



Survival and growth of tree seedlings as a function of seed size in a gallery forest under restoration

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Received: February 24, 2017

Accepted: April 17, 2017

ABSTRACT

Seed size is commonly related to higher rates of emergence and survival, and biomass of seedlings when introduced by direct seeding. However, few studies have evaluated whether this relationship persists when species are reintroduced as seedlings or if this effect persists after seed reserves decline. This study evaluated the effect of seed size (mass) on the probability of survival and growth of seedlings of nine native tree species introduced into a pasture area, which was originally a gallery forest in the state of São Paulo in Southeastern Brazil. The experiment occurred over the course of 24 months, in which was divided into three separate time intervals: 14 to 61 days, 61 days to 12 months, and 12 to 24 months. Seedling survival in the field was high for all three time-intervals. Seed mass positively influenced the probability of seedling survival throughout all three time-intervals after planting, but the intensity of this effect decreased with time. Species with smaller seeds exhibited higher relative growth rates (height), but only until the end of the first year. Our results suggest that seed mass is a functional trait that can predict the probability of the establishment of individual trees during forest restoration.

Keywords: functional trait, life history, nursery-raised seedling planting, pioneering species, species reintroduction

Introduction

The restoration of riparian areas and other terrestrial ecosystems is based on the reconstruction of plant communities through the reintroduction of key species (Davy 2002; Reis *et al.* 2003; Lamb 2005; Pilon & Durigan 2013; Gunaratne *et al.* 2014), mostly through the introduction of nursery-raised seedlings (Klippel *et al.* 2015). The basic premise of this strategy is to decrease high mortality rates of individuals in stages of seeds and seedlings, thereby increasing the success in species establishment (Schmidt 2008; Albuquerque *et al.* 2010; Cole *et al.* 2011; Grossnickle 2012). However, studies on the probabilities of survival and growth rates of seedlings

in degraded areas are still rare (Clark *et al.* 1999; Holl 1999; Martínez-Garza *et al.* 2013; Larson *et al.* 2015), especially in tropical forests.

Several studies showed that individuals of species with larger seeds have higher chances of surviving initial developmental stages than those with smaller seeds, mainly when growing under stressful conditions such as low light, high herbivory rates and low nutrient availability within the soil (Leishman 2001; Moles & Westoby 2004; Baraloto *et al.* 2005; St-Denis *et al.* 2013). Further, Pereira *et al.* (2013), carried out an experiment including seven tree species from Brazilian Savanna which was monitored along 24 months in the field, and found that species with small seeds (smaller than 50 mg) were more vulnerable to competition with exotic grasses than individuals of species

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with larger seeds. However, most studies evaluated the relationship between seed mass and survival in direct sowing experiments (Camargo *et al.* 2002; Baraloto *et al.* 2005; Pereira *et al.* 2013; St-Denis *et al.* 2013).

Moles & Westoby (2004) found that seed mass did not influence the probability of transition from viable seed to newly emerged seedlings of 33 species; however, this trait had a strong effect on the probability of plant survival after the first weeks of emergence. The intensity of the positive effect of seed mass on seedling survival can decline after seed reserves have exhausted (Dalling & Hubbell 2002; Westoby *et al.* 2002), but seed sizes can be negatively correlated with plant relative growth rates (Cornelissen *et al.* 2003; Poorter & Garnier 2007). Seed sizes are also positively related to root mass in the first developmental stages, which could be a decisive factor on the survival of young plants (Larson *et al.* 2015). However, it is not known whether these relationships (seed mass *vs.* survival and seed mass *vs.* growth) persist when species are reintroduced by planting nursery-raised seedlings, and if the intensity of these effects change overtime.

In this study, we evaluated the probabilities of survival and growth of nine tree species in relation to seed sizes over 24 months in a pasture area, which was originally a gallery forest. Since there is a large influence of seasonality on plant survival during the initial life stages, we evaluated three different time periods after transplanting the seedlings to the field: Time Interval I - the first two months, which are critical to plant survival; Time Interval II - the following ten months, when plants face the first unfavorable season; and Time Interval III - when mortality chances strongly decrease (Moles & Westoby 2004). Specifically, we asked: 1) does seed size influence the probability of initial survival of seedlings (Time Interval I) in the same way that is predicted in the literature for plants introduced in seed stage? 2) does this relationship maintain over the time, in Time Interval II and Time Interval III? 3) does seed size influence the relative growth rates of the individuals over time? We expected the effect of seed size on the probability of survival to decrease over time, after the seed reserves have been exhausted.

Materials and methods

Study area

This study was carried out at Estância Dois Irmãos, located in the rural area of the São Carlos district in São Paulo State in southeastern Brazil (21°54'43.569"S and 47°51'37.942"W). The climate is classified as Aw (Rolim *et al.* 2007), subtropical with wet summer from October to March, and dry winter, between April and September. Mean annual temperatures vary between 20 and 25 °C, whereas mean annual rainfall varies between 1,138 and 1,593 mm, averaging 1,429 mm (Rolim *et al.* 2007). The terrain is represented by Serra Geral formations, composed by volcanic

rocks of basaltic flows, sandstone of the Botucatu-Pirambóia formation (Souza Junior *et al.* 2011). The soil of the region is composed by Red-Yellow Latosols (Rhodic Kanhapludalf), Purple Latosol, and Dark Red Latosol, with mean texture of 15 – 34 % clay, and are considered dystrophic, presenting patches of eutrophic soils (Calderano Filho *et al.* 1998). The experimental area had 2,308 m², with approximately 200 m in length, adjacent to a narrow gallery forest remnant, inserted in a Permanent Protection Area, with widths varying between 10 to 20 m, next to Engenho Velho Stream. This experimental area was used as pasture, and therefore the vegetation was basically composed by exotic grasses, mainly *Urochloa brizantha* (A.Rich.) R.D.Webster.

Experimental design

The seedlings of the nine species used in the experiment were produced in the nursery of the Universidade Federal de São Carlos from seeds obtained regionally. The lots were examined and all seeds with any type of anomaly were discarded. Mean seed fresh mass was obtained from 200 seeds from each species from the lots used in the experiment (Tab. 1). Seed dormancy was overcome by mechanical scarification (Carvalho 2003; Salomão 2003), with the exception of *Copaifera langsdorffii* Desf. (Pereira *et al.* 2013). Seeds were disposed on Petri dishes covered with vermiculite and conditioned in a germination chamber with constant temperature (28 °C) and a 12 h photoperiod. After radicle emergence, each seed was transplanted to plastic seedling pots (volume = 290 cm³) containing organic substrate and coconut fiber (20 %). The plants were grown for approximately four months in the nursery, covered by 20 % of shade and the seedlings were irrigated by micro-dispersion for 5 minutes, four times a day. In the last three weeks before transplanting to the field we reduced irrigation to two times a day. Field planting occurred between the 12 and 14 of February 2013. The experimental area was previously isolated from cattle and grasses were chemically removed by applying glyphosate. The whole experimental area received approximately 300 liters of solution in the concentration of 300 ml/100 L. The first application was carried out two weeks before planting the seedlings. After planting, grasses were removed whenever their height was over 20 cm. This procedure was conducted throughout the entire monitoring period of the experiment. After one week of herbicide application, the soil was decompressed to a depth of approximately 30 cm. The control of leaf-cutting ants was done every two weeks during the two years of the experiment conduction. For this, visual searches of the anthills were carried out and, when necessary, we applied Fipronil insecticide.

The nursery-raised seedlings were transplanted to random plots in a grid of 2×2 m and the disposition of species was completely randomized. We introduced 63 seedlings of *Cedrela fissilis* Vell., 63 of *Pterogyne nitens* Tul., 63 of *Cariniana legalis* Kuntze, 64 of *Enterolobium contortisiliquum* (Vell.) Morong, 61



Table 1. Species name, species code, mean seed mass and standard deviation, wood density of the species and ecological categories used in the field experiment.

Family / Species	Code	Seed mass (mg)	Wood density (g/cm ³)	Class ¹
Meliaceae <i>Cedrela fissilis</i> Vell.	CEF	41.99 ± 7.03	0.47 - 0.61*	Early secondary to light-demanding climax
Leguminosae <i>Pterogyne nitens</i> Tul.	PTN	81.09 ± 17.61	0.70 - 0.87*	Pioneering to late secondary
Lecythidaceae <i>Cariniana legalis</i> Kuntze	CAL	91.64 ± 15.81	0.50 - 0.65*	Late secondary
Leguminosae <i>Enterolobium contortisiliquum</i> (Vell.) Morong	ENC	251.66 ± 25.82	0.37 - 0.60*	Pioneering to late secondary
Leguminosae <i>Copaifera langsdorffii</i> Desf.	COL	358.45 ± 80.31	0.64 - 0.86*	Late secondary to climax
Leguminosae <i>Enterolobium timbouva</i> Mart.	ENT	717.25 ± 150.72	0.37 - 0.60**	Pioneering to late secondary
Leguminosae <i>Platypodium elegans</i> Vogel	PLE	748.43 ± 74.15	0.82**	Early secondary
Leguminosae <i>Schizolobium parahyba</i> (Vell.) Blake	SCP	1808.83 ± 259.98	0.32 - 0.40*	Early secondary
Leguminosae <i>Hymenaea courbaril</i> L.	HYC	5125.11 ± 1211.70	0.90 - 1.10*	Late secondary to climax

* Carvalho (2003); ** Lorenzi (2002). ¹ see review by Carvalho (2003)

of *Copaifera langsdorffii*, 64 of *Enterolobium timbouva* Mart., 61 of *Platypodium elegans* Vogel, 62 of *Schizolobium parahyba* (Vell.) Blake and 63 of *Hymenaea courbaril* L.. All individuals were tagged with coloured and numbered seals to enable identification of each individual.

Data collection

Fourteen days after seedling planting, we recorded survival and initial height of aboveground parts to verify if any damage caused during transportation or planting could influence the results or mortality due to changes in water availability and temperature between the nursery and the field. However, very high survival rates in this period were observed, with very low variation among species, indicating that seedling transposition had a negligible effect on plant survival: mortality rates were zero for *P. nitens*, *E. contortisiliquum*, *E. timbouva*, *S. parahyba*, and *H. courbaril*, and lower than 0.066 for the other species.

We carried out 13 observations of plant survival rates, estimated by the fraction of the initial numbers of plants alive per species and time interval that they were alive. Four measurements of aboveground parts were carried out by examining all plants to determine height of seedlings, which were measured from soil surface to apical parts of the primary shoot (0.01 m precision). The monitoring of individual survival was divided into three time intervals: Time Interval I, between 14 days after planting and two months, encompassing 47 days, between late February and mid April 2013; Time Interval II, from two months until the end of the first year (February 2014), encompassing

316 days, and Time Interval III, from the end of the first year to the end of the second year (February 2015), encompassing 351 days.

Data analysis

The survival of all plants per species were graphically described to show when the survival rate declined more drastically and we used Logistic Regression Analysis (Jaccard 2001) to evaluate the effects of seed size (explanatory variable) on survival (binary response variable) of the individuals in the three time intervals. This analysis is recommended when frequency data in response variables are related to continuous explanatory variables. In this analysis, the Odds Ratio predicts how the probabilities of survival vary with increases in the explanatory variable, reflecting the intensity of the effect of seed mass (Jaccard 2001; Quinn & Keough 2002).

Relative Height Increment (RHI) was used as an estimate of growth, since the RHI and RGR (Relative Growth Rate) are strongly related (Baraloto *et al.* 2005). We estimated RHI for Time Interval I, II, and III as:

$$RHI = \frac{(\ln(\text{height in time 2}) - \ln(\text{height in time 1}))}{(\text{time interval in months})}$$

The relationship between RHI and mean seed mass in the three developmental periods were evaluated with linear regression (Sokal & Rolph 1995; Quinn & Keough 2002). The significance level used in the analyses was a



< 0.05. The residuals were graphically checked to verify trends along the estimate. Data were previously log-transformed for variance homogeneity (Sokal & Rolph 1995). All analyses were carried out in Systat 13.0 (Systat 2009).

Results

The survival rates over time varied among species (Fig. 1). The species with the lowest survival after 24 months included *C. langsdorffii* (0.61) and *C. legalis* (0.70). On the other hand, *E. timbouva* and *E. contortisiliquum* presented survival rates equal to 1.0. Among all species, *C. legalis* was the only species whose survival rates did not stabilize over time (Fig. 1); from the beginning of the experiment until the end of the monitoring period we recorded decreases in survival. The species *C. langsdorffii* and *C. fissilis* also presented a high decrease in survival when compared to the other species but, contrary to *C. legalis*, they tended to stabilize (Fig. 1).

During Time Interval I, seed size positively influenced the probability of survival of seedlings in the field ($\chi^2 = 12.377$; Odds Ratio = 3.930; $p < 0.001$) (Fig. 2A). Similarly, seed size positively influenced the probability of survival of seedlings at the end of Time Interval II ($\chi^2 = 11.546$; Odds Ratio = 3.048; $p = 0.001$) (Fig. 2B) and Time Interval III ($\chi^2 = 3.899$; Odds Ratio = 2.431; $p = 0.048$) (Fig. 2C), showing that species with larger seeds had a higher probability of survival than species with smaller seeds. However, the effect of seed size on plant survival in the first two time intervals were stronger than in Time Interval III.

The Relative Height Increment (RHI) varied among species during the experiment. In Time Interval I (Fig. 3A) and II (Fig. 3B), mean seed mass negatively influenced RHI. However, this relationship was weaker at Time Interval II when compared to Time Interval I. In Time Interval III, this relationship was not significant (Fig. 3C).

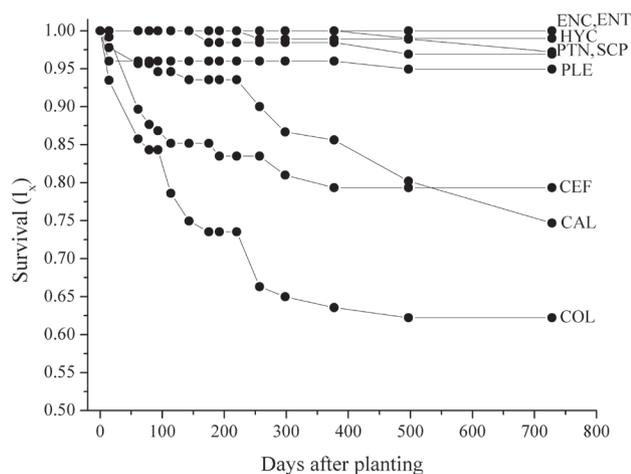


Figure 1. Survival rates of nine tree species during the experimental period. Species codes as in Table 1.

Discussion

The positive relationship between seed size and plant survival was maintained until the end of the second year after planting the seedlings. It was expected that the

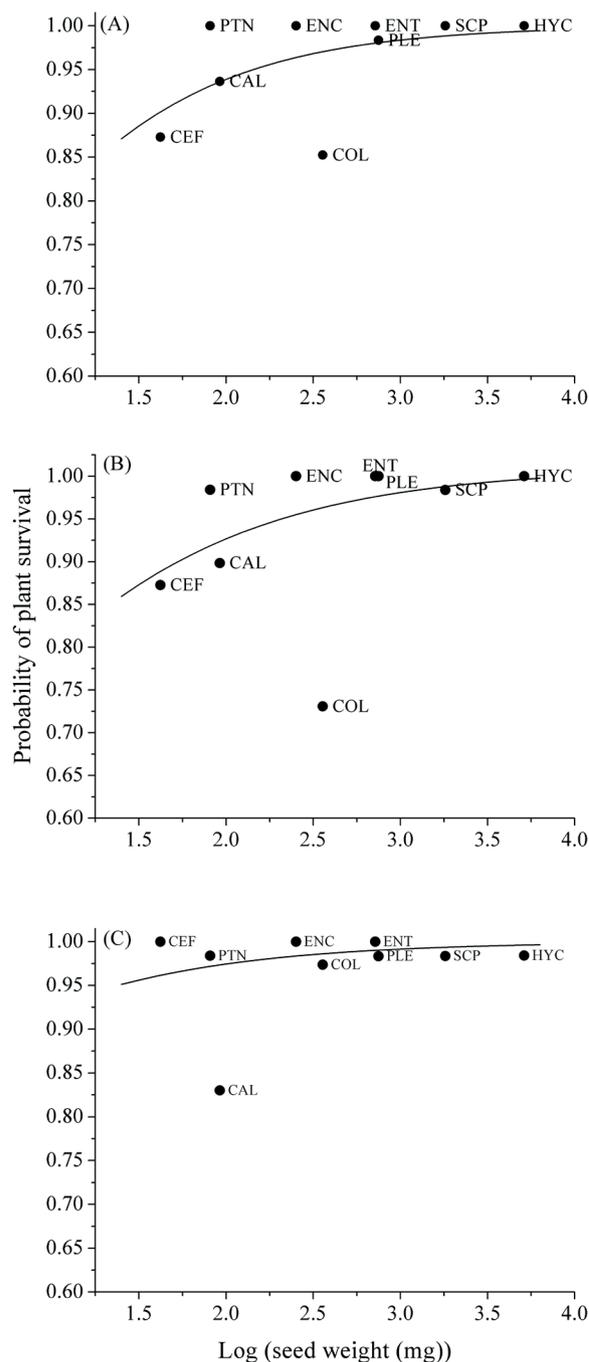


Figure 2. Relationship between the probability of survival of plants and mean seed mass of nine tree species used in the field experiment: (A) at the end of Time Interval I; (B) at the end of Time Interval II and (C) at the end of Time Interval III. Species codes as in Table 1.

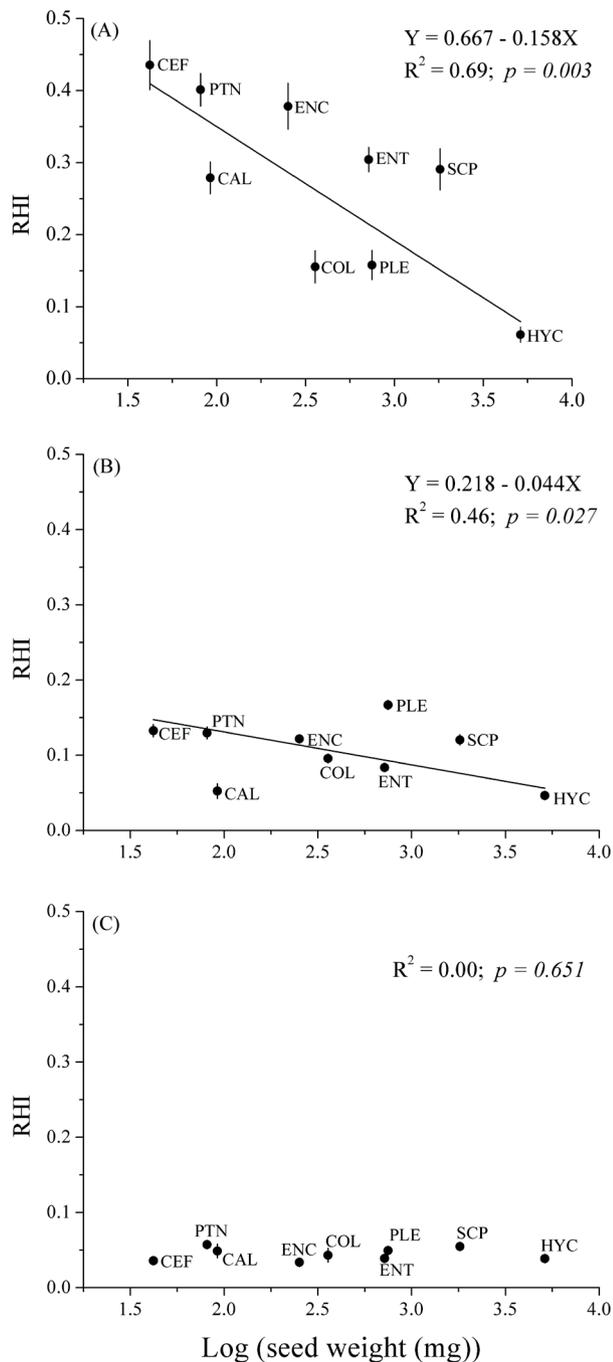


Figure 3. Relationship between Relative Height Increment (RHI) and mean seed mass of nine tree species used in the field experiment: (A) at the end of Time Interval I; (B) at the end of Time Interval II and (C) at the end of Time Interval III. Bars represent standard error. Species codes as in Table 1.

mortality rates would be similar among large seed species and smaller seed species after all the seed reserves had been exhausted, since this relationship is frequently described in the literature, but only for the first developmental periods

of plants introduced by direct seeding (Leishman 2001; Moles & Westoby 2004; Green & Juniper 2004; Martínez-Garza *et al.* 2013; St-Denis *et al.* 2013; Larson *et al.* 2015). The persistence of the positive effect of seed mass on the probability of plant survival over time, for at least two years after planting, suggests that even after the early developmental stage of seedlings is overcome, seed size still positively influences the probability of survival of plants. This relationship can be attributed to the larger amount of energetic reserves within the cotyledons of larger seeds, the reserve effect, which would be directed for the expansion and strengthening of the root system and aboveground parts of the seedlings, guaranteeing higher absorption of nutrients and water (Green & Juniper 2004; Soriano *et al.* 2013; Larson *et al.* 2015). Larger plants with more developed root systems have higher probability of survival (Leishman 2001; Moles & Westoby 2004; Green & Juniper 2004; St-Denis *et al.* 2013).

The negative relationship between Relative Height Increment and seed mass recorded in our experiment corroborate several other studies using different species and environments (Baraloto *et al.* 2005; Larson *et al.* 2015; Visser *et al.* 2016) including in the Brazilian Cerrado (Pereira *et al.* 2013). Turnbull *et al.* (2012) suggest that this relationship can be related with the strategy of growth rates among species (the fast-slow continuum hypothesis). In one extreme, species that grow fast, generally pioneering species, present high capacity to colonize new environments, whereas in the other extreme species that grow slowly have lower capacities of colonization, but with competitive advantages in the long term. Thus, pioneering species generally present smaller seeds, but higher relative growth rates when compared to non-pioneering species (late secondary or climax species), which generally present larger seeds but lower relative growth rates. However, high growth rates can be negatively related to plant survival (Wright *et al.* 2010). Philipson (2014), in a long-term study of 15 species in Malaysian Borneo, found that plant growth rates were positively related to mortality independently of light conditions, suggesting that there is a trade-off between traits that maximize plant growth and traits that minimize mortality. Here the relative height increment rates were negatively influenced by increases in seed mass during the first year, so that plants from larger seeds grew relatively less than those from smaller seeds.

Pioneering species are normally indicated in ecological restoration projects because they are light-dependent, have high growth rates, promote fast covering of the soil and influence the microclimate, favouring the establishment of species from later successional stages, which have larger seeds (Carpanezzi & Carpanezzi 2006; Gris *et al.* 2012; Klippel *et al.* 2015). However, our results suggested that the higher initial relative growth rate of smaller seed species was observed only until the end of the first year after planting, while the larger seeds we recorded a higher probability of survival, which



can extend for at least two years in the field increasing the probability of establishment of plant individuals.

Species classification into ecological groups may vary greatly between authors (Tab. 1), since it is based on many ecological characteristics (Barbosa 2009), imposing difficulties on the choice of species to be used in ecological restoration projects. Further, this categorization into ecological groups has been regarded as limited in relation to measurements of continuous variables as functional traits, because it is often done arbitrarily (Petchey *et al.* 2007; Pillar *et al.* 2013; Pierce *et al.* 2017). Thus, the use of functional traits could be more effective in the selection of the most appropriate species to survive in degraded areas in forest ecological restoration.

This study supported the hypothesis that seed size may be a reliable metric to predict the survival and growth rate of young plants in degraded areas. The persistence of the positive effects of seed mass on survival after the stage of seedlings suggests that other correlated functional attributes can be involved in the mechanisms of this relationship (Baraloto *et al.* 2005; Muller-Landau 2010; Laughlin 2014; Visser *et al.* 2016). It is possible that functional traits studies beyond seed mass could explain with more accuracy questions regarding the recruitment and establishment of species on degraded areas, then improving ecological restoration projects (Sandel *et al.* 2011). Muller-Landau (2010) proposed a model (tolerance-fecundity trade-off) to explain the coexistence of species of different seed sizes within a single habitat, since larger seed species were more likely to survive in habitats under unfavorable conditions (shade, dry and herbivory) whereas smaller seed species had the advantage of being produced in greater numbers, increasing the chances that some individuals survive. Thus, large spatial variation in stress levels could promote the coexistence of species with different seed sizes. Degraded areas have high levels of stress due to the low availability of soil nutrients, high radiation rates, low humidity and high herbivory rates, so that larger seed species would have more chances to establish in these areas. Therefore, the introduction of a greater number of individuals of small seed species in relation to the number of individuals of large seed species could be necessary to compensate for the lower survival of small seed species and to promote a higher diversity of species in these areas.

Acknowledgements

We thank Estância Dois Irmãos for the logistic support, Departamento de Botânica of Universidade Federal de São Carlos for providing equipment support for the experiments, and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the scholarship to the first author (102986/2015-0).

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