SHADE EXPLAINS *Hovenia dulcis* Thunb. INVASIVENESS IN SUBTROPICAL FOREST FRAGMENTS: A MICROCOSM EXPERIMENT

SOMBRA EXPLICA A INVASIBILIDADE DE *Hovenia dulcis* Thunb. EM FRAGMENTOS DE FLORESTA SUBTROPICAL: UM EXPERIMENTO EM CASA DE VEGETAÇÃO

Elivane Salete Capellesso[1]
https://orcid.org/ 0000-0002-2474-9994
Kellin Luana Scronvoski[2]
https://orcid.org/0000-0003-0863-2208
Jean Carlos Budke[3]
https://orcid.org/0000-0003-2035-962X
Luis Morales Salinas[4]
https://orcid.org/0000-0001-8083-0706
Ramiro Bustamante[5]
https://orcid.org/0000-0001-6441-7006
Tanise Luisa Sausen[6]
https://orcid.org/0000-0001-9374-7485

Submetido: 13/04/2021 / Aprovado: 18/08/2022 / Publicado: 11/05/2023

Abstract

Hovenia dulcis is a non-native species in Southern Brazil with high capacity for invasion in subtropical forest fragments. In this study we used a greenhouse experiment simulating field abiotic and biotic conditions to investigate the germination and initial growth to determine the mechanisms associated with the high invasion potential of this species. We evaluated the effects of abiotic factors (light) and biotic factors (litter mass and litter type) on demographic parameters: germination (GR), recruitment rate (RR) and establishment (ER) and initial growth traits (stem height, SH; root length, RL and root:shoot ratio, R:S) in a greenhouse experiment. Interactions between factors were compared using GLM, to select the best model and the factors that influence each parameter evaluated. GR, RR, and ER were influenced by light intensities. GR, ER and RR were higher in low light. The initial growth was influenced by light and litter quality. Higher SH and R:S ratio was observed in low light. Additionally, stem and root growth were higher in exotic

[1]Doutora. Laboratório de Ecologia e Sistemática Vegetal, Departamento de Ciências Biológicas, Universidade Regional Integrada do Alto Uruguai e das Missões – URI, Av. Sete de Setembro, 1621, Centro, CEP 99700-000, Erechim, RS, Brazil. E-mail: elivanesc@gmail.com
[2] Engenheira agrônoma. Universidade Regional Integrada do Alto Uruguai e das Missões – URI, Av. Sete de Setembro, 1621, Centro, CEP 99700-000, Erechim, RS, Brazil. E-mail: kellinscrovonski@hotmail.com
[3] Doutor. Universidade Regional Integrada do Alto Uruguai e das Missões – URI, Av. Sete de Setembro, 1621, Centro, CEP 99700-000, Erechim, RS, Brazil. E-mail: jean@uricer.edu.br
[4]Doutor. Laboratorio para la Investigación en Ciencias Ambientales (LARES), Facultad de Ciencias Agronómicas, Universidad de Chile. Santiago 8820808, Chile. E-mail: lmorales@renare.uchile.cl
[5]Doutor. Departamento de Ciencias Ecológicas, Instituto de Ecología y Biodiversidad, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile. E-mail: rbustama@uchile.cl
[6]Doutora. Laboratório de Ecologia e Sistemática Vegetal, Departamento de Ciências Biológicas, Universidade Regional Integrada do Alto Uruguai e das Missões – URI, Av. Sete de Setembro, 1621, Centro, CEP 99700-000, Erechim, RS, Brazil. E-mail: tasausen@uricer.edu.br

DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)

litter. These results evidence the strategies of establishment and initial growth of *H. dulcis* in the colonization of shaded environments.
Key-words: Biological invasion. Germination. Stem elongation. Understory.

Resumo

Hovenia dulcis é uma espécie exótica com alta capacidade de invasão de fragmentos em floresta subtropical. Neste estudo foi utilizado um experimento em casa de vegetação simulando condições abióticas e bióticas de campo associadas à invasão de *H. dulcis* para investigar a germinação e o crescimento inicial para determinar os mecanismos associados ao alto potencial de invasão desta espécie. Avaliamos os efeitos de fatores abióticos (luz) e fatores bióticos (massa da serapilheira e tipo de serapilheira) sobre parâmetros demográficos e atributos de crescimento inicial: taxa de germinação (TG), taxa de recrutamento (TR) e de estabelecimento inicial (TE) e atributos de crescimento inicial (comprimento do caule, CC; comprimento da raiz, CR e razão raiz:parte aérea, R:PA) em um experimento em casa de vegetação. As interações entre os fatores foram comparadas por meio do GLM, para selecionar o melhor modelo e os fatores que influenciam cada parâmetro avaliado. TG, TR e TE foram influenciados pela intensidade luminosa. TG, TR e TE foram maiores em baixa luz. O crescimento inicial foi influenciado pela luz e qualidade da serapilheira. Um maior CC e R:PA foram observados em baixa luz. Adicionalmente, o crescimento do caule e da raiz foram maiores na serapilheira mista. Estes resultados evidenciam as estratégias de estabelecimento e crescimento inicial de *H. dulcis* na colonização de ambientes sombreados.
Palavras-chave: Invasão biológica. Germinação. Alongamento do caule. Sub-bosque.

1. INTRODUCTION

Invasibility refers to the susceptibility of ecosystems to receive non-native species (WILLIAMSON, 1996; CATFORD *et al.*, 2012). In terrestrial ecosystems attributes such as diversity, cover, and the presence/absence of predators can determine whether one ecosystem is prone or not to be invaded. Tropical forest is regarded with low invasibility due to in general non-native plants are colonizers, shade-intolerant species that invades open spaces where abiotic conditions are more suitable and propagule pressure is higher than in the interior of forests (FINE, 2002). More recently, plant invasion is occurring in these ecosystems due to among other things, forest fragmentation (DENSLOW; DEWALT, 2008). This human-induced change is one of the main drivers of biological invasion (KRUGER *et al.*, 1989). The introduction of non-native invasive species in fragmented forests is responsible for drastic changes in community structure and ecosystem functions (MALLIK; PRESCOTT, 2001; ROTHSTEIN *et al.*, 2004).

Non-native species alter ecosystem services and modify nutrient cycling by changing the composition and amount of litter in forest soils (VITOUSEK; WALKER, 1989; CASTRO-DÍEZ *et al.*, 2009). These changes may in turn affect a number of biotic and abiotic factors, thereby reducing native plant diversity (ROTHSTEIN *et al.*, 2004; RASCHER *et al.*, 2011). Some studies have found that the litter of non-native species can decrease seedling germination and emergence of native species (MYSTER, 1994; FACELLI; LADD, 1996). Seedling recruitment in open forest is higher with litter addition, but an opposite pattern was found in forest understory (DUPUY; CHAZDON, 2008). Litter thickness can affect germination and seedling emergence through changes in microclimate, which produce variation in soil moisture and temperature (FACELLI;

DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)

LADD, 1996; SILVA *et al.*, 2016) and can also serve as a mechanical barrier to seedling establishment (FACELLI; LADD, 1996; HASTWELL; FACELLI, 2000).

Several studies point out that non-native tree species increase invasiveness in open areas due to shade intolerance (BUSTAMANTE *et al.* 2003; BUSTAMANTE; SIMONETTI, 2005; CATFORD *et al.*, 2012). A higher germination of *Hovenia dulcis* Thunb. was observed in semi-open canopy areas with reduced establishment along forest succession (DECHOUM *et al.*, 2015). However, Dupuy and Chazdon (2008) point out that the invasive potential of this species occurs predominantly in canopy gaps, suggesting the positive influence of high light level in the establishment process.

Forest fragments in southern Brazil are characterized by high prevalence of *H. dulcis* (DECHOUM *et al.*, 2015; PADILHA *et al.*, 2015). This pattern seems to contradict the idea that tropical forests have low invasibility. In this study we examined experimentally the effect of litter thickness and composition and light intensity on germination and initial growth of *H. dulcis* seedlings. Given the invasion pattern observed in other studies, we hypothesized that emergence success and initial growth of *H. dulcis* is facilitated under a scenario of intermediate light intensity and a mixed array of litter, characteristics of subtropical forest fragments.

2. MATERIAL AND METHODS

2.1 Plant material and experiment preparation

H. dulcis germination and growth experiments were conducted in a greenhouse at the Regional Integrated University of High Uruguay and Missions, URI – Erechim Campus, southern Brazil, from September to December 2014.

Fruits were collected from eight adult *H. dulcis* in four Atlantic Forest fragments in Southern region of Brazil, totaling twenty - four individuals. After processing the fruits, the seeds were submitted to the water immersion test for the removal of non-viable seeds (supernatants). The seeds classified as viable were disinfected with 2% sodium hypochlorite for 10 minutes followed by four washes in sterilized distilled water. For the germination experiment, 10 pre-treated seeds were placed approximately 5 mm deep in containers (12.5 cm of internal diameter and 9.1 cm height containing 355 grams a mixture of commercial substrate and vermiculite (2:1).

Litter samples were also collected from four Atlantic Forest fragments. Litter collected from locations with predominance of *H. dulcis* trees was characterized as "exotic litter", while litter from areas with a higher diversity of native tree species and without *H. dulcis* was characterized as "native litter." To determine the litter amounts used in containers, litter stock accumulated in soil surface was quantified using a bottom screen (0.25 m^2 area; 0.50 x 0.50 m). The collected material was taken to the laboratory, oven-dried at 60 °C to seven days, and then weighed.

"Mixed" litter was prepared in the laboratory by combining exotic litter (50%) and native litter (50%). We used two litter level treatments, one "x mass" treatment (corresponding to the litter amount accumulated on the sampled soil surface), and one "2x mass" treatment (twice the litter amount accumulated in the sampled soil surface), for a total litter mass of 7.36 (x) and 14.72 grams (2x), being representative of the density of litter found at forest fragments (pers. obs.)

2.2 Experimental design and experimental conditions

DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)

A greenhouse experiment was conducted using a 3x2x3 factorial design, consisting of three different light conditions (low, intermediate, and high), two litter amounts (standard (field conditions) mass (x), and high mass (2x greater than field conditions) and three litter types (exotic, native, and mixed).

The different light conditions in the greenhouse were simulated using nylon mesh with different openings: high (541.8 µmolm^{-2}); intermediate (416.8 µmolm^{-2}) and low (166.7 µmolm^{-2}), which corresponds to 35%, 50%, and 80% of external radiation interception, respectively.

For this experiment were used a total of 180 containers divided in light treatments litter quantity and litter quality, with 10 replicates per treatment (replicates).

In the greenhouse, plants received irrigation twice a day, with duration of 10 minutes, and were maintained under environmental conditions of air temperature and humidity during the experimental period, the soil water conditions were monitored in all treatments to avoid water stress by pots weight.

2.3 Demographic parameters and initial growth traits

Germination rate was monitored daily and at the end of the trials, the number of seedlings that successfully germinated (i.e., with radicle emergence) was counted. Demographic parameters (establishment and recruitment rates) and growth parameters were evaluated at the end of the experiment (60 days). To evaluate the germination rate, all individuals that germinated were considered, including those with emission radicle that did not establish. For establishment rate, all seedlings were considered, i.e., all individuals that showed initial growth with expanded cotyledon leaves. For recruitment rates, we considered all individuals that remained alive at the end of the experimental period (60 days). GR, ER and RR were calculated according to Guerrero and Bustamante (2007). Germination rate (GR) was defined as the total number of seedlings with radicle emergence divided by the total number of initial seeds. Seedling establishment rate (ER) was defined as the total number of plants established divided by the number of germinated seeds. Seedling Recruitment rate (RR) was estimated by the number of established plants divided by the number of germinated seeds. For evaluation of growth parameters, established seedlings (seedlings with true leaves) were removed from the pots and harvest, washed to remove the excess soil from roots, and partitioned in shoot and root components. Shoot length (cm) and root length (cm) were measured using a digital paquimeter.

2.4 Data analysis

For the data analysis, were considered only the intermediate and low intensity treatments, since the high light zero germination and establishment was detected.

Interactions between factors (light intensity, litter mass, and litter type) were compared using a General Linear Model (GLM), with quasi-poison distribution. Our original model (M1) we tested all the variables influenced each parameter (M1 = light + amount of litter + litter quality) and for select the best model used in the Drop 1 command, in order to select the factors that influence each parameter evaluated. We used a 95% CI (p = 0.05). The differences between light intensity and litter quality were compared with Kruskal-Wallis test. All analyses were performed in the 'R' statistical environment (R DEVELOPMENT CORE TEAM, 2021).

3. RESULTS AND DISCUSSION

DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)

Demographic parameters (GR, ER and RR) of *H. dulcis* were influenced only by light intensity (Table 1). The initial growth traits (SH and RL) were influenced by light intensity and litter quality (Table 1).

Table 1. Results of the models tested in the GLM analysis between light and litter quantity and quality treatments for germination (GR), establishment (ER) and recruitment (RR) rates and initial growth (SH, RL and R:S ratio) of *H. dulcis* seedlings. Values for each traits are means and deviation.

Parameter	Factors	Treatments	Mean+SD	Model results		
				Df	F	P(>F)
Germination (GR)	Light intensity	Low	3.53 ± 2.45	1	24.59	<0.0001
		Intermediate	1.83 ± 1.33			
	Litter quality	Native	2.35 ± 2.12	2	0.44	0.65
		Exotic	2.67 ± 2.13			
		Mixed	3.02 ± 2.18			
	Litter quantity	x mass	2.70 ± 2.25	1	0.001	0.99
		2 x mass	2.67 ± 2.05			
Establishment (ER)	Light intensity	Low	2.91 ± 2.13	1	22.27	<0.0001
		Intermediate	0.80 ± 1.1			
	Litter quality	Native	1.60 ± 1.63	2	0.91	0.41
		Exotic	1.82 ± 2.12			
		Mixed	2.15 ± 2.17			
	Litter quantity	x mass	1.78 ± 0.21	1	0.001	0.99
		2 x mass	1.93 ± 1.85			
Recruitment (RR)	Light intensity	Low	0.29 ± 0.21	1	22.27	<0.0001
		Intermediate	0.08 ± 0.11			
	Litter quality	Native	0.16 ± 0.16	2	0.91	0.41
		Exotic	0.18 ± 0.21			
		Mixed	0.21 ± 0.22			
	Litter quantity	x mass	0.17 ± 0.21	1	0.001	0.99
		2 x mass	0.19 ± 0.18			
Stem height (SH)	Light intensity	Low	7.38 ± 3.52	1	10.67	0.001
		Intermediate	3.28 ± 3.88			
	Litter quality	Native	4.87 ± 4.07	2	3.56	0.03
		Exotic	5.21 ± 4.71			
		Mixed	5.91 ± 3.89			
	Litter quantity	x mass	5.09 ± 4.16	1	0.22	0.64
		2 x mass	5.57 ± 4.31			
Root length (RL)	Light intensity	Low	2.35 ± 3.63	1	9.13	0.03

DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)

		Intermediate	3.12 ± 1.91			
	Litter quality	Native Exotic Mixed	2.09 ± 2.17 3.52 ± 3.94 2.60 ± 3.89	2	12.25	<0.0001
	Litter quantity	x mass 2 x mass	2.40 ± 2.54 3.07 ± 3.24	1	1.69	0.18
R:S ratio	Light intensity	Low Intermediate	0.33 ± 0.26 0.12 ± 0.19	1	5.85	0.02
	Litter quality	Native Exotic Mixed	0.21 ± 0.26 0.25 ± 0.27 0.22 ± 0.21	2	2.80	0.07
	Litter quantity	x mass 2 x mass	0.22 ± 0.22 0.23 ± 0.27	1	1.66	0.20

GR and ER were positively affected by both light intensities (Table 2). However, for RR a negative effect of intermediate and low light intensity was observed (Table 2). A higher GR, ER, and RR were observed in low light compared to intermediate light (Fig. 1a, 1b and 1c).

Initial growth traits (SH and RL) were positively influenced by light intensity and litter quality. But the R:S ratio was negatively influenced by light intensity (Table 2).

A higher SH and R:S ratio was observed in low light (Fig. 1d and 1f). But the RL was shorter in low light (Fig. 1e). Additionally, a higher initial growth (SH and RL) was observed on *H. dulcis* litter (exotic litter) (Fig. 2a and 2b).

The litter quantity did not influence the demographic parameters and initial growth traits evaluated (Table 1 and Table 2).

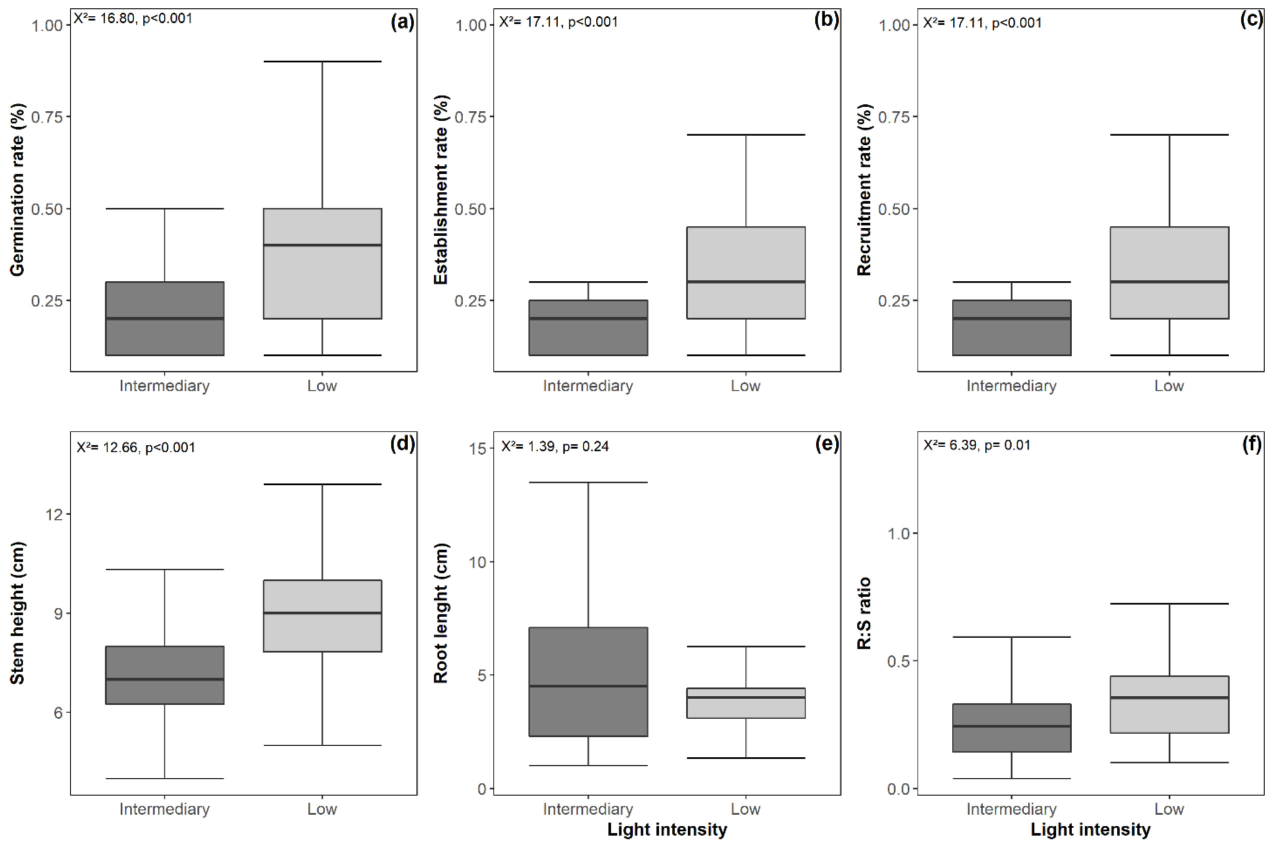
Table 2. Statistical summary of the differences in general linear model with quasipoisson distribution (GLM) and for germination, establishment and recruitment rates and initial growth traits. R^2 values is a proportion of explication. Model 2 is composed by light intensity + litter quality, and Model 3 (M3) is composed only of light intensity.

Parameter	**Model**	**Treatments**	**Estimate**	**St. error**	**t value**	**P(t)**	**R^2**
Germination (GR)	M3	Intermediate Low	0.57 1.3	0.13 0.07	4.40 17.98	<0.0001 <0.0001	57 %
Establishment (ER)	M3	Intermediate Low	0.57 1.23	0.13 0.06	4.39 17.98	<0.0001 <0.0001	57 %
Recruitment (RR)	M3	Intermediate Low	-1.73 -1.07	0.13 0.07	-13.19 -15.60	<0.0001 <0.0001	7%
Stem height (SH)	M2	Intermediate Low	1.98 1.99	0.05 0.08	43.04 23.74	<0.0001 <0.0001	24 %
		Native Mixed Exotic	2.16 2.06 2.20	0.03 0.04 0.05	70.31 47.94 47.99	<0.0001 <0.0001 <0.0001	
Root length (RL)	M2	Intermediate Low	1.65 1.32	0.09 0.08	17.12 15.78	<0.0001 <0.0001	61 %

DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)

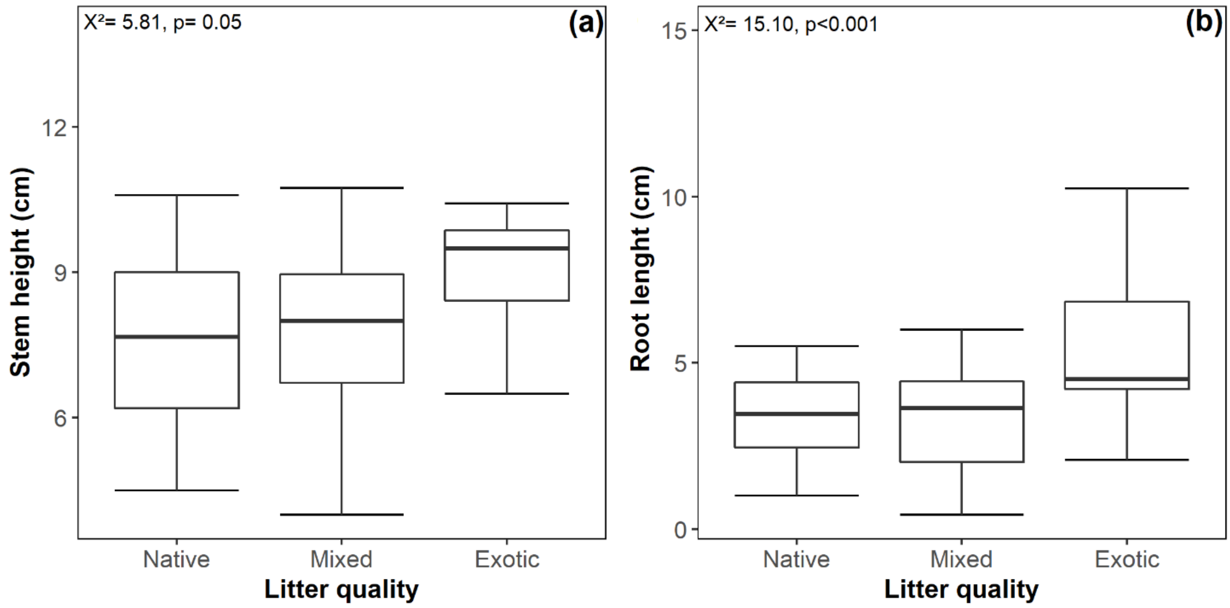
		Native	1.24	0.12	10.59	<0.0001	
		Mixed	1.24	0.10	11.84	<0.0001	
		Exotic	1.81	0.09	20.11	<0.0001	
R:S ratio	M3	Intermediate	-1.34	0.15	-9.15	<0.0001	20
		Low	-0.95	0.09	-10.78	<0.0001	%

Figure 1. Differences between demographic parameters (GR, RR, and ER) and initial growth traits (SH, RL and R:S ratio) of *Hovenia dulcis* seedlings in intermediate and low intensity. The Kruskal-Wallis test showed difference between light intensity. Values are expressed as means + S.D (n = 10).



DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)

Figure 2. Differences between stem height and root length of *Hovenia dulcis* seedlings in native, mixed and exotic litter quality. The Kruskal-Wallis test showed the difference between litter quality. Values are expressed as means + S.D (n = 10).



Our greenhouse study showed that low light intensities influence germination, establishment, and recruitment rates, demonstrating that shading-escape growth strategies can be crucial for successful invasion of conserved forest fragments (shaded). Ecological invasion studies emphasized invasion success in disturbed (more open) environments (BAZZAZ, 1986; REJMÁNEK; RICHARDSON, 1996; GROTKOPP *et al.* 2002). But the plant invasion in well-preserved forests has been observed in temperate and tropical regions indicating the ability of exotic species to invade undisturbed shaded forests (MARTIN *et al.*, 2009). An interesting question is that germination seems to be less affected by light conditions than initial establishment and growth. Additionally, the results of the models tested indicated that for the demographic parameters evaluated (GR, ER and RR) only the light intensity explains the differences observed. Based on these results we suggest that the *H. dulcis* germination and establishment, indicated by GR, ER and RR does not seem to be limited by litter chemical or physical barriers because regardless of litter mass or type, but by only the light intensity. Dechaun *et al.*, (2015) observed that the establishment of *H. dulcis* decreased with the advance of the forest succession; however, older forests tend to have lower light intensity. The results observed in this study point to the capacity of invasion in more shaded areas. After the recruitment process, seedling growth is favored in low light conditions, contrary to the observed by Dechaun *et al.*, (2015).

Most seedlings were able to emerge from all litter mass but was higher under low light. In these conditions, the strategy used by *H. dulcis* to establish itself successfully involves increased allocation to shoot elongation. Stem elongation is a growth strategy associated with shadow avoidance (GOMMERS *et al.*, 2013) and we suggest that the rapid stem elongation is particularly important for this species with small seeds, which facilitates its establishment and appears to be responsible for the ability to competition and invasion. The evaluations were carried out after the initial growth, which included the expansion of cotyledonary leaves and the production of the first leaves. Therefore, we did not observe whether the marked growth in height in low light conditions was associated with other physiological responses associated with shading (leaf chlorosis).

DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)

Our results also indicated that initial growth was influenced by litter quality with a positive effect of exotic litter (*H. dulcis*) on stem height and root length. These results may suggest that in environments with greater abundance of *H. dulcis* individuals, the production of a predominant litter from *H. dulcis* leaves could generate a beneficial effect for the seedlings establishment and successful colonization. In field conditions, Padilha *et al.* (2015) observed a high abundance of *H. dulcis* saplings close to adult trees pointed out the successful colonization of recently invaded Atlantic Forest remnants.

Initial establishment of *H. dulcis* in subtropical Brazilian forest fragments occurs mainly in undisturbed subtropical Atlantic Forest habitats, highlighting the potential for invasion of shaded environments with well-developed understory, opposite to that observed in other studies that indicate that the invasiveness is higher in open areas (BUSTAMANTE *et al.*, 2003; BUSTAMANTE; SIMONETTI, 2005; CATFORD *et al.*, 2012). Light intensity can be considered as the main factor associated with the initial invasion of *H. dulcis* in well-preserved fragments, due to the positive effects of low light on establishment and initial growth. But the goal of this work was to verify that under low light conditions, the rapid growth associated with stem elongation seems to be the fundamental strategy for success in establishment. The rapid growth, observed in stem elongation in low light conditions, characteristic of the forest understory, seem to be determinant for the high competitiveness of *H. dulcis* compared with to native tree species.

This study highlights the initial growth of *H. dulcis* that enable their establishment in preserved forest fragments, which is characterized by having developed understory with litter of multiple species and strong shade conditions. Although the litter amount does not interfere in the germination and establishment of new individuals in already invaded areas. Thus, the non-native *H. dulcis* seems to have higher invasion potential in shading areas, leading to negative effects for conservation of forest fragments in southern Brazil. In addition, the results of this study, added to the work observed by Padilha *et al.*, (2015) and Dechoum *et al.*, (2015) emphasize the high phenotypic plasticity to light conditions. Other factors associated with seed number and size and the landscape of the fragments may be associated with the potential for invasiveness of this species.

5. ACKNOWLEDGEMENTS

We acknowledge the Fundação de Amparo à Pesquisa do Rio Grande do Sul (FAPERGS) for financial support for the experiment and international missions' study between researchers at the Universidad de Chile (RO Bustamante and L Morales-Salinas) and the Program for Postgraduate in Ecology of Universidade Regional Integrada do Alto Uruguai e das Missões (JC Budke and TL Sausen) for the International Project (252.299.16450.13122013). ES Capellesso received grants from the FAPERGS. RO Bustamante acknowledges the partial support of project ICM P05–002.

4. REFERENCES

BAZZAZ, FA. Life history of colonizing plants: some demographic, genetic, and physiological features. In: MOONEY HA, DRAKE JA (orgs). **Ecology of biological invasions of North America and Hawaii**. Springer New York. 1986. p. 96-110.

DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)

BUSTAMANTE, RO; SEREY, IA; PICKETT, STA. Forest fragmentation, plant regeneration and invasion processes across edges in Central Chile. In: BRADSHAW GA, MARQUET PA (orgs.). **How landscapes change: human disturbance and ecosystem fragmentation in the Americas.** Springer Berlin Heidelberg. 2003. p. 145-160.

BUSTAMANTE, RO; SIMONETTI, JA. Is Pinus radiate invading the native vegetation in central Chile? Demographic responses in a fragmented forest. **Biological Invasions**, v. 7, p. 243-249, 2005.

CASTRO-DÍEZ, P; GONZÁLES-MUÑOZ, N; ALONSO, A; GALLARDO, A; POORTER, L. Effects of exotic invasive trees on nitrogen cycling: a case study in Central Spain. **Biological Invasions**, v. 11, p. 1973-1986, 2009.

CATFORD, JA; VESK, PA; RICHARDSON, DM; PYŠEK, P. Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. **Global Change Biology**, v. 18, p. 44-62, 2012.

DECHOUM, MS; ZENNI, RD; CASTELLANI, TT; ZALBA, SM; REJMÁNEK, M. Invasions across secondary forest successional stages: effects of local plant community, soil, litter, and herbivory on *Hovenia dulcis* seed germination and seedling establishment. **Plant Ecology**, v. 216, 823-833, 2015.

DENSLOW, JS; DEWALT, SJ. Exotic plant invasions in tropical forests: patterns and hypotheses. In: CARSON, WP; SCHNITZER, SA (Orgs.). **Tropical forest community ecology**. Oxford, UK: Wiley-Blackwell. 2008. p. 409-426.

DUPUY, JM; CHAZDON, RL. Interacting effects of canopy gap, understory vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. **Forest Ecology and Management**, v. 255, p. 3716-3725, 2008.

FACELLI, JM; LADD, B. Germination requirements and responses to leaf litter of four species of eucalypt. **Oecology**, v. 107, p. 441-445, 1996.

FINE, PVA. The invasibility of tropical forests by exotic plants. **Journal of Tropical Ecology**, v. 18, p. 687-705, 2002.

GOMMERS, CMM; VISSER, EJW; ONGE, KR St; VOESENEK, LACJ; PIERIK, R. Shade tolerance: when growing tall is not an option. **Trends in Plant Science**, v. 18, n. 2, p. 65-71, 2013.

GROTKOPP, E; REJMÁNEK, M; ROST, TL; SIMBERLOFF, D. **The American Naturalist**, v. 159, n. 4, p. 396-419, 2002.

GUERRERO, PC; BUSTAMANTE, RO. Can native tree species regenerate in Pinus radiata plantations in Chile? Evidence from field and laboratory experiments. **Forest Ecology and Management**, v. 253, p. 97-102, 2007.

HASTWELL, GT; FACELLI, JM. Effects of leaf litter on woody seedlings in xeric successional communities. **Plant Ecology**, v. 148, p. 225-231, 2000.

DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)

KRUGER, FJ; BREITENBACH, GJ; MACDONNALD, IAW; RICHARDSON, DM. The characteristics of invaded mediterranean-climate regions. In: DRAKE, JA; MOONEY, HA; DI CASTRI, F; GROVES, RH; KRUGER, FJ; REJMNANEK, M; WILLIAMSON M. (Eds). **Biological Invasions:** a Global Perspective, Wiley, Chichester, UK. 1989.

MALLIK, AU; PRESCOTT, CE. Growth inhibitory effects of salal on western hemlock and western red cedar. **Agronomy Journal**, v. 93, p. 85–92, 2001.

MARTIN, PH; CANHAM, CD; MARKS PL. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. **Frontiers in Ecology and the Environment**, v. 7, n. 3, p. 142-149, 2009.

MYSTER, RW. Contrasting litter effects on old field tree germination and emergence. **Vegetatio**, v. 114, p. 169-174, 1994.

PADILHA, DL; LOREGIAN, AC; BUDKE, JC. Forest fragmentation does not matter to invasions by *Hovenia dulcis*. **Biodiversity Conservation**, v. 24, p. 2293-2304, 2015.

RASCHER, KG; GROSSE-STOLTENBERG, A; MAGUAS, C; MEIRA-NETO, JAA; WERNER, C. Acacia longifolia invasion impacts vegetation structure and regeneration dynamics in open dunes and pine forests. **Biological Invasions**, v. 13, p. 1099-1113, 2011.

ROTHSTEIN, DE; VITOUSEK, PM; SIMMONS, BL. An exotic tree alters decomposition and nutrient cycling in a Hawaiian montane forest. **Ecosystems**, v. 7, p. 805-814, 2004.

R DEVELOPMENT CORE TEAM. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing,Vienna, Austria. 2021.

REJMÁNEK, M; RICHARDSON, DM. What attributes make some plant species more invasive? **Ecology**, v. 77, n. 6, p. 1655-1661, 1996

SILVA, RHM; BOUILLET, JP; PAULA,,RC. Assessing the invasive potential of commercial Eucalyptus species in Brazil: Germination and early establishment. **Forest Ecology and Management**, v. 374, p. 129-135, 2016.

WILLIAMSON, M. **Biological Invasions**. Springer Netherlands. 1996, 244p.

VITOUSEK, PM; WALKER, LR. Biological invasion by Myrica faya in Hawaii: plant demography, nutrient fixation, ecosystem effects. **Ecological Monographs**, v. 59, p. 247–265, 1989.

DOI: http://dx.doi.org/10.24021/raac.v20i1.6026 V. 20, N. 1 (2023)