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Effect of rhizome exposure to contrasting abiotic conditions on the performance of the
invasive macrophyte *Hedychium coronarium* J. Koenig (Zingiberaceae)

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Abstract

Although invasive species are often better competitors than native species, broad environmental tolerance may also drive invasion success. Tolerance to abiotic heterogeneity in riparian ecosystems tends to favour the establishment of alien clonal species, as well as their dispersion by vegetative fragments. *Hedychium coronarium* J. Koenig is a rhizomatous emergent macrophyte native to Asia, and has invaded Neotropical riparian ecosystems. We assessed the effect of *H. coronarium* rhizome exposure to distinct abiotic conditions on ramet growth. We exposed rhizomes to different desiccation periods (1 to 90 days), temperatures (15°C, 25°C and 35°C) and light regimes (0h, 12h, 16h), and then assessed the effect of each of these variables on subsequent clonal growth (aboveground biomass production per plant and per ramet, and number and height of ramets) under ambient conditions. While no rhizome survived desiccation periods longer than 30 days, ramet growth among surviving rhizomes was not affected by the period of desiccation. Biomass production per rhizome, ramet biomass and ramet height were significantly lower at 35°C than at 25°C. Constant darkness increased rhizome survival but decreased ramet growth. Although rhizome exposure to extremes of each abiotic variable may hinder the invasion success of *H. coronarium*, the subsequent aboveground biomass production of surviving rhizomes did not decrease strongly in response to any treatment. This resilience may contribute to successful establishment of *H. coronarium* after dispersal through rhizome fragments and to varying abiotic conditions.

Keywords: desiccation, clonal growth, extreme conditions, stress tolerance, invasiveness.

Declarations

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Authors' contributions - D.M.S.M and A.M.P. conceived the ideas and designed the methodology. A.M.P. collected the data. R. O. X. analysed the data. R.O.X and W.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

1. Introduction

Invasive species are important drivers of biodiversity loss (Simberloff and Rejmánek 2010), and correctly predicting which introduced species are more likely to succeed and exert negative impacts on invaded ecosystems is vital. Although invasion success is often associated with traits that confer greater competitive ability than native species (Valéry et al. 2008; Van Kleunen et al. 2009), introduced species with broad environmental tolerance may also be favoured (Chown et al. 2007). Not surprisingly, a high proportion of invasive plant species exhibit clonal growth (Liu et al. 2006), which is often associated with high resource use efficiency and persistence under a wide range of conditions (de Kroon et al. 2005; Hutchings and Wijesinghe 2008). In many successful invasive plants this effective clonal growth is based on an extensive system of rhizomes (Keser et al. 2014), which often allows rapid emergence of new ramets and may store a large amount of resources (Asaeda et al. 2006; Jones et al. 2018).

Clonal plant species often succeed under spatially heterogeneous conditions as a result of effective physiological integration (de Kroon et al. 2005). However, the establishment success of clonal plants may depend on the extent to which previous unsuitable conditions affect the subsequent performance of the clonal individuals (Portela et al. 2020), which are critical to the persistence and spread of the clonal population in a given site (Jongejans et al. 2008). For example, for the invasive grass *Arundo donax* severe drought increased rhizome mortality and decreased ramet productivity and size (Mann et al. 2013). Conversely, low light availability decreased ramet growth and depleted rhizome reserves of the marine grass *Posidonia oceanica*, but these effects did not affect subsequent clonal generations (Ruiz and Romero 2001).

Clonal species are subjected to a natural process of loss of the physical connections among their modular units, thus generating new clonal individuals (Oborny

and Kun 2002). For species occurring on aquatic ecosystems, this process of clonal fragmentation tends to be accelerated by soil erosion processes, so that vegetative fragments of clonal emergent macrophytes may be dispersed by water currents to distant sites (Konlechner 2008; Berković et al. 2014). Accordingly, clonal fragmentation is likely a major driver of introduction and spread of many invasive plants in these ecosystems (Bart and Hartman 2003; Konlechner 2008; Catford and Jansson 2014), although, disposal of fragments of rhizomes by humans may also drive the spread of invasive clonal species in terrestrial ecosystems (Rusterholz et al. 2012; Krajšek et al. 2020). Clonal establishment from rhizome fragments depends on multiple factors, including their sprouting ability under suitable growing conditions (Konlechner et al. 2016). Therefore, producing underground organs with high longevity and tolerance to a wide range of conditions may play an important role in the dispersal of invasive clonal species (Juneau and Tarasoff 2013; Konlechner et al. 2016).

Many clonal species are highly invasive in riparian ecosystems (Fleming and Dibble 2015), where abiotic conditions are often spatially and temporally heterogeneous (Lawson et al. 2015), for example due to repeated flooding and desiccation periods (Westwood et al. 2006; Chu et al. 2012). However, invasive emergent macrophytes may also withstand general changes in environmental conditions, such as daily and inter-annual temperature variation (Rooney and Kalff 2000) and spatial variation in the light regime (Glover et al. 2015), as well as temporarily unsuitable abiotic conditions, such as during extreme climatic events or dispersal by fragmentation (Juneau and Tarasoff 2013). Accordingly, the extent to which the clonal offspring is affected by previous exposure to these stressful conditions may play a central role in the dominance and spread of invasive macrophytes in riparian ecosystems.

The macrophyte *Hedychium coronarium* J. Koenig (Zingiberaceae) has been

introduced from Asia to the Neotropics, where it is invasive in a wide range of riparian ecosystems. The success of this species has been linked to high aboveground biomass production associated with an extensive rhizome system (Chiba de Castro et al. 2016; Chiba De Castro et al. 2019). Even though *H. coronarium* occurs under multiple abiotic conditions and may be dispersed through rhizome fragmentation, it is still unknown how previous exposure to stressful abiotic conditions affects rhizome survival and the performance of the subsequent clonal offspring of the species under ambient growing conditions. In this study we assessed the effect of rhizome exposure to contrasting desiccation, temperature and photoperiod conditions on the subsequent vegetative growth of *H. coronarium*. We specifically aimed to answer the following questions: i) Does rhizome exposure to longer desiccation periods decrease the survival and subsequent biomass production of ramets? ii) How are ramet abundance, size and biomass production affected by distinct temperature and light conditions? Considering that *H. coronarium* occurs under contrasting light regimes in both tropical and temperate ecosystems (Chiba De Castro et al. 2019) and may disperse through rhizome fragmentation, we expected that survival and biomass production of rhizomes would not differ significantly in relation to photoperiod or temperature. However, we predicted that survival and biomass production of *H. coronarium* would decrease as a result of longer desiccation periods, since drought stress can often have a large negative effect on the performance of clonal herbaceous species (Mann et al. 2013).

2. Material and methods

2.1. Species description

Hedychium coronarium is a rhizomatous herbaceous plant growing up to 2 m high (Kissmann and Groth 1991). It has been widely introduced outside its native range as an ornamental and has become a highly successful invader in many Brazilian ecosystems,

including wetlands, floodplains and riparian zones in the Atlantic Forest and Cerrado. *Hedychium coronarium* forms dense monospecific stands, leading to high biomass production and litter accumulation (Chiba De Castro et al. 2019), as well as allelopathic effects on Neotropical riparian tree species (Costa et al. 2019). Although the role of rhizome fragments in the spread of *H. coronarium* remains unknown, dispersal in watercourses after trampling or grazing by native animals has been reported (Chiba de Castro et al. 2013), as well as following floods and soil erosion.

2.2 Methods

We collected rhizomes of *H. coronarium* from five sites in southeastern Brazil. The local climate is a transition between Cwa (humid subtropical climate) and Aw (tropical savanna climate). The study sites included: 1) the border of a permanent lake (21°58'16.80"S, 47°53'18.35"W); 2) a reservoir border (21°59'06.87"S, 47°52'48.17"W); 3) a river border (21°59'13.01"S, 47°52'21.87"W); 4) an agricultural site (21°58'48.71"S, 47°55'17.94"W); 5) and an urban fragment (21°59'31.51"S, 47°54'13.52"W) .

Rhizomes were haphazardly collected in all sites in October 2016 to control for the effect of seasonality on ramet viability (Juneau and Tarasoff 2017). The rhizomes were washed, dried at room temperature for 24h and divided into 10 cm fragments. Rhizome fragments were randomly assigned to distinct experiments assessing the effect of desiccation period, temperature and light regime on rhizome survival and ramet growth.

2.2.1. Desiccation experiment

For the desiccation experiment, we oven dried three rhizome fragments of each site at the average annual maximum temperature in the region (30°C) for 12 distinct time

periods: 2h, 5h, 15h, 30h, 60h, 120h, seven days, 14 days, 21 days, 30 days, 60 days and 90 days (3 fragments by site x 5 sites x 12 treatment levels = 180 rhizome fragments)). These periods were used to simulate a wide range of water loss conditions in rhizomes, including both short to intermediate periods of low soil moisture that occur naturally during the dry season in riparian sites invaded by *H. coronarium* (Almeida 2015) and more prolonged desiccation that may occur after rhizome fragments are naturally dispersed or disposed by humans.

Following desiccation treatments, three rhizome fragments from each site were transplanted to 10 x 10 cm trays with a 5 cm layer of commercial organic soil. These trays were maintained in a room at 24°C and 12h:12h light-dark photoperiod for 60 days. Twice a week, we added 500 mL of water to each tray, counted the number of emergent ramets and measured their heights. We obtained the dry biomass of each ramet at the end of the experiment after oven drying at 60°C for 48h. Thus, we measured biomass per ramet from a rhizome fragment and total biomass across ramets per rhizome fragment.

2.2.2. Light and Temperature Experiments

To assess the effect of rhizome exposure to distinct temperatures on ramet growth, we placed five 10 cm x 10 cm trays with five rhizome fragments in germination chambers at three conditions ((T1) 15°C, (T2) 25°C and (T3) 35°C) and a 12h:12h light-dark photoperiod (5 fragments by tray × 5 trays by treatment (1 tray by site) × 3 treatment levels = 75 rhizomes). These temperatures were chosen as they are low (15°C), ambient (25°C) or high (35°) compared to average annual temperatures in the native range of *H. coronarium* (Manish 2013).

To assess the effect of light availability on ramet growth, five rhizome fragments from each site were transplanted to 10 x 10 cm trays with a 5 cm layer of soil rich in

organic matter, which were then exposed to four photoperiods: ((L1) 16h light, (L2) 12h light (L3) 0h light (5 fragments by tray $\times$ 5 trays by treatment (1 tray by site) $\times$ 4 treatment levels = 100 rhizome fragments). In the constant darkness treatment trays were covered with aluminum foil and placed into black plastic bags, whereas in the other treatments they remained in rooms subjected to distinct photoperiods; in all treatments, samples were subjected to a 24°C air temperature. Photoperiods with 12 and 16 h of light occur at the latitude of sites invaded by *H. coronarium*, whereas constant darkness simulates light conditions when rhizomes remain buried under substrate such as soil or alluvial material. In both experiments, samples also were watered with 500 mL water twice a week, and the abundance and height of emergent ramets was recorded weekly for 30 days. After this period the trays were transferred without removal of the already emerged ramets to a room at 24°C with a 12h:12h light:dark photoperiod, where they remained under the same watering regime for an additional 60 day period. At the end of this period, we oven dried all the ramets at 60°C for 48h and weighed the dry biomass. Thus, we measured biomass per ramet from a rhizome fragment and total biomass across ramets per rhizome fragment. We assumed that rhizomes failing to produce ramets during the entire experimental period had not survived.

2.3. Data analysis

We used Generalized Linear Mixed Models (GLMMs) to assess the effect of desiccation period, temperature and photoperiod on rhizome survival, number of ramets produced per rhizome fragment, aboveground biomass production per rhizome fragment, ramet height and ramet biomass of *H. coronarium* at the end of the experiments. For the models assessing effects on ramet growth we only included rhizomes that produced ramets during the experiment, as failing to produce ramets was our criterion for rhizome

mortality. We considered desiccation period as a continuous fixed effect, given the high number of treatment levels in the experiment, whereas temperature and light conditions were categorical fixed effects. In the models assessing effects of abiotic conditions on total biomass and ramet production per rhizome fragment, we included site as a random effect (intercept only). In the models assessing effects of abiotic conditions on ramet biomass and height, we included site and rhizome fragment as random effects (intercept only).

All GLMMs were done using the packages “lme4” (Bates et al. 2016) and “nlme” (Pinheiro et al. 2018). We assumed a Gaussian error distribution for continuous response variables, a binomial distribution for rhizome mortality and a negative binomial distribution for the number of ramets. We observed variance heterogeneity in residuals among temperature and light treatments; in this case we modelled distinct variances for each treatment by adding a variance structure to the models in the R package “nlme”. A few ramets that failed to develop (height < 5 cm) were excluded from analysis assessing effects on ramet height and biomass. We assessed the overall main effect of temperature and photoperiod treatments using Wald tests in the package “car” (Fox and Weisberg 2019). When the effects of temperature and light were significant, we performed *post-hoc* pairwise comparisons in the R package “multcomp” (Hothorn et al. 2008). All the analyses were done with the program R (R Core Team 2020).

3. Results

3.1. Desiccation period effects

Rhizome survival was low under all desiccation conditions and GLMMs showed an only marginally significant negative relationship between rhizome survival and desiccation period, largely as a result of the lack of survival among ramets subjected to

desiccation period longer than 40 days (Fig. 1a, Table 1). However, the aboveground biomass production and the number of ramets by rhizome, as well as the height and biomass of ramets, were not significantly related to the desiccation period (Table 1, Fig. 1).

3.2. Temperature effects

We found large differences in rhizome survival among temperature treatments (Table 2, Fig. 2a); *post-hoc* pairwise comparisons showed that mortality at 25°C (36%) was over two times lower than at 15°C (80%, $z=3.00$, $p=0.007$) and 35°C (80%, $z=3.00$, $p=0.007$). The aboveground biomass production per rhizome and the biomass and height of ramets differed significantly among temperature treatments (Table 2); pairwise comparisons showed that aboveground biomass production per rhizome (Fig. 2b, $t=2.82$, $p=0.012$), ramet biomass (Fig. 2d, $t=2.67$, $p=0.020$) and ramet height (Fig. 2e, $t=2.70$, $p=0.019$) were at least 30% greater at 25°C than at 35°C, and significantly so. The number of ramets produced per rhizome did not significantly differ among temperature treatments (Fig. 2c).

3.3. Photoperiod effects

Rhizome mortality differed among photoperiod treatments (Table 2, Fig. 3); *post-hoc* tests showed that mortality under constant darkness (4%) was much lower than under a 12h (56%, $z=3.14$, $p=0.004$) or 16h (64%, $z=3.42$, $p=0.002$) photoperiod. However, the aboveground biomass production per rhizome and the biomass and height of ramets differed significantly among photoperiod treatments (Table 2). Average biomass production per rhizome under constant darkness was more than two times lower than that of rhizomes under a 12h photoperiod (Fig. 3b, $t=-5.10$, $p<0.001$) and 70% higher than under a 16h photoperiod ($z=3.27$, $p=0.003$). Consistent with the biomass finding, rhizomes exposed to constant darkness produced ramets with almost 50% lower biomass

than those exposed to a 12h photoperiod ($t=3.37$, $p=0.005$; Figure 3d). However, ramet height and number of ramets produced by rhizome did not differ among light treatments (Table 1, Figure 3).

4. Discussion

In this study we assessed how exposure of rhizomes of *H. coronarium* to contrasting abiotic conditions affects their survival and subsequent ramet production. Although rhizomes did not survive prolonged desiccation (>40 days), the subsequent productivity among the surviving rhizomes was not affected by the initial desiccation period. We also found that *H. coronarium* shows optimal rhizome survival and ramet growth at 25°C, whereas exposure to constant darkness decreased the aboveground biomass. Our findings suggest that rhizomes of *H. coronarium* tolerate a wide range of abiotic conditions with little consequence for the next generation of ramets under suitable conditions.

We found that most rhizomes of *H. coronarium* did not survive to exposure to desiccation for 60 to 90 days and hence failed to produce ramets. Plants may exhibit a range of mechanisms to tolerate desiccation, such as increased production of compounds (e.g. sugars) that increase tolerance to water deficit (Alpert 2006). Therefore, aquatic macrophytes often survive and resprout after exposure to a few hours of desiccation (1 or 3h) (Barnes et al. 2013), whereas few or no rhizomes of clonal species typical from riparian sites survive after exposure to over a month of desiccation (Michelan et al. 2010). We found that even a few hours of desiccation led to high mortality of rhizomes of *H. coronarium*, which suggests a low level of tolerance to drought stress for this species. Although metabolic costs associated with desiccation tolerance also tend to decrease individual performance (Hartung et al. 1998), rhizomes surviving up to 30 days of

desiccation surprisingly did not produce less ramet biomass or lower ramets with increasing desiccation period. We acknowledge that the 10% surviving rhizomes in our desiccation experiment were possibly a subset including the most robust and productive clones. However, these findings do suggest that a few rhizomes of *H. coronarium* may survive and perform well even after exposure to severe soil water deficit during up to one month. Producing rhizomes that tolerate moderate desiccation possibly enables *H. coronarium* to persist even in riparian ecosystems subjected to seasonally dry climates (Chiba de Castro et al. 2016); in addition, it may favour dispersal of rhizome fragments, as they would be more likely to overcome drought during transportation and establish clonal populations in suitable sites.

We found that rhizome survival and aerial biomass production by rhizome, as well as the height and biomass of ramets, were lower at 35°C than 25°C,. This is surprisingly because rhizomes can tolerate short exposure to temperatures over 50°C (Flinn and Pringle 1983), and *H. coronarium* occurs in regions where maximum air temperatures exceed 35°C (Ray et al. 2018). Nevertheless, increased evapotranspiration from soils at 35°C possibly also increased drought stress and hence further contributed to the inferior performance of *H. coronarium* at high temperatures, given that watering was constant across all treatments. However, our results show that high temperatures may decrease the size and biomass of ramets and then be limiting to the success of *H. coronarium* in low latitude tropical ecosystems in South America, where average annual and maximum temperatures often exceed 25° and 35°C, respectively (da Silva 2004; Almeida et al. 2017). By contrast, although we also found lower rhizome survival at 15°C than 25°C, the current annual average temperatures (20- 25°C) in most Atlantic Forest sites (Colombo and Joly 2010) are in the optimum temperature range for this species, which is already widely distributed and often dominant in the southern part of this biodiversity

hotspot (Maciel et al. 2011).

Exposure to constant darkness resulted in higher rhizome survival but decreased ramet biomass and the overall aboveground biomass production compared to rhizomes exposed to light.. Rhizomes remain underground and hence are naturally subjected to low light availability. It is unclear why exposure to light should decrease rhizome survival, but an implication is that it could decrease establishment success of dispersed rhizome fragments. Conversely, light availability is often limiting for macrophytes (Glover et al. 2015), and hence heavy shading may decrease growth of invasive clonal macrophytes (Maurer and Zedler 2002). *H. coronarium* tolerates shading and is found both in riparian forests and forest edges (Serra do Vale Duarte et al. 2015). However, complete darkness often causes dramatic changes in patterns of resource allocation on underground organs, thus affecting morphological attributes and productivity (Voesenek et al. 1998), consistent with the low biomass of ramets and overall aboveground production of *H. coronarium* after rhizome exposure to this condition. Although further experimental studies should investigate the effect of contrasting canopy cover conditions on ramet growth, our findings point to the likelihood that the species will not dominate the understory of riparian forests with very dense canopy.

We found that the number of ramets produced by *H. coronarium* was not affected by the abiotic variation. This is surprising because altering ramet production in response to environmental conditions can be critical to the success of clonal species (de Kroon et al. 2005). Indeed, stressful abiotic conditions may either increase rhizome growth and bud activity in rhizomes (Pumisutapon et al. 2012). A lack of responsiveness of ramet number production may favour the initial establishment of clonal populations, but it may also limit the spread of the species in riparian ecosystems, where these abiotic conditions also often spatially and temporally heterogeneous (Lawson et al. 2015). Nevertheless, the plant growth

period after experimental treatments (two months) possibly did not allow substantial rhizome growth and hence the detection of ramet production differences. Longer experimental studies assessing how abiotic conditions interact to affect rhizome survival and growth compared to functionally similar native species would shed more light on the abiotic limits to success of this invader.

Although the response of *H. coronarium* to abiotic variation in this study is consistent with its success in multiple riparian ecosystems, we also demonstrate that there are abiotic limits to the survival and biomass production of the species. We found that even short periods of desiccation have a large negative effect on rhizome survival and, hence, may limit the persistence of *H. coronarium* in seasonally dry sites. In addition, high temperatures decrease both the survival and biomass production of *H. coronarium* and may limit the success of the species at low latitudes, whereas constant darkness leads to lower aboveground biomass production. We conclude that prolonged desiccation and high temperatures may decrease the survival of *H. coronarium*, but subsequent clonal generations from surviving rhizomes are not severely hindered by the abiotic conditions experienced previously. This resilience to abiotic stress may play a central role in the success of the species. Given the predictions of higher frequencies of extreme events, we need to understand further how lower rhizome survival but resilient growth after drought and higher temperatures will affect ongoing invasion by this species.

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Tables

507 Table 1 – Results of generalized linear mixed models assessing the effect of exposure to
508 distinct desiccation periods (1 to 90 days), on rhizome mortality, aboveground biomass
509 production per rhizome, number of ramets per rhizome and height and biomass of ramets
510 of *Hedychium coronarium*. Error = standard error.

Model	Estimate	Error	z value	P value
Rhizome survival	0.035	0.019	1.81	0.070
Biomass by rhizome (g)	0.062	0.027	1.87	0.079
Ramets per rhizome	0.026	0.015	1.65	0.098
Ramet biomass (g)	0.013	0.013	1.05	0.302
Ramet height (cm)	-0.027	0.136	-0.20	0.846

Table 2 – Results of Wald tests based on generalized linear mixed models assessing the effect of rhizome exposure to different temperature (15°C, 25°C and 35°C) and light conditions (00h, 12h, 16h) on the aboveground biomass production per rhizome, number of ramets per rhizome and height and biomass of ramets of *Hedychium coronarium*. df= degrees of freedom.

	Chisq	df	P value
	value		
Temperature treatments			
Rhizome survival	12.5	2	0.002
Biomass per rhizome (g)	10.77	2	0.005
Number of ramets per rhizome	0.42	2	0.811
Ramet biomass (g)	7.18	2	0.028
Ramet height (cm)	8.68	2	0.013
Light treatments			
Rhizome survival	11.85	2	0.003
Biomass per rhizome (g)	26.40	2	<0.001
Number of ramets per rhizome	0.72	2	0.697
Ramet biomass (g)	16.08	2	<0.001
Ramet height (cm)	3.61	2	0.164

List of Captions

Fig. 1. Relationship between period of rhizome exposure to desiccation at 30°C and the aboveground biomass per rhizome (a), number of ramets per rhizome (b), rhizome survival rate (c), ramet biomass (d) and ramet height (e) in *Hedychium coronarium*. Lines are predicted values based on results of Generalized Linear Mixed models, with dotted and dashed lines indicating, respectively, marginally significant and non-significant

relationships.

Fig. 2. Aboveground biomass per rhizome (a), number of ramets per rhizome (b), rhizome survival rate (c), ramet biomass (d) and ramet height (e) of *Hedychium coronarium* after rhizome exposure to different temperatures (15°, 25° and 35°C). Solid and dashed horizontal lines indicate the median and the mean, respectively, and the absence of the same letter/s between two treatments indicates significant differences ($p < 0.05$).

Fig. 3. Aboveground biomass per rhizome (a), number of ramets per rhizome (b), rhizome survival rate (c), ramet biomass (d) and ramet height (e) of *Hedychium coronarium* after rhizome exposure to different photoperiods (0h, 12h, 16h). Solid and dashed horizontal lines indicate the median and the mean, respectively, and the absence of the same letter/s between two treatments indicates significant differences ($p < 0.05$).