Ramet specialization allows similar performance of the invasive macrophyte *Hedychium coronarium* under different light and intraspecific competition levels

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Abstract

Invasive species can affect ecosystems functioning by forming dense monospecific stands and outcompeting native plants. However, the performance of the invader depends on its plastic responses to abiotic attributes of invaded communities. Understanding the interplay between intraspecific competition and environmental conditions is important to elucidate the domain and aggressive potential of invasive species. Here, we assessed the performance of the invasive *Hedychium coronarium* in two levels of intraspecific competition created through rhizome density under full light and partial shade. We tested the influence of light, density and their interaction on ramet length and number of ramets during the first three months after planting (phase 1) and after 22 months (phase 2), and on rhizome dry weight and the ramet/rhizome biomass ratio in phase 2. In both phases, ramets were longer under shade and the number of ramets was higher under low rhizome density indicating lower intraspecific competition. In phase 2, there was a negative effect of rhizome density on ramet length, but it was restricted to shade, probably due to the aggravation of competition for light. Rhizome dry weight was greater under shade conditions and it was not affected by rhizome density, and ramet/rhizome ratio did not differ between treatments. Our results supported a large phenotypic plasticity of *H. coronarium* ramets, which allowed similar performances despite variations in environmental conditions and population densities. We suggest that this mechanism of energy allocation enhances the success of this invasive plant in varied habitats, such as open and closed, forested sites.

Introduction

Invasive species are currently among the major threats to global biodiversity, affecting ecosystems through changes in the habitat and harming ecological processes of the community (Elton 1958). The understanding of how exotic species become invaders may avoid their proliferation and reduce their impact on communities (Kolar and Lodge 2001). The success of invasive species depends on their biological traits as well as on biotic and abiotic characteristics of invaded communities (Simberloff and Rejmanek 2011). Several studies described how traits of invader species enhance their capacity of occupation and dominance (Marco et al. 2002), while others investigated habitat conditions and its susceptibility to invasion (Batisteli et al. 2020; Davis et al. 2000). However, associating biological aspects of invasive species and environmental factors is important to improve the knowledge about the invasion process (Jeschke et al. 2012).

The competition between invasive and native species has been investigated to explore the dominance strategies of invaders (Vila and Weiner 2004, Herrera et al. 2016), but the role of intraspecific competition in constraining the performance of invasive species remains poorly studied (Huang and Peng 2016). Conspecific individuals are similar and compete for resources, which can affect their growth, survival and reproduction (Wang et al. 2014). These effects are greater as higher the density of conspecific individuals in consequence of intraspecific or environmental pressures (Wang et al. 2014). Generally, species respond negatively to the density effect, which can regulate their population size (Müller-Schärer et al. 2004).

Nevertheless, some invasive species are known to grow in dense monospecific stands, and the role of intraspecific competition in limiting their performance is barely studied.

Invasive plants usually show high phenotypic plasticity than native species (DeWalt et al. 2004; Davidson et al. 2011), which allows them to occupy a wide range of habitats. Nevertheless, environmental factors such as nutrient availability, temperature and light can limit their growth and spread, thus regulating their spatial distribution (El-Keblawy and Al-Rawai 2005; Lannes et al. 2016; Pinheiro et al. 2021). Although the distribution of most invasive species can be constrained by environmental factors, some clonal plants present compensation mechanisms through phenotypic plasticity as an adaptive strategy to growth under different abiotic conditions (Ming 1996; Ikegami et al. 2007; Pinheiro et al. 2021). Among clonal invasive species, light is a major driver of responses of phenotypic plasticity rather than nutrient or water availability (Xie et al. 2014), and different light levels elicit adjustments on the ratio between aboveground and belowground biomass, sprouting and ramet morphology (Chen et al. 2019).

The white-ginger lily *Hedychium coronarium* J. König (Zingiberaceae) is an amphibious macrophyte native from tropical Asia that became an aggressive invader in Brazilian riparian zones and other American zones due to rapid growth, impacting on the maintenance of biodiversity and ecosystem services in open and forested sites (Kissmann and Groth 1999; De Castro et al. 2016). It presents efficient vegetative reproduction through rhizomes from which small fragments can be dispersed by water flow and originate new invasion spots (Stone et al. 1992; Kissmann and Groth 1999). Despite evidence of its phytotoxicity against native seeds and harmful effects on ecosystem functioning (De Castro et al. 2016; Costa et al. 2019), little is known about the response of *H. coronarium* to intraspecific competition and light availability. Understanding internal and external (i.e. environmental) regulatory mechanisms of invasive plant populations is useful to predict fluctuations in their birth rates, growth and mortality (Davis et al. 2000).

Here, we experimentally assessed the effects of intraspecific competition simulated by different rhizome densities on sprouting and growth of *H. coronarium* under two environmental conditions (full light and partial shade). We expected that ramet morphology (i.e. length) should differ regarding length between different light conditions due to phenotypic plasticity. We also predict 1) higher number of ramets, after controlled for the number of rhizomes, under full light because this condition stimulates sprouting, and under low rhizome density due to lower intraspecific competition, 2) greater rhizome growth on the shade condition, as a strategy to reach new, more favorable areas via subterranean propagation, 3) lower mean rhizome biomass on high density treatments, due to space and nutrient limiting, and 4) higher proportion of aerial/belowground biomass (hereafter “ramet/rhizome ratio”) under lower rhizome density because of reduced intraspecific competition.

Materials And Methods

Experimental Design

We conducted the experiment at an external area in the Center of Hydric Resources and Environmental Studies of University of São Paulo (CRHEA-USP) in Itirapina, São Paulo State, southeastern Brazil (22°10'08"S, 47°53'59"W). The climate is humid subtropical with hot summers and dry winters (Cwa according Köppen), with mean monthly temperatures ranging from 15.6 to 22.0 °C and annual rainfall around 1400 mm (Alvares et al. 2013). The experiment was carried out using ten circular 500 L tanks (diameter 1.5 m, height 0.6 m) with a drain exhaust system at the bottom. We divided each tank in half with impermeable canvas and both sides were filled with a soil layer of ~ 40 cm height. In each half, we transplanted *H. coronarium* rhizomes of ~ 20 cm length, establishing two paired density treatments: high density (25 rhizomes) and low density (five rhizomes). We choose these densities according a previous study on the population dynamics of *H. coronarium* in the region (De Castro et al. 2016).

To assess the environmental effects on *H. coronarium* growth, we distributed five tanks in each light condition: 50 % (hereafter "shade") and 100 % of light (hereafter "full light"). We constructed the shade treatment covering the tanks with 50 % black screen. In the first three months of the experiment, we used a dispersion irrigation system over the tanks to enhance rhizome establishment and stimulate sprouting.

Each ramet received a tag with a unique code to allow repeated measurements. We measured the length (to the nearest 0.5 cm using a ruler) of all ramets every 15 days in the first three months (hereafter "phase 1"). At the end of the experiment, after 22 months (April 2016, hereafter "phase 2"), we counted the number of ramets and measured their length. Right after this last measurement, the rhizomes and ramets were removed and dried at $60 \pm 2^\circ\text{C}$ for one week, and their dry weight was obtained using a digital scale (precision 0.01 g).

Statistical Analyses

To assess the effect of treatments in *H. coronarium* sprouting, we pondered the number of ramets per replicate by multiplying per five the number of ramets in each replicate in both phase 1 and 2, since the high density treatment have five times the initial number of rhizomes of the low density treatment.

We created linear mixed-effects models (LMMs) to test the influence of Light and Density as fixed factors on ramet length and number of ramets (both square-root transformed) in phase 1, setting ramet identity and tank number as random effects, respectively. Due to the temporal autocorrelation within repeated measurements in phase 1, we included an auto-regressive level 1 correlation structure in these models. The presence of the Density $\times$ Light interaction was assessed through a likelihood-ratio test and this term was removed when did not improve the model.

Based on data from phase 2, we estimated the total rhizome dry weight and the ramet/rhizome ratio (total ramet dry weight/total rhizome dry weight) per replicate. The same procedure described above to ponder the number of ramets per replicate was used when analyzing rhizome dry weight. To analyze the phase 2 data, we tested for the use of LMMs with tank number as a random effect following Zuur et al. (2009). The use of this random effect improved significantly the model on ramet length, but not the further models (all $p > 0.189$), and we retained linear models in the models on number of ramets, rhizome

dry weight and ramet/rhizome ratio. In all phase 2 models, light and density were set as fixed factors, and the presence of the Density $\times$ Light interaction was tested as described above. Square-root transformation of the response variables of phase 2 was employed in the models on ramet length, number of ramets and rhizome dry weight.

Model validation was assessed by testing residual normality in a Shapiro-Wilk test and checking visually heteroscedasticity, and. All analysis and graphs were performed in the R environment (R Development Core Team 2017), using "*lme*" function of "*nlme*" package (Pinheiro et al. 2017).

Results

In phase 1, ramet length differed between light treatments, being 38.2 % longer in shade than in full light (Fig. 1A). Ramet length averaged 19.9 ± 9.5 cm in shade and 14.4 ± 6.3 cm in the full light treatment ($n = 1246$ measurements from 285 ramets). The Density treatment did not affect ramet length. Otherwise, the number of ramets in phase 1 was higher in low rhizome density (Fig. 1C), indicating a negative effect of intraspecific competition, and did not differ between light treatments (Table 1). The interaction Density $\times$ Light was absent from the models on length and number of ramets (Table 1).

Table 1

Results of linear models (LM) and linear mixed-effects (LMM) models testing the effects of light level (Light = full light/shade), rhizome density (Density = high/low), and their interaction (Density $\times$ Light) on ramet length, number of ramets, total rhizome dry weight, and ramet/rhizome biomass ratio (ramet biomass divided by rhizome biomass in each replicate) of *Hedychium coronarium* in two phases of a controlled experiment. SE = standard error; df = degrees of freedom; bold denotes statistical significance of p-values ($\alpha = 0.05$). Parameters of the interaction term not shown when it was absent from final models

Phase 1 (first three months)					Phase 2 (after 22 months)			
	Estimate (SE)	df	t ratio	p	Estimate (SE)	df	t ratio	p
<i>Ramet length</i>								
Intercept	3.666 (0.076)	944	48.351	< 0.001	2.819 (0.147)	302	19.192	< 0.001
Density	-0.041 (0.103)	287	-0.400	0.689	-0.364 (0.173)	302	-2.107	0.036
Light	0.631 (0.102)	8	6.180	< 0.001	1.678 (0.217)	8	7.748	< 0.001
Density $\times$ Light				0.297	-0.723 (0.253)	302	-2.856	0.005
<i>Number of ramets</i>								
Intercept	3.971 (0.191)	55	20.841	< 0.001	4.803 (0.718)		6.693	< 0.001
Density	0.505 (0.1397)	55	3.636	0.001	1.991 (0.829)		2.403	0.028
Light	0.242 (0.253)	8	0.958	0.366	-0.325 (0.829)		-0.393	0.699
Density $\times$ Light				0.946				0.5792
<i>Total rhizome dry weight</i>								
Intercept					17.477 (3.019)		5.789	< 0.001
Density					3.671 (3.553)		1.033	0.317
Light					10.482 (3.553)		2.951	0.009
Density $\times$ Light								0.411
<i>Ramet/rhizome ratio</i>								

Phase 1 (first three months)	Phase 2 (after 22 months)		
Intercept	35.383 (4.674)	7.569	< 0.001
Density	1.697 (5.398)	0.314	0.757
Light	-6.745 (5.398)	- 1.250	0.228
Density × Light			0.256

In phase 2, ramet length also differed between light treatments, with ramets more than twice (2.17 times) longer in shade than in full light treatment (vs. 8.4 cm in average, Fig. 1B, Table 1). Ramet length averaged 18.3 ± 9.8 cm in shade and 8.4 ± 5.9 cm in the full light treatment ($n = 314$ ramets). A positive effect of rhizome density on ramet length also expressed in phase 2 (Fig. 1B). However, the interaction term Density × Light was significant, and a post-hoc test revealed that the effect of rhizome density on ramet length was restricted to the shade treatment. Under shade, ramets were in average 8.0 cm (i.e. 60.7 %) longer in high than in low rhizome density, whereas this difference was only 1.3 cm (i.e. 17.7 %) under full light treatment. Similarly to the phase 1 results, the number of ramets in phase 2 suffered a negative effect of rhizome density, and did not differ between shade and full light (Table 1, Fig. 1D), neither was the interaction Density × Light significant in this model (Table 1).

At the end of the experiment, the total rhizome dry weight was significantly higher under shade than in full light (Table 1, Fig. 2), but it was not affected by density treatments. Although the proportion of rhizome dry weight in low and high density treatments has averaged around 1:2 at the end of the experiment, this was not enough for deviating from the initial proportion of rhizomes in these treatments (1:5). The ramet/rhizome ratio did not differ between the light or density treatments. The interaction Density × Light was removed from both the models on rhizome dry weight and ramet/rhizome ratio (Table 1).

Discussion

We found a clear variation in ramet length in response to different light conditions, indicating a high phenotypic plasticity of *H. coronarium*. The effect of light levels in this aspect of ramet morphology was intensified by the intraspecific competition created by rhizome density treatments over time. The number of ramets, when controlled for the initial number of rhizomes, initially suffered a negative effect of intraspecific competition, but this difference was no longer evident in the phase 2. Moreover, the number of ramets was similar regardless of light levels, which indicates that environmental conditions had a secondary role in predicting *H. coronarium* sprouting. Our results also showed that the proportion of aerial and subterraneous biomass is roughly constant despite variations in light and rhizome density, probably owe to the adjustments in ramet morphology mediated by phenotypic plasticity mechanisms.

Together, these results suggest that *H. coronarium* maintains similar performances under different environmental conditions, being little affected by the negative effects of intraspecific competition resulting from population growth.

Ramet length showed a fast adaptation to the differences between light treatments, being higher in shade treatment at both density treatments since the early stages of invasion, represented by phase 1. In fact, the length of *H. coronarium* ramets can be positively affected by shading levels (Santos et al. 2005). Accordingly, some clonal species can exhibit higher growth rates in shaded environments, increasing investment on height under low-light conditions (Huber and Wiggerman 1997; Ikegami et al. 2007). Furthermore, higher rhizome density in the shade treatment was related to higher ramet length during phase 2, reinforcing that ramet elongation occurs due to the aggravation of resource scarcity by intraspecific competition. Considering the invasiveness of *H. coronarium*, as registered in Brazil and other American countries (Kissmann and Groth 1999), our results indicate that closed canopy forests, as riparian forests, can facilitate the growth of ramets, being as susceptible as disturbed, deforested water stream margins to the spatial expansion of this invasive plant.

Contradicting our initial hypothesis, rhizome biomass at the end of the experiment was similar between high and low density treatments, although this result may have accrued from the wide variation between replicates. This result indicates that stochasticity had a considerable effect on the levels of rhizome growth reached during the experiment, which probably masked the consequences of intraspecific competition. On the other hand, our prediction regarding the effect of light treatments on rhizome dry weight was corroborated. Considering that rhizomes are an important propagule (Lange and Marshall 2016), the higher rhizome biomass under shade may allow a greater subterraneous propagation and the effort to colonize new areas as an attempt to escape competition for light.

We expected to find a negative effect of rhizome density on aerial biomass resulting from higher intraspecific competition (Müller et al. 2016). However, although the morphology of ramets have differed between the treatments, the proportion of aerial/belowground biomass (i.e., ramet/rhizome ratio) did not vary between them. The number of ramets was similar regardless of environmental conditions, indicating that light did not increase sprouting of *H. coronarium*, unlike other invasive clonal plants (Ikegami et al. 2007; Martin et al. 2020; Chen et al. 2019). Our hypothesis on the negative effect of rhizome density on the number of ramets was corroborated in both phases of the experiment, which suggests an important effect of belowground competition on sprouting in both the initial and later stages of *H. coronarium* invasion. This is in line with other studies reporting that the neighborhood density affects the growth, survival and fitness of clonal species (De Kroon and Kwant 1991; Kleunen et al. 2001; Van Kleunen et al. 2005). This negative effect of rhizome competition, however, seems to be attenuated by other mechanisms in field conditions given the typical formation of dense monospecific stands of *H. coronarium*, and the comprehension of the multiple factors underlying the population dynamics of this invasive species deserves further studies.

In conclusion, our results suggest a large phenotypic plasticity in *H. coronarium* pronounced in ramet length. The capacity of such adjustment is analogous to the mechanism of division of labor (Ikegami et al. 2008), and probably is an important compensation strategy to maintain the relation of aerial/subterranean biomass through variations in environmental conditions and population densities (Pinheiro et al. 2021). These alternative ways of energy allocation may have a key role in the colonization of different habitat types, since *Hedychium coronarium* can keep biomass production constant on varied environmental conditions and intraspecific competition levels, establishing a compensation mechanism of energy investment in above and belowground biomass. These traits may confer an important competitive advantage over native species and enhance spatial expansion of *H. coronarium* to different areas, such as opened water lands and closed, forested sites.

Declarations

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Availability of data and material – The data supporting the findings of this study are available from the corresponding author upon reasonable request.

Code availability – The R code used in the statistical analyses is available from the corresponding author upon reasonable request.

Authors' contributions – Conceptualization: WACC, ELGE, DMSM; Data curation: ROC, AFB, RVA; Formal analysis: ROC, AFB; Investigation: ROC, AFB; Methodology: ROC, WACC; Project administration: DMSM; Supervision: ELGE, DMSM; Writing – original draft: ROC, AFB; Writing – review & editing: ROC, AFB, WACC, ELGE, DMSM.

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Figures

Figure 1

Ramet length and number of ramets of *Hedychium coronarium* on different conditions of rhizome density (High and Low) and light (Full light and Shade), on phase 1 (first three months) and phase 2 (after 22 months) of a controlled experiment. *indicates significant differences

Figure 2

Total rhizome dry weight of *Hedychium coronarium* on different conditions of rhizome density (High and Low) and light (Full light and Shade) on phase 2 (after 22 months) of a controlled experiment. *indicates significant differences