

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.

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## 1 **1. Introduction**

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

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

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

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

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

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

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

## 71 **2. Material and methods**

### 72 2.1. Species description

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

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

83

## 84 2.2 Methods

85 We collected rhizomes of *H. coronarium* from five sites in southeastern Brazil.  
86 The local climate is a transition between Cwa (humid subtropical climate) and Aw  
87 (tropical savanna climate). The study sites included: 1) the border of a permanent lake  
88 (21°58'16.80"S, 47°53'18.35"W); 2) a reservoir border (21°59'06.87"S, 47°52'48.17"W);  
89 3) a river border (21°59'13.01"S, 47°52'21.87"W); 4) an agricultural site  
90 (21°58'48.71"S, 47°55'17.94"W); 5) and an urban fragment (21°59'31.51"S,  
91 47°54'13.52"W) .

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

### 98 2.2.1. Desiccation experiment

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

101 periods: 2h, 5h, 15h, 30h, 60h, 120h, seven days, 14 days, 21 days, 30 days, 60 days and  
102 90 days (3 fragments by site x 5 sites x 12 treatment levels = 180 rhizome fragments)).  
103 These periods were used to simulate a wide range of water loss conditions in rhizomes,  
104 including both short to intermediate periods of low soil moisture that occur naturally  
105 during the dry season in riparian sites invaded by *H. coronarium* (Almeida 2015) and  
106 more prolonged desiccation that may occur after rhizome fragments are naturally  
107 dispersed or disposed by humans.

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

115

#### 116 2.2.2. Light and Temperature Experiments

117         To assess the effect of rhizome exposure to distinct temperatures on ramet growth,  
118 we placed five 10 cm x 10 cm trays with five rhizome fragments in germination chambers  
119 at three conditions ((T1) 15°C, (T2) 25°C and (T3) 35°C) and a 12h:12h light-dark  
120 photoperiod (5 fragments by tray × 5 trays by treatment (1 tray by site) × 3 treatment  
121 levels = 75 rhizomes). These temperatures were chosen as they are low (15°C), ambient  
122 (25°C) or high (35°) compared to average annual temperatures in the native range of *H.*  
123 *coronarium* (Manish 2013).

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

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

143

### 144 2.3. Data analysis

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

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

158 All GLMMs were done using the packages “lme4” (Bates et al. 2016) and “nlme”  
159 (Pinheiro et al. 2018). We assumed a Gaussian error distribution for continuous response  
160 variables, a binomial distribution for rhizome mortality and a negative binomial  
161 distribution for the number of ramets. We observed variance heterogeneity in residuals  
162 among temperature and light treatments; in this case we modelled distinct variances for  
163 each treatment by adding a variance structure to the models in the R package “nlme”. A  
164 few ramets that failed to develop (height < 5 cm) were excluded from analysis assessing  
165 effects on ramet height and biomass. We assessed the overall main effect of temperature  
166 and photoperiod treatments using Wald tests in the package “car” (Fox and Weisberg  
167 2019). When the effects of temperature and light were significant, we performed *post-*  
168 *hoc* pairwise comparisons in the R package “multcomp” (Hothorn et al. 2008). All the  
169 analyses were done with the program R (R Core Team 2020).

170

### 171 **3. Results**

#### 172 3.1. Desiccation period effects

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

176 desiccation period longer than 40 days (Fig. 1a, Table 1). However, the aboveground  
177 biomass production and the number of ramets by rhizome, as well as the height and  
178 biomass of ramets, were not significantly related to the desiccation period (Table 1, Fig.  
179 1).

### 180 3.2. Temperature effects

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

### 191 3.3. Photoperiod effects

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

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

204

#### 205 **4. Discussion**

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

215 We found that most rhizomes of *H. coronarium* did not survive to exposure to  
216 desiccation for 60 to 90 days and hence failed to produce ramets. Plants may exhibit a  
217 range of mechanisms to tolerate desiccation, such as increased production of compounds  
218 (e.g. sugars) that increase tolerance to water deficit (Alpert 2006). Therefore, aquatic  
219 macrophytes often survive and resprout after exposure to a few hours of desiccation (1 or  
220 3h) (Barnes et al. 2013), whereas few or no rhizomes of clonal species typical from  
221 riparian sites survive after exposure to over a month of desiccation (Michelan et al. 2010).  
222 We found that even a few hours of desiccation led to high mortality of rhizomes of *H.*  
223 *coronarium*, which suggests a low level of tolerance to drought stress for this species.  
224 Although metabolic costs associated with desiccation tolerance also tend to decrease  
225 individual performance (Hartung et al. 1998), rhizomes surviving up to 30 days of

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

236         We found that rhizome survival and aerial biomass production by rhizome, as well  
237 as the height and biomass of ramets, were lower at 35°C than 25°C,. This is surprisingly  
238 because rhizomes can tolerate short exposure to temperatures over 50°C (Flinn and  
239 Pringle 1983), and *H. coronarium* occurs in regions where maximum air temperatures  
240 exceed 35°C (Ray et al. 2018). Nevertheless, increased evapotranspiration from soils at  
241 35°C possibly also increased drought stress and hence further contributed to the inferior  
242 performance of *H. coronarium* at high temperatures, given that watering was constant  
243 across all treatments. However, our results show that high temperatures may decrease the  
244 size and biomass of ramets and then be limiting to the success of *H. coronarium* in low  
245 latitude tropical ecosystems in South America, where average annual and maximum  
246 temperatures often exceed 25° and 35°C, respectively (da Silva 2004; Almeida et al.  
247 2017). By contrast, although we also found lower rhizome survival at 15°C than 25°C,  
248 the current annual average temperatures (20- 25°C) in most Atlantic Forest sites  
249 (Colombo and Joly 2010) are in the optimum temperature range for this species, which is  
250 already widely distributed and often dominant in the southern part of this biodiversity

251 hotspot (Maciel et al. 2011).

252           Exposure to constant darkness resulted in higher rhizome survival but decreased  
253 ramet biomass and the overall aboveground biomass production compared to rhizomes  
254 exposed to light.. Rhizomes remain underground and hence are naturally subjected to low  
255 light availability. It is unclear why exposure to light should decrease rhizome survival,  
256 but an implication is that it could decrease establishment success of dispersed rhizome  
257 fragments. Conversely, light availability is often limiting for macrophytes (Glover et al.  
258 2015), and hence heavy shading may decrease growth of invasive clonal macrophytes  
259 (*H. coronarium* tolerates shading and is found both in riparian  
260 forests and forest edges (Serra do Vale Duarte et al. 2015). However, complete darkness  
261 often causes dramatic changes in patterns of resource allocation on underground organs,  
262 thus affecting morphological attributes and productivity (Voesenek et al. 1998),  
263 consistent with the low biomass of ramets and overall aboveground production of *H.*  
264 *coronarium* after rhizome exposure to this condition. Although further experimental  
265 studies should investigate the effect of contrasting canopy cover conditions on ramet  
266 growth, our findings point to the likelihood that the species will not dominate the  
267 understory of riparian forests with very dense canopy.

268           We found that the number of ramets produced by *H. coronarium* was not affected  
269 by the abiotic variation. This is surprising because altering ramet production in response  
270 to environmental conditions can be critical to the success of clonal species (de Kroon et al.  
271 2005). Indeed, stressful abiotic conditions may either increase rhizome growth and bud  
272 activity in rhizomes (Pumisutapon et al. 2012). A lack of responsiveness of ramet number  
273 production may favour the initial establishment of clonal populations, but it may also  
274 limit the spread of the species in riparian ecosystems, where these abiotic conditions also  
275 often spatially and are heterogeneous (Lawson et al. 2015). Nevertheless, the plant growth

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

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

295

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301

302 **References**

303 Almeida CT, Oliveira-Júnior JF, Delgado RC, Cubo P, Ramos MC (2017)

304 Spatiotemporal rainfall and temperature trends throughout the Brazilian Legal

305 Amazon, 1973–2013. *International Journal of Climatology* 37:2013–2026 .

306 <https://doi.org/10.1002/joc.4831>

307 Almeida RV de (2015) Invasividade de *Hedychium coronarium* J. Koenig

308 (Zingiberaceae) em diferentes umidades do solo. Universidade Federal de São

309 Carlos

310 Alpert P (2006) Constraints of tolerance: why are desiccation-tolerant organisms so

311 small or rare? *Journal of Experimental Biology* 209:1575–1584

312 Asaeda T, Rajapakse L, Manatunge J, Sahara N (2006) The effect of summer harvesting

313 of *Phragmites australis* on growth characteristics and rhizome resource storage.

314 *Hydrobiologia* 553:327–335 . <https://doi.org/10.1007/s10750-005-1157-6>

315 Barnes MA, Jerde CL, Keller D, Chadderton WL, Howeth JG, Lodge DM (2013)

316 Viability of aquatic plant fragments following desiccation. *Invasive Plant*

317 *Science and Management* 6:320–325

318 Bart D, Hartman JM (2003) The role of large rhizome dispersal and low salinity

319 windows in the establishment of common reed, *Phragmites australis*, in salt

320 marshes: New links to human activities. *Estuaries* 26:436–443 .

321 <https://doi.org/10.1007/BF02823720>

322 Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B,

323 Grothendieck G (2016) Package lme4: Linear mixed-effects models using Eigen

324 and S4. CRAN Repos 1:1–113

325 Berković B, Cabaço S, Barrio JM, Santos R, Serrão EA, Alberto F (2014) Extending the  
326 life history of a clonal aquatic plant: Dispersal potential of sexual and asexual  
327 propagules of *Zostera noltii*. *Aquatic Botany* 113:123–129 .  
328 <https://doi.org/10.1016/j.aquabot.2013.10.007>

329 Catford JA, Jansson R (2014) Drowned, buried and carried away: effects of plant traits  
330 on the distribution of native and alien species in riparian ecosystems. *New*  
331 *Phytologist* 204:19–36 . <https://doi.org/10.1111/nph.12951>

332 Chiba de Castro WA, Moitas ML, Lobato GM, Cunha-Santino MB & Matos DMS  
333 (2013). First record of herbivory of the invasive macrophyte *Hedychium*  
334 *coronarum* J. König (Zingiberaceae). *Biota Neotropica* 13: 3–5.  
335 <http://dx.doi.org/10.1590/S1676-06032013000400030>.  
336

337 Chiba de Castro WA, Almeida RV, Leite MB, Marrs RH, Matos DS (2016) Invasion  
338 strategies of the white ginger lily *Hedychium coronarium* J. König  
339 (Zingiberaceae) under different competitive and environmental conditions.  
340 *Environmental and Experimental Botany* 127:55–62

341 Chiba De Castro WA, Almeida RV, Xavier RO, Bianchini I, Moya H, Silva Matos DM  
342 (2019) Litter accumulation and biomass dynamics in riparian zones in tropical  
343 South America of the Asian invasive plant *Hedychium coronarium* J. König  
344 (Zingiberaceae). *Plant Ecology & Diversity* 1–13 .  
345 <https://doi.org/10.1080/17550874.2019.1673496>

346 Chown SL, Slabber S, McGeoch MA, Janion C, Leinaas HP (2007) Phenotypic

347 plasticity mediates climate change responses among invasive and indigenous  
348 arthropods. *Proceedings of the Royal Society B: Biological Sciences* 274:2531–  
349 2537 . <https://doi.org/10.1098/rspb.2007.0772>

350 Chu SH, Zhang QS, Liu SK, Tang YZ, Zhang SB, Lu ZC, Yu YQ (2012) Tolerance of  
351 *Sargassum thunbergii* germlings to thermal, osmotic and desiccation stress.  
352 *Aquatic Botany* 96:1–6

353 Colombo AF, Joly CA (2010) Brazilian Atlantic Forest lato sensu: the most ancient  
354 Brazilian forest, and a biodiversity hotspot, is highly threatened by climate  
355 change. *Brazilian Journal of Biology* 70:697–708 .  
356 <https://doi.org/10.1590/S1519-69842010000400002>

357 Costa RO, José CM, Grombone-Guaratini MT, Silva Matos DM (2019) Chemical  
358 characterization and phytotoxicity of the essential oil from the invasive  
359 *Hedychium coronarium* on seeds of Brazilian riparian trees. *Flora* 257:151411 .  
360 <https://doi.org/10.1016/j.flora.2019.05.010>

361 de Kroon H, Huber H, Stuefer JF, Van Groenendael JM (2005) A modular concept of  
362 phenotypic plasticity in plants. *New Phytologist* 166:73–82 .  
363 <https://doi.org/10.1111/j.1469-8137.2004.01310.x>

364 Decruyenaere JG, Holt JS (2001) Seasonality of clonal propagation in giant reed. *Weed*  
365 *Science* 49:760–767 . [https://doi.org/10.1614/0043-](https://doi.org/10.1614/0043-1745(2001)049[0760:SOCPIG]2.0.CO;2)  
366 [1745\(2001\)049\[0760:SOCPIG\]2.0.CO;2](https://doi.org/10.1614/0043-1745(2001)049[0760:SOCPIG]2.0.CO;2)

367 Fleming JP, Dibble ED (2015) Ecological mechanisms of invasion success in aquatic  
368 macrophytes. *Hydrobiologia* 746:23–37 . [https://doi.org/10.1007/s10750-014-](https://doi.org/10.1007/s10750-014-2026-y)  
369 [2026-y](https://doi.org/10.1007/s10750-014-2026-y)

- 370 Flinn MA, Pringle JK (1983) Heat tolerance of rhizomes of several understory species.  
371 Canadian Journal of Botany 61:452–457
- 372 Fox J, Weisberg S (2019) An R Companion to Applied Regression, 3rd edn. Sage
- 373 Glover R, Drenovsky RE, Futrell CJ, Grewell BJ (2015) Clonal integration in *Ludwigia*  
374 *hexapetala* under different light regimes. Aquatic Botany 122:40–46 .  
375 <https://doi.org/10.1016/j.aquabot.2015.01.004>
- 376 Hartung W, Schiller P, Dietz K-J (1998) Physiology of poikilohydric plants. In:  
377 Progress in botany. Springer, pp 299–327
- 378 Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric  
379 Models. Biometrical Journal 50:346–363 <https://doi.org/10.1002/bimj.200810425>
- 380 Hutchings MJ, Wijesinghe DK (2008) Performance of a clonal species in patchy  
381 environments: effects of environmental context on yield at local and whole-plant  
382 scales. Evolutionary Ecology 22:313–324 . <https://doi.org/10.1007/s10682-007->  
383 [9178-4](https://doi.org/10.1007/s10682-007-9178-4)
- 384 Jones D, Bruce G, Fowler MS, Law-Cooper R, Graham I, Abel A, Street-Perrott FA,  
385 Eastwood D (2018) Optimising physiochemical control of invasive Japanese  
386 knotweed. Biol Invasions 20:2091–2105 . <https://doi.org/10.1007/s10530-018->  
387 [1684-5](https://doi.org/10.1007/s10530-018-1684-5)
- 388 Jongejans E, de Vere N, de Kroon H (2008) Demographic vulnerability of the clonal  
389 and endangered meadow thistle. Plant Ecol 198:225–240 .  
390 <https://doi.org/10.1007/s11258-008-9397-y>
- 391 Juneau KJ, Tarasoff CS (2013) The Seasonality of Survival and Subsequent Growth of

392 Common Reed (*Phragmites australis*) Rhizome Fragments. Invasive plant sci  
393 manag 6:79–86 . <https://doi.org/10.1614/IPSM-D-12-00051.1>

394 Juneau KJ, Tarasoff CS (2017) The Seasonality of Survival and Subsequent Growth of  
395 Common Reed (*Phragmites australis*) Rhizome Fragments. Invasive Plant  
396 Science and Management 6:79–86 . <https://doi.org/10.1614/IPSM-D-12-00051.1>

397 Keser L, Dawson W, Song Y-B, Yu F-H, Fischer M, Dong M, van Kleunen M (2014)  
398 Invasive clonal plant species have a greater root-foraging plasticity than non-  
399 invasive ones. Oecologia 174:1055–1064 . [https://doi.org/10.1007/s00442-013-](https://doi.org/10.1007/s00442-013-2829-y)  
400 2829-y

401 Kissmann KG, Groth D (1991) Plantas invasoras e nocivas. São Paulo: BASF 2:

402 Konlechner TM (2008) The management challenge posed by marine dispersal of  
403 terrestrial plants in coastal dune systems. New Zealand Geographer 64:154–156  
404 . <https://doi.org/10.1111/j.1745-7939.2008.00139.x>

405 Konlechner TM, Orlovich DA, Hilton MJ (2016) Restrictions in the sprouting ability of  
406 an invasive coastal plant, *Ammophila arenaria*, from fragmented rhizomes. Plant  
407 Ecol 217:521–532 . <https://doi.org/10.1007/s11258-016-0597-6>

408 Krajšek SS, Bahčič E, Čoko U, Koce J (2020) Disposal methods for selected invasive  
409 plant species used as ornamental garden plants. MBI 11:293–305 .  
410 <https://doi.org/10.3391/mbi.2020.11.2.08>

411 Lawson JR, Fryirs KA, Lenz T, Leishman MR (2015) Heterogeneous flows foster  
412 heterogeneous assemblages: relationships between functional diversity and  
413 hydrological heterogeneity in riparian plant communities. Freshwater Biology

414 60:2208–2225 . <https://doi.org/10.1111/fwb.12649>

415 Liu J, Dong M, Miao S, Li Z, Song M, Wang R (2006) Invasive alien plants in China:  
416 role of clonality and geographical origin. *Biological Invasions* 8:1461–1470 .  
417 <https://doi.org/10.1007/s10530-005-5838-x>

418 Maciel LA, Siles MFR, Bitencourt MD (2011) Alterações na vegetação herbácea de  
419 floresta ombrófila densa decorrentes do uso em uma trilha turística na Serra do  
420 Mar em São Paulo, Brasil. *Acta Botanica Brasilica* 25:628–632

421 Manish M (2013) Current status of endangered medicinal plant *Hedychium coronarium*  
422 and causes of population decline in the natural forests of Anuppur and Dindori  
423 districts of Madhya Pradesh, India. *Int Res J Biol Sci* 2:1–6

424 Mann JJ, Barney Jacob N, Kyser Guy B, Di Tomaso Joseph M (2013) *Miscanthus* ×  
425 *giganteus* and *Arundo donax* shoot and rhizome tolerance of extreme moisture  
426 stress. *GCB Bioenergy* 5:693–700 . <https://doi.org/10.1111/gcbb.12039>

427 Maurer DA, Zedler JB (2002) Differential invasion of a wetland grass explained by  
428 tests of nutrients and light availability on establishment and clonal growth.  
429 *Oecologia* 131:279–288 . <https://doi.org/10.1007/s00442-002-0886-8>

430 Michelan TS, Thomaz SM, Carvalho P, Rodrigues RB, Silveira MJ (2010)  
431 Regeneration and colonization of an invasive macrophyte grass in response to  
432 desiccation. *Nat & Conserv* 8:133–139

433 Oborny B, Kun Á (2002) Fragmentation of clones: how does it influence dispersal and  
434 competitive ability? In: Stuefer JF, Erschbamer B, Huber H, Suzuki J-I (eds)  
435 *Ecology and Evolutionary Biology of Clonal Plants: Proceedings of Clone-2000.*

436 An International Workshop held in Obergurgl, Austria, 20–25 August 2000.  
437 Springer Netherlands, Dordrecht, pp 97–124

438 Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC (2018) nlme: linear and nonlinear  
439 mixed effects models. R package version 3.1-137. Vienna, Austria: R  
440 Foundation

441 Portela R, Dong B-C, Yu F-H, Barreiro R, Roiloa SR, Silva Matos DM (2020) Trans-  
442 generational effects in the clonal invader *Alternanthera philoxeroides*. J Plant  
443 Ecol 13:122–129 . <https://doi.org/10.1093/jpe/rtz043>

444 Pumisitapon P, Visser RGF, de Klerk G-J (2012) Moderate abiotic stresses increase  
445 rhizome growth and outgrowth of axillary buds in *Alstroemeria* cultured in vitro.  
446 Plant Cell Tiss Organ Cult 110:395–400 . [https://doi.org/10.1007/s11240-012-](https://doi.org/10.1007/s11240-012-0160-7)  
447 0160-7

448 R Core Team (2020) R: a language and environment for statistical computing, version  
449 4.0.1. Vienna, Austria: R Foundation for Statistical Computing; 2013

450 Ray A, Jena S, Dash B, Kar B, Halder T, Chatterjee T, Ghosh B, Panda PC, Nayak S,  
451 Mahapatra N (2018) Chemical diversity, antioxidant and antimicrobial activities  
452 of the essential oils from Indian populations of *Hedychium coronarium* Koen.  
453 Industrial crops and products 112:353–362

454 Rooney N, Kalff J (2000) Inter-annual variation in submerged macrophyte community  
455 biomass and distribution: the influence of temperature and lake morphometry.  
456 Aquatic Botany 68:321–335 . [https://doi.org/10.1016/S0304-3770\(00\)00126-1](https://doi.org/10.1016/S0304-3770(00)00126-1)

457 Ruiz JM, Romero J (2001) Effects of in situ experimental shading on the Mediterranean

458 seagrass *Posidonia oceanica*. Marine Ecology Progress Series 215:107–120

459 Rusterholz H-P, Wirz D, Baur B (2012) Garden waste deposits as a source for non-  
460 native plants in mixed deciduous forests. Applied Vegetation Science 15:329–  
461 337 . <https://doi.org/10.1111/j.1654-109X.2011.01175.x>

462 Serra do Vale Duarte G, Pott VJ, Lemke AP, Rondon Suárez Y (2015) Efeito das  
463 características ambientais sobre a riqueza e composição de macrófitas aquáticas  
464 em córregos urbanos. Ciência e Natura 37:74–94

465 Simberloff D, Rejmánek M (2010) Encyclopedia of Biological Invasions. University of  
466 California Press

467 Valéry L, Fritz H, Lefeuvre J-C, Simberloff D (2008) In search of a real definition of  
468 the biological invasion phenomenon itself. Biological Invasions 10:1345–1351

469 Van Kleunen M, Weber E, Fischer M (2009) A meta-analysis of trait differences  
470 between invasive and non-invasive plant species. Ecology Letters 13:235–245 .  
471 <https://doi.org/10.1111/j.1461-0248.2009.01418.x>

472 Voesenek LACJ, van der Putten WH, Maun MA, Blom CWPM (1998) The role of  
473 ethylene and darkness in accelerated shoot elongation of *Ammophila*  
474 *breviligulata* upon sand burial. Oecologia 115:359–365 .  
475 <https://doi.org/10.1007/s004420050528>

476 Westwood CG, Teeuw RM, Wade PM, Holmes NTH, Guyard P (2006) Influences of  
477 environmental conditions on macrophyte communities in drought-affected  
478 headwater streams. River Res Appl 22:703–726

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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.

511

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

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

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	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

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### 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

559 relationships.

560

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

567

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

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