These results must be considered at restoration programs of reservoirs margins.

Key-words: *restoration ecology, hydrobiology, water stress, plant recruitment, flood tolerance*

1. Introduction

The occurrence of flooding in riparian habitats may happen in different frequencies, periodicity and reaching different water levels (Poff *et al.* 1997). As a consequence of waterlogging, soil O_2 concentration can be drastically reduced and physicochemical alterations in the soil can be displayed (Kozlowski 1984). Habitats closer to streams are more prone to flooding than habitats farther or higher in the landscape which are less or not subjected to waterlogging (Junk, Bayley & Sparks 1989). This lateral gradient of water in the soil may characterize a stress or a disturbance, acting as an environmental filtering, and as such, may select different plant species (Kraft *et al.* 2015). Thus, different functional groups of species, or guilds, may be identified in the community in means of its responses (Merritt *et al.* 2010), such as related to flood tolerance.

Flooding, considered as the soil waterlogging or submergence (Jackson & Colmer 2005) occurs naturally in some riverscapes. Nonetheless, when the flow and rhythmicity of the stream are artificially controlled, such as in the case of dam construction (Ward & Stanford 1995), the flooding spatial and temporal patterns may change. Depending on the intensity of those changes, the area influenced by flooding may be exposed to very different environmental conditions. In these new formed habitats, i.e. the margins of what was once a non-flooded forest, now occurs periodical flooding, affecting established plants, seedlings and seed banks. Since during the first stages of development plants are more fragile, this disturbance must be more harmful to seeds and seedlings (Ferreira *et al.* 2007). Thus, the plant regeneration process at the community must be affected by the disturbance of flooding and the spatial distribution of species and ecological processes must be altered in this novel ecosystem (Hobbs *et al.* 2006). The community structure must then change and new species may establish or even dominate the area depending on its ability to survive flooding.

To analyze the effects of flooding on the recruitment proccess of different riparian species we ran a laboratory experiment. We hypothesize that the prolonged flooding can interfere with the plant recruitment by negatively affecting seed germination or seedling development. The seeds of tolerant species should have higher germination rate and for a longer period. Also the seedlings must have a better development and exhibit morphological and physiological adaptations to survive to prolonged flooding periods when compared with sensitive species. Understanding how seeds and seedlings respond to induced flooding may contribute to the restoration of riparian areas affected by dams and reservoirs. The comprehension of these factors is important in face of the growing energy demand worldwidely and the great hydro-electrical power dams constructions employed to face it, especially in tropical developing countries (Palmeirim, Peres & Rosas 2014).

2. Methods

2.1 Plant material

We selected arboreal species indicated by Martins (2014) for the restoration of flooded and non-flooded riparian areas, here considered as from flooded habitats (FH) or non-flooded habitats (NH) for means of expected tolerances. Of those, we chose eight species (Fig. 1), being four from each group. The species from FH were: *Hymenea courbaril* L. (Fabaceae-Caesalpinioideae), *Psidium guajava* L. (Myrtaceae), *Pterogyne nitens* Tul. (Fabaceae-Caesalpinioideae) and *Schinus terebinthifolius* Raddi (Anacardiaceae); and the species from NH were: *Apuleia leiocarpa* (Vog.) Macbr. (Fabaceae-Caesalpinioideae), *Enterolobium contortisiliquum* (Vell.) Morong. (Fabaceae-Mimosoideae), *Handroanthus serratifolius* (Vahl) S. Grose (Bignoniaceae), botanical synonim *Tabebuia serratifolia* (Vahl) G. Nich., and *Peltophorum dubium* (Spreng.) Taub. (Fabaceae-Caesalpinioideae).

Seeds of these species were acquired from the Laboratory of Analysis of Forest Seeds; Forest Engineer Department at Federal University of Viçosa (UFV), MG, Brazil. They are usually colected from more than 5 plants, in cities in a maximum distance of 100 Km away from Viçosa, in the Rio Doce and Rio Paraíba do Sul Basins.

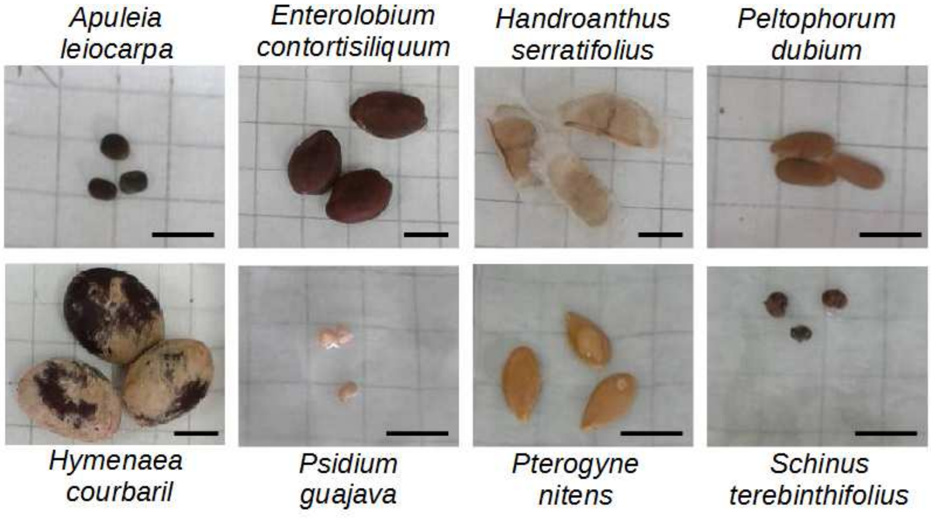

Figure 1: Seeds from the species used in the floodig experiment. The upper four species are indicated for the restoration of flooded areas and the bottom ones for restoration of non-flooded areas. *Bars* approximately 1cm

2.2 Germination under flooding

The seeds were disinfected by submersion in water solution of commercial sodium hypochlorite 1% for two minutes (Marques & Joly 2000) and washed in distilled water. No procedure was taken for overcoming seed dormancy, since it would change the natural characteristics of the seeds tegument that could allow some species to tolerate prolonged submergion. Plastic recipients of 50 ml were filled with tap water, forming a 5 cm water column, to set the flooded treatment (F). To set the non-flooded treatment (N), representing the control situation, the recipients had its bottom lined with two layers of filter paper (Brasil Ministério da Agricultura Pecuária e Abastecimento 2009). Three seeds were put in each recipient and were totally covered by water in F and were put over soaked filter papers in N. Seeds of all species used in the study did not float, except those of *H. Serratifolius*, which sank after embebition. In each treatment we used 129 seeds distributed in 43 recipients.

The seeds were observed daily during 90 days looking for germination, which was characterized by the emission of radicule (Bernhardt *et al.* 2008). Seeds that were visibly deteriorated were removed and registered as dead. We measured total germination, percentage of germination, time to 50% of seeds germination (Paz, Mazer & Martínez-Ramos 1999), and the percentage of dead seeds.

To simulate the receding of flooding in the floodplain margins at different time periods we run a parallel germination test with submerged seeds in the same conditions as described above. We set six periods of flooding: 15, 30, 45, 60, 75 and 90 days for each species. Each 15 days the seeds of seven recipients were removed from water and transferred to recipients lined with wet filter paper, amounting 21 seeds per period. After transference, these seeds were observed for more 90 days looking for germination. Seeds that germinate or decompose before water removal were registered as germinated underwater.

These experiments were carried out in a growing chamber with humidity of 70% and mean temperature of 25 ºC (± 2), under photo-period of 12h and light intensity between 700 and 1000 LUX (Brasil Ministério da Agricultura Pecuária e Abastecimento 2009). The water of each recipient was changed weekly to avoid toxin accumulation (Marques & Joly 2000).

2.2.1 Statistical Analysis

We ran ANOVA adopting Weibull distribution to analyze the data of time to germination (Souza & Fagundes 2014), assuming time as explanatory variable and the germination percentage as the response variable. To this Survival Analysis we did not consider the 0 (zeros), generated by non-germinated or dead seeds.

We chose to present germination and death data as absolute numbers and as percentages. To calculate the percentages we adopted the formula: (ni/N)*100, where: ni=germinated or dead seeds of a given species; N=total number of seeds of this given species. We ran a Tukey-Kramer test to compare the germination between treatments for each species. For this we joined the data of germination in 3 groups of 43 seeds.

2.3 Seedling development under flooding

Seedlings from *Psidium guajava* and *Handroanthus serratifolius* that germinated in the first experiment were taken to a greenhouse and planted in commercial substrate (Tropstrato®) in pots of 250 ml. After 75 days the seedlings were transplanted to pots of 2000 ml to allow a better rooting (Kawaletz *et al.* 2014). Eight pots of each species were waterlogged, with a 1 cm layer of water above the soil (F), and eight were just wet (N). The experimental units were daily watered. To avoid algae formation the pots were bagged in black plastic and a circular tap of Tetrapak® covered the soil. The temperature was measured daily, and had a mean of 24,6 ºC (±1,8). Also the pH of the water in the flooded pots were measured for each species. The mean pH in the *P. guajava* pots were of 6,83 (± 0,22) and in the *H. serratifolius* pots were of 6,95 (± 0,14).

2.3.1 Morphophisiological analysis

Every 15 days we measured height, collar diameter and number of leaves of each plant. Also, we observed and registered the presence of hypertrophied lenticels, chlorosis and of adventitious roots above the ground. After 90 days of experiment, when the plants had almost 6 months, we measured the net assimilation rate of CO_2 (A) under an irradiance of 2000 μmol photons m^{-2} s^{-1} using a IRGA, Infra Red Gas Analyzer (Mielke *et al.* 2005). For each treatment we used five plants and in each of two leaves, we made six continuous measurements. After that, three plants were cut in the collar region separating the aerial part and the root system (Kolb *et al.* 1998). They were dried in a stove at 70ºC for 72 hours to obtain the dry biomass of each part.

2.3.2 Anatomical analysis

We took three plants to analyze their anatomical structure of stems at the collar region and at 5 cm above the apex of the main root. The cuts were fixed in FAA 50, following the ethanol series from ethanol 70% until 95%. After fixation procedure, the plant material was embedded in methacrylate (Historesin, LEICA Instruments). Cross sections of 5µm were taken using an automatic rotary microtome (model RM2255; Leica Mycrosystems). The slices were stained with toluidine blue and mounted in synthetic resin (Permount, Fisher Scientific) (Dalvi *et al.* 2014).

2.3.3 Statistical Analysis

To analyze the prediction that in P. guajava the growth in height, the collar diameter and the number of leaves would be less altered by the flooding, opposing to the expected for H. serratifolius, a t-test was carried out to each parameter. Also, a t-test was adopted to compare the net photosynthetic rate and the shoot:root ratio between the different treatments. We chose not to consider the outliers of photosynthesis data.

3. Results

Among the NH species, *A. leiocarpa* and *H. serratifolius* seeds showed significant differences in the patterns of time to germination. Seeds of both species germinated under water (Fig. 2) (χ^2=87.37, p=0.00 and χ^2=10.45, p=0.001, respectively). *E. contortisiliquum* and *P. dubium* time to germination was similar on both treatments (χ^2=0.04, p=0,84 and χ^2=2.4, p=0.12). The percentage of germination was significantly different for *A. leiocarpa* ($F_{(1, 5)}$=76.25; p<0.01), *H. serratifolius* ($F_{(1, 5)}$=34.76; p<0.01), *H. courbaril* ($F_{(1, 5)}$=57.23; p<0.01), *P. guajava* ($F_{(1, 5)}$=44.66; p<0.01), *P. nitens* ($F_{(1, 5)}$=20.65; p<0.05) and *S. terebinthifolius* ($F_{(1, 5)}$=325.25; p<0.001), but was similar for *E. contortisiliquum* ($F_{(1, 5)}$=1.04; p=0.36) and *P. dubium* ($F_{(1, 5)}$=6.28; p=0.06).

H. courbaril and *S. terebinthifolius* seeds did not germinate in F (Figs 2 and 3) although both were classified as FH. The submerged seeds of *H. courbaril* had its interior melted by the prolonged flooding, and the seeds were dead by the end of the experiment (Table 1). On the opposite, flooded *P. guajava* seeds showed the greatest germination rate (Fig. 3) and a fast time to germination (χ^2=200.91, p<0.001). Seeds of *P. nitens* did not show difference in the time to germination between treatments (χ^2=0.47, p=0.49), but differences were found in the number of germinated seeds (Fig. 3).

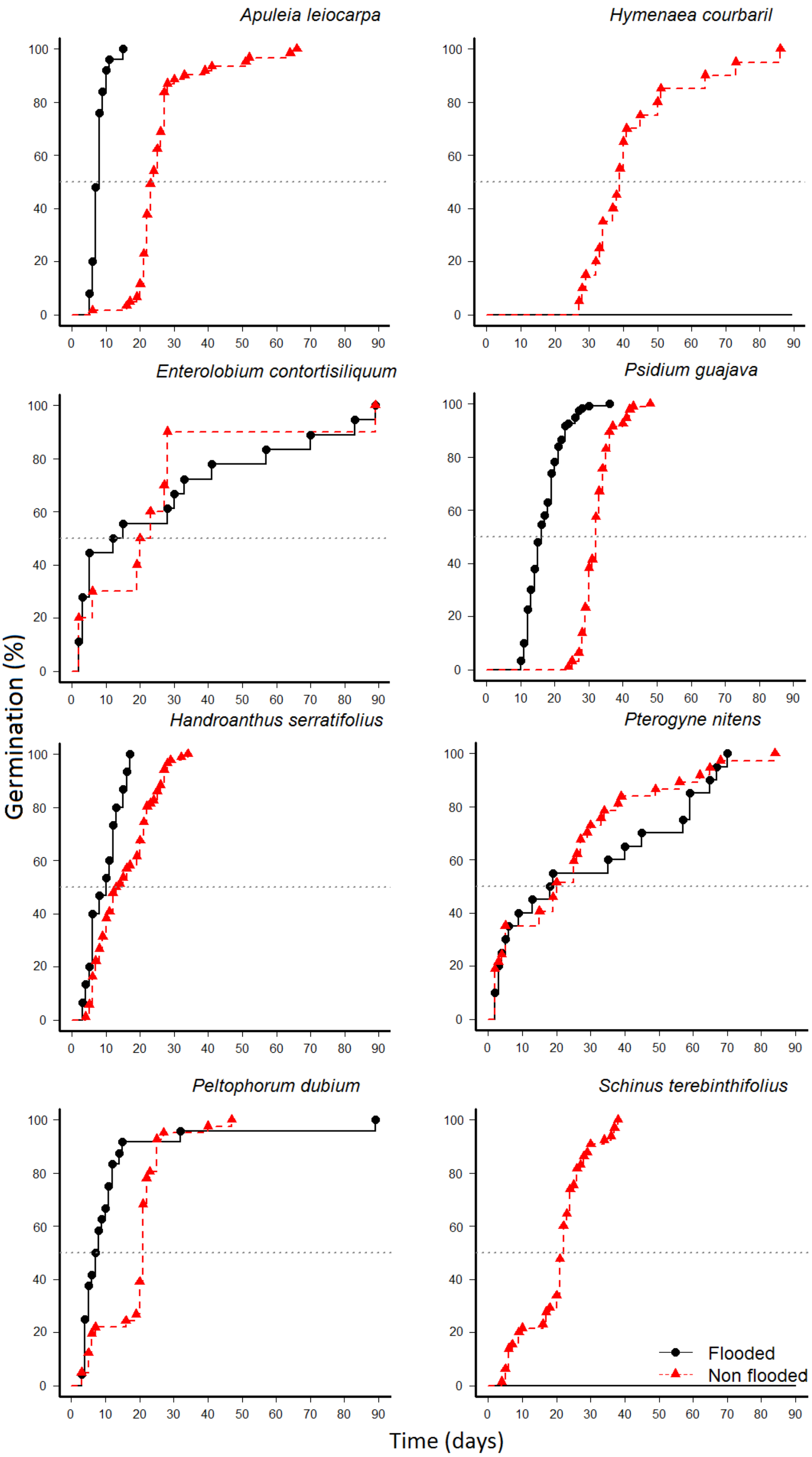

Figure 2: Time for germination of arboreal species seeds indicated for the restoration of naturally flooded and non-flooded habitats submitted to flooding and non-flooded conditions.

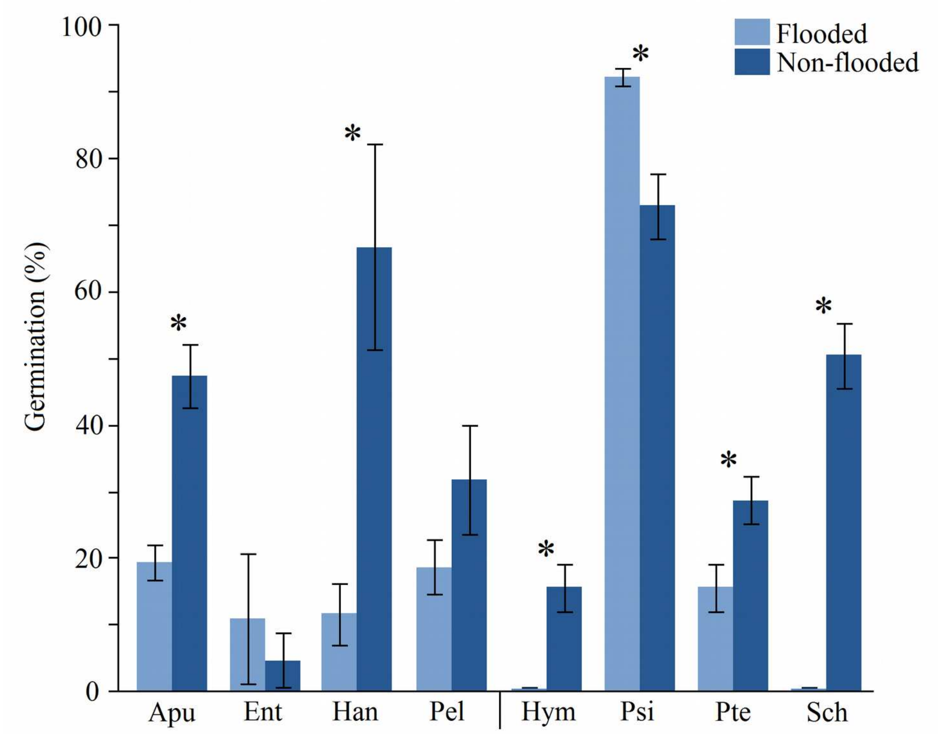

Figure 3: Percentage of germination of arboreal species seeds indicated for the restoration of naturally flooded and non-flooded habitats submitted to prolonged flooding (90 days). No germination was observed in the flooded treatment for Hym and Sch. Apu= *Apuleia leiocarpa;* Ent= *Enterolobium contortisiliquum;* Han= *Handroanthus serratifolius;* Pel= *Peltophorum dubium*; Hym= *Hymenaea courbaril*; Psi= *Psidium guajava*; Pte= *Pterogyne nitens*; Sch= *Schinus terebinthifolius*. Significant differences between treatments for each species is represented by an asterisk. The Tukey-Kramer analysis was ran with 3 groups of 43 seeds to obtain the variance.

Table 1: Number of germinated and dead seeds from plants of flooded and non-flooded habitats after 90 days of flooded (F) and non-flooded control (N) conditions. "Days to 50%" means the amount of days passed until germination of half of the viable seeds were observed. Total number of seeds per treatment per species= 129.

Species		Germination		Death	
	Treatment	N° seeds	Days to 50%	N° seeds	% of seeds
Non-flooded habitats species					
Apuleia leiocarpa	F	25	7	44	34.11
	N	61	27	13	10.08
Enterolobium contortisiliquum	F	18	12	11	8.53
	N	10	20	10	7.75
Handroanthus serratifolius	F	15	9	103	79.84
	N	86	13	33	25.58
Peltophorum dubium	F	24	8	28	21.71
	N	41	21	5	3.88
Flooded habitats species					
Hymenaea courbaril	F	0	-	28	21.71
	N	20	39	6	4.65
Psidium guajava	F	119	16	0	0
	N	94	32	2	1.55
Pterogyne nitens	F	20	18	9	6.98
	N	37	20	1	0.78
Schinus terebinthifolius	F	0	-	27	20.93
	N	65	22	6	4.65

Seeds of *E. contortisiliquum, H. serratifolius, P. dubium, P. guajava* and *S. terebinthifolius* were not viable after 15 days of flooding (Table 2). On the other hand, *H. courbaril* and *P. nitens* seeds germinate after, at least, 75 days of flooding, even if in a small percentage.

Table 2: Viability of arboreal species seeds from naturally flooded and non-flooded habitats after periods of 15 days of flooding. "Germination under water" represents seeds that germinated before the remotion of water .

Species	Days of Flooding	Viability (%) After flood	Germination Underwater (%)
Non-flooded habitats species			
Apuleia leiocarpa	0	33,3	
	15	9,5	
	30	9,5	
	45	0,0	
	60	0,0	
	75	0,0	9,5
	90	4,8	4,8
Enterolobium contortisiliquum	0	14,3	
	15	23,8	
Handroanthus serratifolius	0	66,7	
	15	19,0	
Peltophorum dubium	0	47,6	
	15	19,0	
Flooded habitats species			
Hymenaea courbaril	0	42,9	
	15	23,8	
	30	4,8	
	45	14,3	
	60	4,8	
	75	4,8	
	90	4,8	
Psidium guajava	0	81,0	
	15	85,7	
	30	14,3	9,5
	45	0,0	9,5
	60	0,0	14,2
	75	0,0	4,8
	90	0,0	4,8
Pterogyne nitens	0	42,9	
	15	9,5	
	30	0,0	
	45	0,0	
	60	9,5	
	75	4,8	
Schinus terebinthifolius	0	52,4	
	15	28,6	

3.2 Seedling development under flooding

3.2.1 Morphophisiological analysis

P. guajava plants has grown less under flooding ($F_{(1, 15)}$=8.17; p=0.01) compared to non-flooded ones (Table 3), but the stem diameters growth were similar ($F_{(1,15)}$=3.20; p=0.093). We did not register significant differences between treatments for heights ($F_{(1,16)}$=0.02; p=0.87) nor diameters of steams ($F_{(1,16)}$=0.06; p=0.80) of *H. serratifolius* plants. There was a greater number of leaves in *P. guajava* plants in N ($F_{(1,15)}$=7.73; p=0.01), and we registered foliar abscission for *H. serratifolius* in F (Table 3). In spite of that, there was no significant difference in the number of leaves between treatments ($F_{(1,16)}$=1.56; p=0.23). In *H. serratifolius* the shoot:root ratio was greater in the flooded treatment ($F_{(1,6)}$=12.15; p=0.01) and there was no significant difference for *P. guajava* ($F_{(1, 6)}$=2.64; p=0.15).

The net photosynthetic rate was higher in the non-flooded plants of *P. guajava* ($F_{(1,9)}$=8.14; p=0.02) and *H. serratifolius* ($F_{(1,9)}$=13.40; p<0.00). Morphological alterations as response to flooding were observed in both species (Table 2), and after 30 days half of *H. serratifolius* flooded plants had lost at least one leaf.

Table 3: Development and responses of seedlings of *Handroanthus serratifolius* and *Psidium guajava* subjected to 90 days of waterlogging. Development parameters are shown as the difference between the final and the first measurements. S/R ratio = shoot/root ratio. Within each species same letters means no statical differences.

Measurements		*Handroanthus serratifolius*		*Psidium guajava*	
		N	F	N	F
Relative Development	Heigh (cm)	1.11 (±1.90)^a	1.22 (±0.97)^a	14.25 (±3.34)^a	8.05 (± 5.24)^b
	Diameter (cm)	0.54 (±0.24)^a	0.58 (±0.35)^a	1.20 (±0.46)^a	0.76 (±0.53)^a
	Nº of leaves	0.44 (±3.46)^a	-1.55 (±3.32)^a	6.6 (±1.84)^a	3 (±3.24)^b
Responses (first appearence)	Chlorosis	-	60 days	-	-
	Leaf abscision	-	15 days	-	90 days
	Adventitious roots	-	-	-	60 days
Net Photosynthetic Rate	A_{net} (µmol CO_2 $m^{-2}s^{-1}$)	2.64 (±1.58)^a	-0.68 (±1.27)^b	5.35 (±1.79)^a	2.78 (±0.92)^b
Biomass	S/R ratio	0.41 (±0.06)^a	1.92 (±0.86)^b	1.81 (±1.33)^a	3.15 (±0.96)^a

3.2.2 Anatomical analysis

There were no significant differences in any of the analyzed anatomical parameters for stems or roots of *P. guajava*. However, for *H. serratifolius* there were lenticels in the stems of plants of both treatments, but in the waterlogged plants they were much more pronounced with a bigger space between the cells, characterizing hypertrophic lenticels formation (Fig. 4). The thickness of the phloem and xylem layer were different between treatments. In the flooded one the production of cells of xylem was proportionally lower than of the phloem tissue (Fig. 4). The roots of flooded *H. serratifolius* plants were, on the majority, damaged and died (Fig. 5).

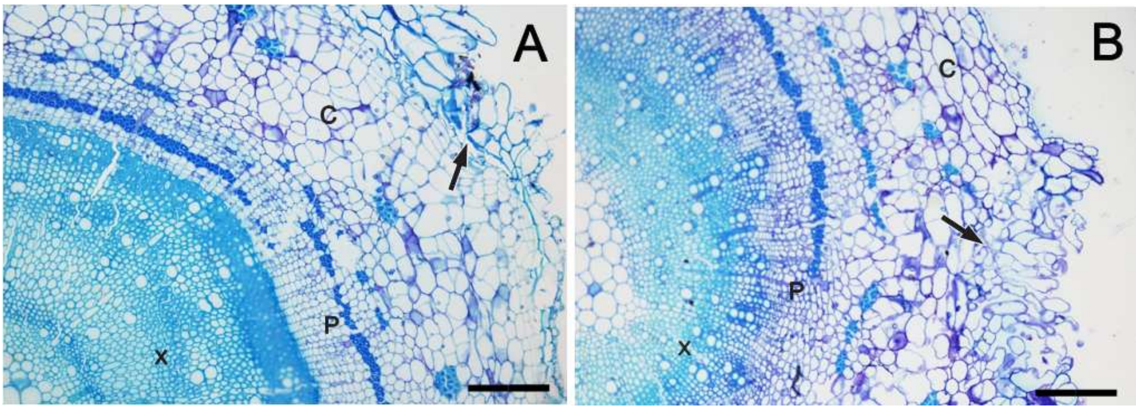

Figure 4. Cross sections at the collar region of *Handroanthus serrratifolius* stems, where lenticels (*arrows*) are seen with different sizes between **A** non-flooded treatment, and **B** flooded treatment. Different thickness of phloem (*P*) and xylem (*X*) can be seen between treatments. (*C* cortex). *Scale bars* 100 µm.

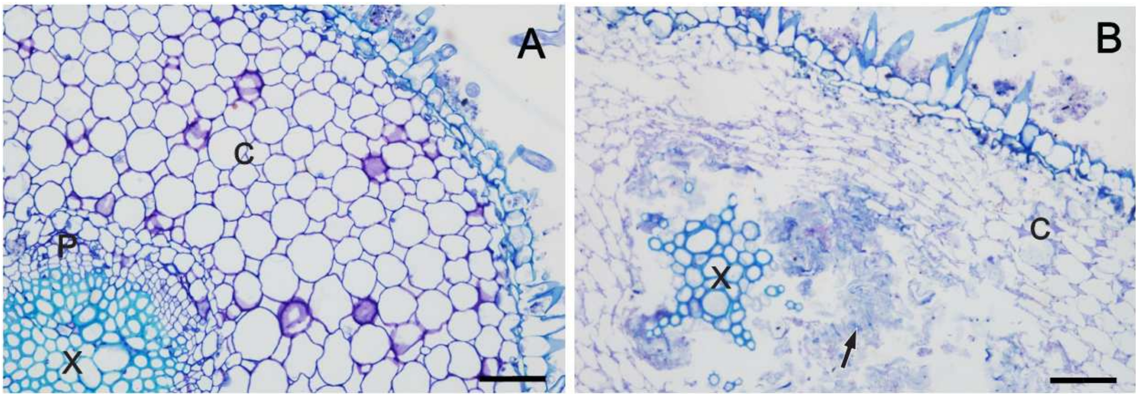

Figure 5. Cross sections at the maturation region of *Handroanthus serrratifolius* roots in primary growth. **A** Non-flooded treatment. **B** Flooded treatment, with generalized deformation (*arrow*) of the tissue around de xylem (*X*). (*P* phloem, *C* cortex). *Scale bars* 40 µm.

4. Discussion

As contrary to the expected, seeds of plants indicated for restoration of FH (Martins 2014) were not more affected by the flooding filtering. In general, submerged seeds had lower germination rate (Fig. 3) and faster germination (Fig. 2). Two species had their germination inhibited by flooding, and two showed no differences between time to germination among treatments. For *H. courbaril* and *S. terebinthifolius,* indicated for restoration of FH, there were no germination in F, meaning that the excess of water represents a filtering for its seeds. This is the opposite of what is reported for some flood tolerant species, e.g. in the Amazonian floodplains, where seeds need submersion to keep its germination potential (Parolin 2012). In spite of the very different seed sizes (Fig. 1), which means different amounts of stored energy and seed coat thickness (Paz *et al.* 1999), the prolongued submersion affected both species in the same negative way. It is important to notice that seeds of *H. courbaril* can germinate in a small rate if the water stress is not prolongued (Table 2). This tolerance to short-periods of flooding and the delay to start germination in the control treatment may be explained by the thick tegument of its seeds and its tegumentary dormancy (Nassif & Perez 1997). Therefore, caution should be taken when suggesting those species for restoration of flooded areas, since there may be no germination in the long-term and no natural succession.

The tegument thickness may likewise explain the prolonged germination period of other species, i.e. *E. contortisiliquum*, *P. dubium* and *P. nitens* seeds (Fig. 2), for whom time to germination was similar on both flooded and nonflooded treatments. This means that flooding did not alter significantly their germination process, even though may have diminished the germination percentage. An exception occurred with seeds of *E. contortisiliquum* and *P. guajava*, in which germination percentage was greater for flooded seeds (Table 1). Moreover, species of flooded habitats removed from water at different periods (Table 2) were able to germinate after a longer time of flooding, even if in a smaller percentage. Therefore, some seeds of those species may endure in the flooded soil seed bank and have a higher probability to survive this stress. Furthermore, *P. nitens* dispersal occurs by an alate fruit (Lorenzi 2002) that may float over the water and may keep the oxygenation of the seed for a longer time. The fruits of those species disperse for two to three months, or four in *P. Guajava* (Lorenzi 2002), and have a bigger chance to escape flooding or stay a shorter time underwater. Those seed behaviors are favoured in flooded prone forests such as at the margins of dammed rivers, where flooding duration vary along the years, from days to months (Jansson *et al.* 2000).

It is well known that individuals of species whose niche does not comprehend waterlogging and flooding will have its development and reproduction limited (Merritt *et al.* 2010). We found a high percentage of death in the flooded seeds (Table 1) and in almost all species the seeds became non-viable after 15 days of flooding (Table 2). Since anoxia stress plays an important role in flooded conditions (Guilloy-Froget *et al.* 2002; Souza 2009), this must be the main filter for the studied seeds. The saturated condition was lethal to the *H. serratifolius* seeds (Table 1), probably because they have less endosperm and a membranaceus tegument that allows a fast germination but favors pathogens (Mattos *et al.* 2015) or may enhance seed death and decomposition.

Therefore, in communities affected by periodic and unpredictable flooding the natural recruitment of individuals of species not tolerant may not happen throughout the years, and as the established mature individuals die, there will be no seeds or seedlings in the soil bank to replace them. According to ours results, the species whose seeds are most probable to survive the flooding filtering and succeed in the natural regeneration, from the most to the least probable are: *P. guajava, E. contortisiliquum, P. nitens, P. dubium, A. leiocarpa, H. serratifolius, H. courbaril* and *S. terebinthifolius.*

The occurrence of germination is just one step in the recruitment process and may not generate adult individuals if seedling development is compromised (Oliveira-Wittmann *et al.* 2007). As observed in the second part of the study, flooding also negatively affected plant growth. There were no observed differences in the collar diameter for any species (Table 3), but the thickness of the xylematic tissue in the *H. serratifolius* flooded plants was smaller than in plants of the control. It points to slower activity of the cambium and reduced ATP consumption, a common physiological response of tolerance (Bailey-Serres *et al.* 2012). We observed hypertrophied lenticels in the stem (Fig. 4), which enhance the interchange of gases between the stem and the air, diminishing hipoxia locally. Since no aerenchyma was formed (Fig. 4) the ethanol produced during the fermentation (Marques & Joly 2000) might have accumulated in the roots leading to cell death in the *H. serratifolius* plants, which lost their root apical meristem and partially decompose (Fig. 5).

Flooding may also lead to leaf chlorosis (Parolin *et al.* 2004), followed by foliar abscission and affecting photosynthesis, as observed in *H. serratifolius* plants (Table 3). The net CO_2 assimilation was lower in the flooded individuals of both species, being positive in *P. guajava* but negative in *H. serratifolius* plants. This suggests that respiration was greater than photosynthesis, and the energy expenditure was higher than the production, probably because of stomatal closure and lower water absorption in the roots (Herrera 2013). In some species photosynthesis can recover a few days or few hours after the disturbance period (Sapeta *et al.* 2013), what may have happened to *P. guajava* plants.

Furthermore, damming of rivers causes flooding in some seasons but drought in others, selecting a restricted number of species that must have a large niche width related to soil hydric conditions (Parolin 2001). It seems to be, at least partially, the case of individuals of *P. guajava* which had their growth decreased but kept their mainly activities positive, such as shown by photosynthesis. Reversely, individuals of *H.*

serratifolius were injured by flooding and did not grow. Nonetheless, both species survived the 90 days, and showed tolerance responses to flooding. Taking into account the seed and seedling characteristics of *P. guajava,* this seems to be the most tolerant species of the whole study. As seen in riparian communities there is a high frequency of individuals of this species (Durães *et al.* 2014), what may represent a menace for local biodiversity since this species is exotic and may dominate the community. Future works related to the effects of flooding in juvenile seedlings and mature plants are necessary to complement the knowledge about the possible responses of native tree species to unpredicted and prolonged waterlogging. Also, studies with complete submersion of the plants may show different responses. Furthermore, comprehending responses of plants to flooding in different seasons, with different temperatures and day lengths, is also important.

In the restoration of the flooded margins of reservoirs decision makers should take into account the various life stages of a plant. Even though the adult plant is flood-tolerant, the seeds and seedlings may not be, because there may exist a conflict between the niches of the different life stages (Collins & Good 1987; Schupp 1995). Since at naturally flooded habitats the recruitment generally occurs when the water recedes (Goodson et al. 2001), in the restoration process of riparian areas, the best period to sow the seeds is when the water is low, or better, to plant developed seedlings that are more prone to thrive. As the anthropic transformations of environments, such as induced flooding or drought, generally occurs at variable times during the year, it makes its effects on plant communities much more difficult to predict. Since the energy demand is growing and more hydroelectrical power dams are being constructed to meet this request (Palmeirim *et al.* 2014) it is important to know the general impacts on nature and to understand how species deal with it.

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Conclusões Gerais

O alagamento induzido prejudicou as sementes e plântulas da maior parte das espécies estudadas e representou um filtro ambiental até mesmo para plantas indicadas para recuperação de áreas alagadas. Para as sementes dos dois grupos de espécies estudados houve respostas semelhantes. A germinação é acelerada, mas o número de sementes germinadas quando submetidas ao alagamento prolongado é, em geral, menor. Ao contrário do esperado, no grupo de espécies indicadas para recuperar áreas alagadas houve duas espécies que não germinaram sob essas condições. No entanto, em geral elas permanecem viáveis por períodos maiores do que as espécies de hábitats não-alagáveis. As plantas jovens de goiaba (*Psidium guajava)* e de Ipê-amarelo (*Handroanthus serratifolius)* também foram afetadas pelo alagamento e tiveram seu desenvolvimento comprometido, mas apresentaram tolerância. O crescimento vegetativo foi menor, o investimento em folhas diminuiu e a atividade metabólica foi comprometida. As plantas de goiaba cresceram em altura e mantiveram sua atividade fotossintética positiva, enquanto as plantas de Ipê-amarelo cresceram pouco, perderam grande parte de suas raízes e folhas e a fotossíntese foi drasticamente inibida, porém resistiram vivas ao período de alagamento. A indicação de espécie para recuperar áreas alagadas parece seguir apenas as respostas de indivíduos adultos, e não leva em conta os estágios iniciais, como observado. Dessa forma, na restauração ecológica deve-se usar plantas mais desenvolvidas e sabidamente aptas a suportar o alagamento e que tenham, portanto, maiores chances de se fixar e de se estabelecer na comunidade. Há que se ressaltar, no entanto, que florestas às margens de represas estão sujeitas ao alagamento mas também à seca, que pode ocorrer durante o período de retrocesso das águas. Neste momento, o solo pode ficar seco e inibir o desenvolvimento de indivíduos que são originários de habitas alagáveis. Esses novos ecossistemas são complexos e a dinâmica de morte, germinação e sucessão também são complexas, o que exige mais cuidado e planejamento ao se construir e manter grandes reservatórios. Nesses locais a vegetação pode tender a uma homogeneização com o passar do tempo, uma vez que um limitado número de espécies é capaz de sobreviver às condições extremas de alagamento e seca. Isso demonstra mais uma vez a importância em se estudar a dinâmica dessas matas, a fim de se auxiliar em sua recomposição e manutenção.