Invasion strategies of the white ginger lily *Hedychium coronarium* J. König (Zingiberaceae) under different competitive and environmental conditions

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Abstract

The success of an invasive plant depends on its competitive advantage in the new community. This advantage can be attributed to high phenotypic plasticity, which either allows the plant to develop under a broad variety of environmental conditions, or grants it with a higher fitness compared to native species. In the present study, we assessed the development of the invasive white ginger lily, *Hedychium coronarium,* and plant community through removal experiments, under different conditions of soil moisture in riparian areas. We observed that *H. coronarium* exhibited different invasion strategies according to soil moisture, plant community species life form, and intensity of intra- and interspecific competition. In areas with high soil moisture and high competitive pressure, *H. coronarium* invests in height growth rather than new ramets. In areas with drier soils and lower competitive pressure, *H. coronarium* expands its population through new ramets. Our results suggest *H. coronarium* has a negative influence on the recruitment of plants from the plant community, with consequences to the biodiversity of invaded areas.

Highlights

- A trade- off for invasive *Hedychium coronarium* new ramets is proposed.
- As higher competition, lower number and higher heights of new ramets.
- As lower soil moisture, higher number and lower heights of new ramets.

Keywords: plant invasion; competition; phenotypic plasticity; riparian areas; white ginger lily; trade- off.

Introduction

Biological invasions can represent a threat to the ecological balance and conservation of native plant communities (Simberloff, 2005) because they can suppress native species (Pyšek et al., 2012). A species is considered invasive when it acquires a competitive advantage because natural obstacles to its proliferation disappear and this allows fast dispersal and colonization of new areas, where it can become dominant (Valery et al., 2008). This competitive advantage is frequently related to high phenotypic plasticity, which allows the invasive species to grow and reproduce under a broad variety of environmental conditions (Rejmánek et al., 2005). However, morphological or physiological plasticity only contributes to invasion success if it allows the invasive plant to develop under a broad range of environmental conditions or it provides a competitive advantage in favorable environments (Richards et al., 2006). Hence, to understand the success of invasive species, a knowledge of the role of morphological and phenotypic adaptations in the face of biotic (Burns and Winns, 2006) and abiotic interactions (Williams et al., 2008) is necessary.

Height is an essential component of ecological strategy for plants as individuals compete for light, favoring taller plants over shorter plants (Westoby et al., 2002). This competitive advantage depends on relative rather than absolute height (Falster and Westoby, 2003). Exotic species that grew slightly taller than those already present would have an advantage in light capture, presenting potential for invasion (Kollmann and Banuelos, 2004). Many herbaceous plants enhance elongation of stems, when the stand density or the leaf area index is high, as a shade avoidance strategy (Nishimura et al., 2010). However, any resources allocated to one function are unavailable for other functions, requiring investment trade-offs (Klinkhamer et al., 1990). Height investment incurs disadvantages in the transport of water (Midgley, 2003), increased risk of breakage (Williams and Douglas, 1995), and decreases of leaf investment (Givnish, 1982) and reproduction (Kawecki, 1993). Thus, the relationship between the accumulation of biomass and its allocation to structures and functions is the core of plant life-history strategies (Moles et al., 2009).

Riparian ecosystems have been identified as environments with a high risk of plant invasion (Richardson et al., 2007), partly because they are influenced by substantial human disturbance, from local to global scales. Such disturbance can result from dams and flow regulation (Shafroth et al., 2002), land use (Patten, 1998), deforestation (Iwata et al. 2003), trampling and extensive livestock farming (Meeson et al., 2002), water use for consumption (An et al., 2003), and leisure activities (Washitani, 2001), all of which can alter the physical and chemical characteristics of water. These disturbances, together with cyclic floods (Naiman and Décamps, 1997), which enhance rapid propagule dispersal through lotic environments (Planty-Tabacchi et al., 1996), can lead to extensive changes in wetland extension and its floristic composition, making these riparian environments highly susceptible to biological invasion (Richardson et al., 2007). Invasive species not only respond to environmental conditions, but can also modify the invaded sites (Wardle et al., 1998). Thus, knowledge of the intrinsic functional characteristics of an exotic invasive plant species provides a better understanding of its impact on the ecosystem, via changes in shading, soil temperature, and nutrient cycling (Westoby and Wright, 2006).

Hedychium coronarium is a perennial, rhizomatous, herbaceous macrophyte that occurs in wet environments and can reach up to two meters in height (Macedo, 1997). The species is self-incompatible, presenting low rates of fruit set and the flowering follows an annual pattern, showing asynchrony in the population level (Souza and Correia, 2007). It is native to tropical Asia and is commonly used as an ornamental plant due to its white and fragrant flowers (Kissmann & Groth, 1991). Because of its fast growth and rapid dispersal, *H. coronarium* is considered a weed in many tropical and subtropical areas worldwide (Kissmann, 1997; Villaseñor and Espinosa-Garcia, 2004; Vargas, 2009; Foxcroft and Richardson, 2003;

Govaerts, 2015; PIER, 2015). It invades wetlands, marshes, lake banks, streams, and drainage channels where it can form dense populations (Lorenzi, 1991) and replace native vegetation (Lorenzi and Souza, 2001). *Hedychium coronarium* is difficult to control because of its extremely efficient vegetative reproduction through rhizome fragments (Kissmann and Groth, 1991).

Testing the response of native plants to invasion experimentally, with a focus on the first stages of its development, can provide information on both the degree of influence of the invasive plant on the community, and how the ecosystem responds to a reduction or removal of the invasion (Cushman and Gaffney, 2010). Understanding the mechanisms leading to an invasive species success is, therefore, key to comprehend and mitigate their impacts (Byers et al., 2002). In this study, we used a removal experiment to assess development in height and numbers of new individuals of the invasive white ginger lily *Hedychium coronarium* J. König (Zingiberaceae) and other plants within the plant community in riparian areas under different competitive and environmental conditions. Our hypothesis was there would exist a trade- off between investments in vegetative (plant height) and clonal reproductive growth (new ramets) by *H. coronarium* in response to (1) different soil moisture levels and (2) differing levels of plant competition produced by removing different groups of species. We expected greater invasive success in soils with higher moisture levels, expressed by the number of *H. coronarium* recruits. Regarding removal treatments, with higher competition (i.e., with fewer plants removed), we expected taller *H. coronarium* recruits and lower recruitment.

Material and methods

Vegetation removal experiment

This study was carried out from September to December 2013, in four natural riparian (first or second orders) floodplains near São Carlos city (21°30’-22°30’S; 47°30’-48°30’W), São Paulo state, south-eastern Brazil. The sites were 10 km apart, in different river systems, inserted in riparian vegetation and fragments of semideciduous mesophytic forest (Brazilian Atlantic Forest vegetation), with some stretches of *Cerrado* (Soares et al., 2003). The soils presents dark coloration due to high organic matter content. The regional climate is classified as a transition between Cwa.i and Aw.i (Tolentino, 1967), with a dry winter from April to September and a warm, humid summer, from October to March, presenting seasonal pattern of flooding in the summer. Wetlands species such as *Typha domingensis* (Pers.) Steud. (Thyphaceae), *Salvinia auriculata* Aubl. (Salviniaceae) and Cerrado/Brazilian Atlantic Forest species as *Guarea guidonia* (L.) Sleumer (Meliaceae), *Sapium glandulosum* (L.) Morong (Euphorbiaceae) were highly represented. The exotic species *Monstera deliciosa* Liebm. (Araceae), *Tithonia diversifolia* (Hemsl.) A. Gray (Asteraceae), *Cenchrus purpureus* (Schumach.) Morrone (Poaceae), *Urochloa decumbens* (Stapf) R.D.Webster (Poaceae), *Impatiens walleriana* Hook. f. (Balsaminaceae), and *Urochloa subquadripara* (Trin.) R.D.Webster (Poaceae) were found in low frequency (Table 1).

The removal experiment was established with a split- plot design, with 4 independent blocks, 2 sub- blocks each block (moisture treatment), and 3 plots in each sub- block (removal treatment). In each of the four sites (independent blocks), with a dominant 50-80% *H. coronarium* cover and without any other dominant species, we delimited one transect with two experimental sub-blocks. One sub-block was close to the margin of the main water body (denoted Wet moisture treatment) at the riparian zone, which is very susceptible to flooding.

The other was 20 m away from the main water body (denoted Dry moisture treatment) at the semi-deciduous vegetation, not susceptible to flooding. In each sub- block, we delimited three 1.5 x 1.5 m plots, at least 2 m from each other, and allocated a vegetation management treatment (removal treatment) randomly to each one. The three vegetation management treatments were:

(1) Untreated control (denoted Ctr) where no plants were removed, including *H. coronarium*.

(2) *Hedychium coronarium* removal; all *H. coronarium* ramets were removed at the start of the experiment (September 2013), but all other plant species were left intact. This treatment assessed the natural regeneration capacity of the plant community in the available niches left after *H. coronarium* removal (denoted Nat).

(3) Complete removal; all plants were removed at the start of the experiment including *H. coronarium*. This treatment assessed the regeneration capacity of both *H. coronarium* and plant community species (denoted All).

We considered the plant community to be all plant species other than *H. coronarium* found in the area. At the beginning of the experiment, we marked all plants in the plots with numbered plates. In the removal experiment, we cut the plants at ground level, taking care to minimize soil disturbance, and then removed all above ground material from the plots (Blane and Tricia, 2011). At fortnightly intervals, we monitored the survival, recruitment, and height of all marked individuals, marking new recruits. We considered each *H. coronarium* ramet and each emerged community plant as an individual. We also classified all individuals according to life- form: herbaceous or arboreal/shrubby. We measured the soil moisture content using the gravimetric method (50 g of humid sediment dried at 60 °C for 48 h). At the end of the experiment (January 2014), we identified all plants to the lowest possible taxonomic level.

Although we assessed height of all plants in the plots, the data used in the analyses reported are those of the individuals recruited during the study, i.e., under direct influence of the treatments during the experiment.

Statistical analysis

To test for significant differences between treatments, we used a split-plot analysis of variance (function 'aov' within the R statistical environment). We used the average height and number of the recruits of each plot on the last sampling day of the experiment as the response variables; removal treatments (Ctr, Nat, All), moisture content (dry versus wet treatments), and their interaction as fixed factors with a nested error structure (Blocks/Moisture/Treatment). To verify differences between soil moisture treatments, we used a generalized linear mixed model (GLMM with function 'lme' within the R statistical environment), testing for differences between sub-blocks moisture data obtained fortnightly (8 samplings). To test which treatments in each sub-blocks showed differences between the height and number of *H. coronarium* and plant community recruits, we used an Analysis of Variance test (ANOVA) with a post hoc Tukey test. We used a linear regression between the recruit average heights as a function of the number of recruits per plot to verify investment trade-offs for both *H. coronarium* and plants community. To verify the treatment influences at growth in height of *H. coronarium* and plant community recruits, we analyzed the height data obtained fortnightly (7 samplings), using a generalized linear mixed model (GLMM with function 'lme' within the R statistical environment) testing for differences between (1) sub-blocks, (2) *H. coronarium* and plant community, and (3) removal treatments. All analyses were run in either Past 3.10 or the lme4 and nlme packages within the R statistical environment (R Development Core Team, 2013).

Results

The Wet moisture treatment had a greater average soil moisture content (Figure 1) than the Dry moisture treatment over the sample period (GLMM: df = 14; t- value = 13.645; $p<0.001$). Over the four months, we monitored 2,932 individual plants of which 2,497 plants were recruits, i.e., they regenerated or sprouted. Of the recruits, 2,069 were *H. coronarium* ramets and 428 were plant community recruits (Table 1). In the wet plots, herbaceous species were dominant, whereas in Dry plots species of the shrub and tree strata were dominant (Figure 2).

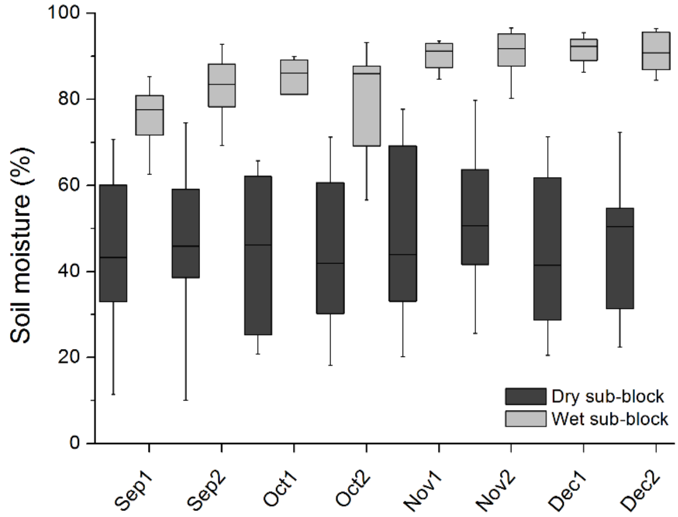

FIGURE 1. Differences in soil moisture content in the two riverine moisture treatments (sub blocks dry and wet moisture treatments) during the removal experiment of *Hedychium coronarium* and plant community species. Each boxplot presents the moisture percent of the four sites (block) according the moisture treatment.

Table 1. Species and life- forms recorded within the species-removal experiment under two moisture regimes (dry and wet moisture treatments) in the four months between September to December 2013. Key to: H = herbaceous, S = shrubs, T= trees and E = exotic.

	Dry sub- blocks			Wet sub- blocks	
Family	**Species**	**Life-form**	**Family**	**Species Species**	**Life-form**
Araceae	*Philodendron* sp.	H	Asteraceae	*Ageratum conyzoides* L.	H
	Monstera deliciosa Liebm.[E]	S			
Asteraceae	*Chromolaena* sp.	S		*Bacharis* sp.	S
	Eupatorium sp.	S		*Campuloclinium macrocephalum* (Less.) DC.	H
	Tithonia diversifolia (Hemsl.) A. Gray [E]	S		*Mikania cordifolia* (Linnaeus f.)	H
Bignoniaceae	*Handroanthus heptaphyllus* (Vell.) Mattos	T		*Chromolaena* sp.	S
Clusiaceae	*Clusia criuva* Cambess.	T	Balsaminaceae	*Impatiens walleriana* Hook. f. [E]	H
	Clusia sp.	T	Convolvulaceae	*Merremia* sp.	H
Convolvulaceae	*Merremia* sp.	H	Cyperaceae	*Cyperus* sp.	H
Dennstaedtiaceae	*Pteridium aquilinum* (L.) Kuhn in Kersten	H		*Cyperus surinamensis* Rottb.	H
Euphorbiaceae	*Sapium glandulatum* (Vell.) Pax	T		*Eleocharis acutangula* (Roxb.) Schult	H
Fabaceae	*Crotalaria incana* L.	S		*Eleocharis interstincta* (Vahl) Roem. & Schult.	H
Melastomataceae	*Miconia chamissois* Naud.	T		*Eleocharis sellowiana* Kunth.	H
	Tibouchina granulosa (Desr.) Cogn.	S	Dennstaedtiaceae	*Pteridium aquilinum* (L.) Kuhn in Kersten	H
	Tibouchina sp.1	S	Euphorbiaceae	*Sapium gladulatum* (Vell.) Pax	T
	Tibouchina sp.2	S	Fabaceae	*Crotalaria incana* L.	S
Meliaceae	*Guarea guidonia*(L.) Sleumer	T	Lamiaceae	*Hyptis atrorubens* J.A.Schmidt	H
Phyllanthaceae	*Phyllanthus tenellus* Roxb.	H	Onagraceae	*Ludwigia leptocarpa* (Nutt.) H. Hara	H
Poaceae	*Panicum* sp.	H	Poaceae	*Urochloa subquadripara* (Trin.) R.D.Webster [E]	H
	Cenchrus purpureus (Schumach.) Morrone [E]	H	Pontederiaceae	*Eichhornia azurea* (Swartz) Kunth	H
	Urochloa decumbens (Stapf) R.D.Webster [E]	H	Primulaceae	*Rapanea gardneriana* (A. DC.) Mez.	T
Rubiaceae	*Spermacoce* sp.	S	Salviniaceae	*Salvinia auriculata* Aubl.	H
	Indet. 4	H	Typhaceae	*Typha domingensis* (Pers.) Steud.	H
			Xyridaceae	*Xyris* sp.	H
				Indet 1	T
				Indet 2	H
				Indet 3	T
				Indet 4	H

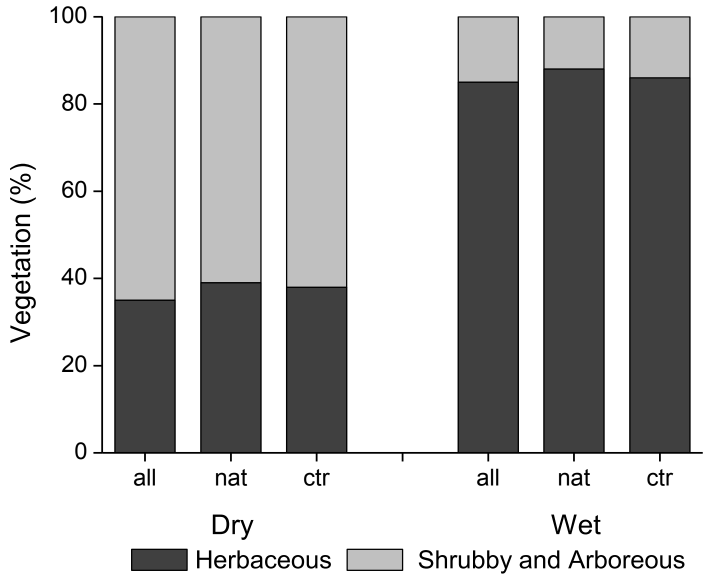

FIGURE 2. Proportion of recruits present as Herbaceous and Shrubby/arboreal life- forms colonizing the riverine plant communities in each moisture treatment, following removal treatments. Treatment Key to: all = all species removed; nat = only *Hedychium coronarium* removed; ctr = control – no removal.

There was no significant effect of moisture treatment, removal treatment, or their interaction on plant community species, but a significant effect of removal treatment and its interaction with moisture (Table 2). Average height was lower and the number of *H. coronarium* new ramets was greater in the Dry moisture treatment compared to the Wet moisture treatment (Table 3 and Figure 3). In the Dry moisture treatment, the average height of *H. coronarium* recruits showed the following ranking for the removal treatments: All < Nat < Ctr. As for plant community recruits, the average height showed the following ranking: All > Nat > Ctr. In the Wet moisture treatment, the average height of *H. coronarium* recruits showed the following ranking: Nat > All = Ctr. As for plant community recruits, the average height showed the following ranking: All > Nat = Ctr. The number of recruits per plot of *H. coronarium* in the Dry moisture treatment showed the following ranking for the removal treatments: All = Nat, Nat = Ctr and All > Ctr. As for plant community recruits: All = Nat < Ctr. In the Wet moisture treatment, the number of recruits for both *H. coronarium* and plant community recruits showed the following ranking: All = Ctr = Nat. For *H. coronarium,* as higher number of recruits, lower the recruits average height (Figure 4). This pattern was not confirmed for the plant community recruits.

Table 2. Results of a split-plot analysis of variance (ANOVA) testing for significant effects of moisture treatment (Moisture), removal treatment (Treatment) and their interaction on the average height and number of recruits per plot of both *Hedychium coronarium* and plant community species at the end of the experiment. Asterisks represent significance levels.

Parameter	Error stratum	Factor	df	*H. coronarium*				Plant community species			
				Sums of Squares	Mean Square	F	P	Sums of Squares	Mean Square	F	P
Height	Error: Block	Residuals	3	161.9	53.98	-	-	286.8	95.6	-	-
	Error: Block x Moisture	Moisture	1	1386	1386	115.6	0,001*	167.5	167.5	2.5	0.223
		Residuals	3	36	12	-	-	205.8	68.58	-	-
	Error: Within	Treatment	2	413.2	206.6	8.0	0.006*	495.4	247.7	2.7	0.177
		Moisture x Treatment	2	314.0	157.0	6.1	0.023*	230.1	115.0	1.2	0.311
		Residuals	12	308.2	25.7	-	-	1107.4	92.3	-	-
Number of recruits	Error: Block	Residuals	3	11396	3799	-	-	494.3	164.8	-	-
	Error: Block x Moisture	Moisture	1	28291	28291	64.18	0.004*	468.02	468.02	6.05	0.091
		Residuals	3	1322	441	-	-	232.2	77.4	-	-
	Error: Within	Treatment	2	5842	2921	6.69	0.011*	320.3	160.17	2.96	0.090
		Moisture x Treatment	2	9674	4882	11.17	0.002*	140.3	70.17	1.29	0.309
		Residuals	12	5242	437	-	-	650	54.17	-	-

Table 3. Results of an analysis of variance (ANOVA) testing for the different removal treatments according soil moisture on the average height and number of recruits per plot of *Hedychium coronarium* and plant community species at the end of the experiment. Asterisks represent significance levels.

Parameter	Sub-block	*H. coronarium*					plant community species				
		df	Sums of Squares	Mean square	F	P	df	Sums of Squares	Mean square	F	P
Height	Dry	2	43706.4	21853.2	44.6	***	2	2.16081	1.08041	13.85	<0.0001*
	Wet	2	23863.1	11931.5	17.7	***	2	0.5002	0.25014	3.348	0.037*
Number of recruits	Dry	2	14465.2	7232.58	7.91	0.010*	2	429.167	214.58	15.61	0.001*
	Wet	2	1140.17	570.08	0.5	0.607	2	31.5	15.75	0.11	0.894

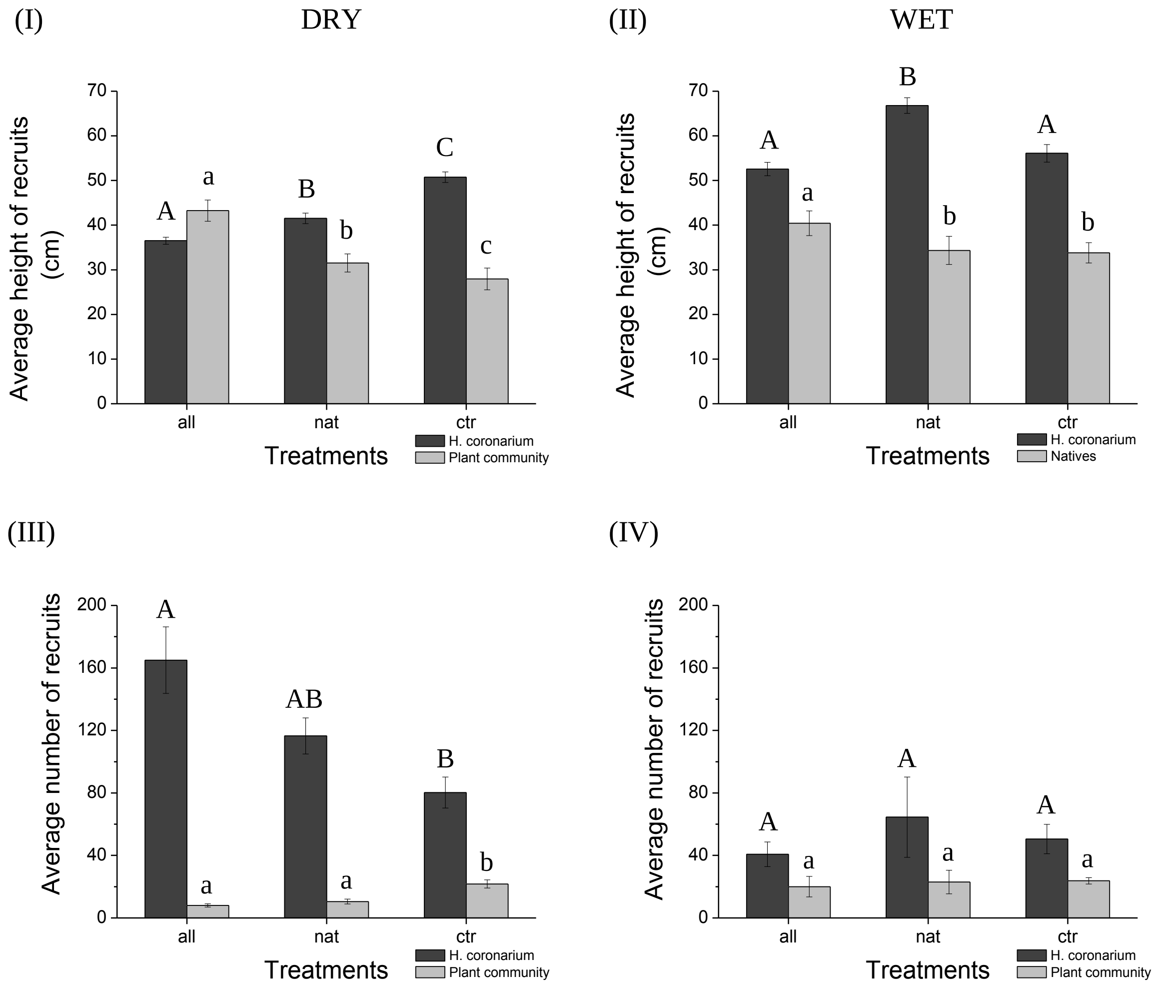

FIGURE 3. Average height (I and II) and average number of recruits per plot (III and IV) of *Hedychium coronarium* and plant community species in sub-blocks with dry (I and III) and wet (II and IV) moisture treatments. Treatment Key to: all = all species removed; nat = only *Hedychium coronarium* removed; ctr = control – no removal. Error bars indicate Standard Error. Different letters indicate significant differences (ANOVA in Table 3, with a *post hoc* Tukey test; p<0.05) between treatments.

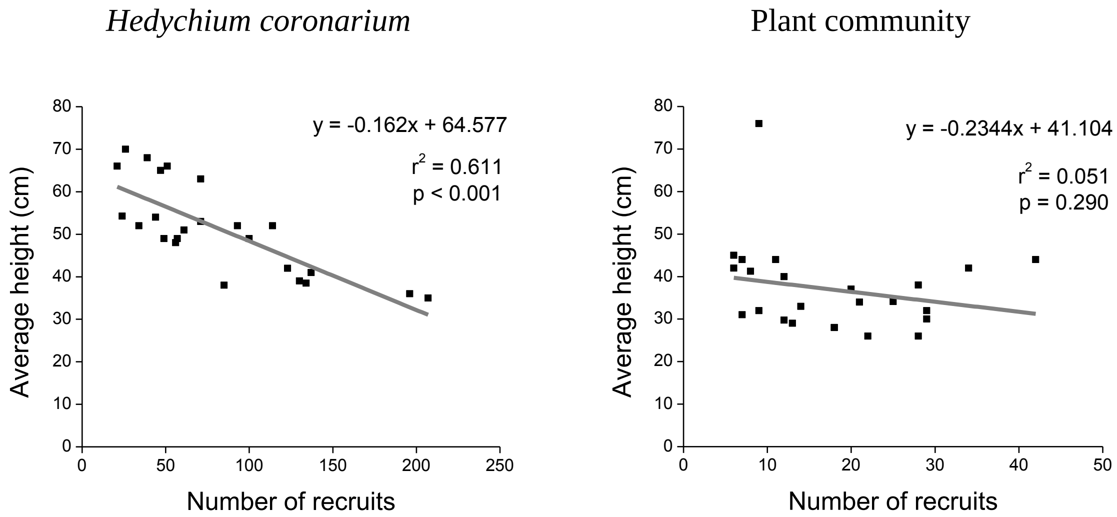

Figure 4. Scatter plot and linear regression between average height in function of number of recruits for *Hedychium coronarium* and plant community per plot.

The pattern of recruit´s growth in height throughout time (Table 4, Figure 5) showed no differences between the moisture treatment, removal treatments, or their interaction either for *H. coronarium* or for plant community recruits. There were significant differences, though, between *H. coronarium* and plant community species in height according to each moisture treatment.

Table 4. Results of the Generalized Linear Mixed Models adjusted to differences between Sub-blocks, invasive and plant community species and removal treatments. We utilized the height data of *Hedychium coronarium* and plant community species that regenerated during the experiment (from September to December 2013). Significance levels are represented by asterisks.

Scale	Variable	Value	Std.Error	DF	t-value	p-value
Between sub-blocks moistures (Dry and Wet)	Intercept	23.6137	1.9246	82	12.2692	-
	H. coronarium + plant community species	2.4727	2.7218	82	0.9084	0.3663
	Intercept	27.3832	3.0326	40	9.0297	
	Just *H. coronarium*	2.9738	4.2887	40	0.6934	0.4921
	Intercept	19.8442	2.0900	40	9.4944	
	Just plant community species	1.9715	2.9558	40	0.7000	0.5086
Same moisture but different plants (*H. coronarium* and plant community species)	Intercept	27.3832	2.4378	40	11.2326	
	Dry sub-block	-7.5390	3.4476	40	-2.1867	0.0347 *
	Intercept	30.3570	2.7608	40	10.9958	
	Wet sub-block	-8.5413	3.9043	40	-2.1876	0.0346 *
Same moisture, same plants but different removal treatments (*All* comparing with *Ctr* and *Nat*)	Intercept	23.3667	4.3435	18	5.3797	
	H. coronarium in dry sub-block and *Ctr*	8.8517	6.1426	18	1.4410	0.1667
	H. coronarium in dry sub-block and *All*	3.1977	6.1426	18	0.5206	0.6090
	Intercept	25.3207	3.9820	18	6.3587	
	Plant community species in dry sub-block and *Ctr*	-9.4379	5.6315	18	-1.6759	0.1110
	Plant community species in dry sub-block and *All*	-6.9915	5.6315	18 -	1.2415	0.2304
	Intercept	27.9049	6.2699	18	4.4506	
	H. coronarium in wet sub-block and *Ctr*	1.7827	8.8670	18	0.2010	0.8429
	H. coronarium in wet sub-block and *All*	5.5739	8.8670	18	0.6286	0.5375
	Intercept	24.8107	3.1370	18	7.9091	
	Plant community species in wet sub-block and *Ctr*	-4.8321	4.4364	18	-1.0892	0.2904

	Plant community species in wet sub-block and *All*	-4.1528	4.4364	18	-0.9361	0.3616

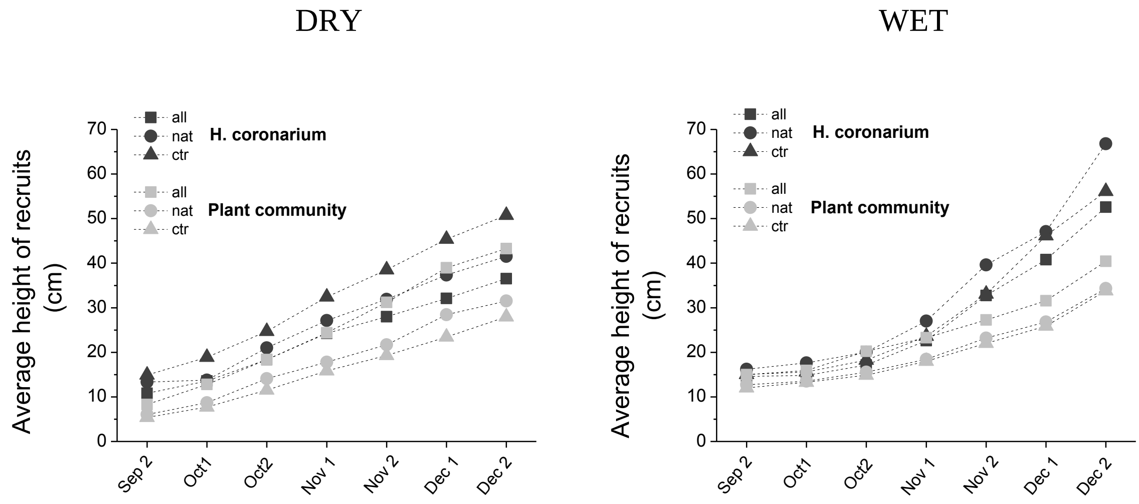

FIGURE 5. Average height of *Hedychium coronarium* and plant community recruits in different plant removal treatments under Dry and Wet moisture treatment obtained fortnightly from September to December 2013. Treatment Key to: all = all species removed; nat = only Hedychium coronarium removed; ctr = control – no removal.

Discussion

Our results demonstrated that *H. coronarium* shows different invasion strategies in response to soil moisture and presence of other species from the plant community. In dry soil, the growth strategy of both *H. coronarium* and the plant community species varied with removal treatment. In the treatment in which all plants were removed (All), *H. coronarium* showed the lowest growth in height, but a greater ramet production. Hence, this invasive plant invested in new sprouts to quickly expand its cover. Conversely, plants of the community had a lower recruitment, but a greater average height. This may be interpreted as evidence of a competitive pressure of *H. coronarium* on the plant community species, whose individuals invest in height to overgrow the dense foliage of invasive plants (Nishimura et al., 2010). In the control treatment (Ctr), the new ramets of *H. coronarium* are subjected to higher intra- and interspecific competition, with the presence of already-established individuals, both of the plant community species and *H. coronarium*. Plant community regeneration was higher in this treatment, probably due to a lower competitive pressure exerted by *H. coronarium*, with a proportionally smaller number of new ramets comparing with All, and a higher amount of adult individuals initially present in the experiment. Where all *H. coronarium* was removed (Nat), we obtained intermediate values for number of new ramets and average height for *H. coronarium* and plant community species. We believe the intermediate values due to relationship among resource availability (e.g., light and space), lack of intra-specific competition, and presence of inter-specific competition. The treatments in wet soil differed from the treatments in dry soil in growth and number of ramets. The average height of *H. coronarium* in all Wet moisture treatments was higher than in the Dry moisture treatments, but the number of new ramets was less. These results may be associated with higher competition with plant community species and with rhizome adaptability to anaerobic stress (Chen and Qualls, 2003).

Differences in life form between native and exotic species play an important role in invasion and establishment, with exotic species having higher invasion success in areas with fewer morphologically - and functionally - similar plants (Scharfy et al., 2011). Pyšek et al. (2012) observed the most successful invasive plants in Central Europe were herbaceous species in areas dominated by perennial grasses. In our experiment, the plant community associated with wet areas is composed of mainly herbaceous plants. These plants have higher metabolic rates compared to arboreal and shrub species (Grime et al., 1997), which dominated the plant community in the dry areas of our experiment. Hence, we believe herbaceous plants can compete more efficiently with *H. coronarium* than shrubby and arboreal plants. Therefore, in areas dominated by herbaceous plants, *H. coronarium* invests more in vertical growth than in the production of new ramets. According to Blaine and Tricia (2011), the impact of the invasive plant *Melilotus alba* Medik. (Fabaceae) on the recruitment of native species varied with the life forms found in the invaded community, and, therefore, this invasive plant was a superior competitor than native grasses.

Plant invasions are frequently associated with different types of disturbance, among them floods (Catford et al., 2012). Floods can favor invasions through a decrease in interspecific competition, an increase in allochthonous nutrient input (White and Jentsch 2001), and disturbances in trophic structure (McCann, 2007). However, high soil moisture can be stressful for rhizomes and stimulates metabolic processes associated with anaerobic sediments, such as fermentation (Chen et al., 2002). The use of fermentation in the metabolism of glucose is less efficient than cellular respiration and increases the need for soluble sugars. Consequently, the high soil moisture promotes decrease in the starch content of rhizomes in situations of anaerobic stress, such as long floods (Chen et al., 2005). Some unpublished data collected by us showed lower amounts of amyloplasts in the rhizomes of *H. coronarium* in wet areas than in dry areas. Hence, we believe that floodable areas are less favorable to the development of the rhizomes of *H. coronarium* than not floodable areas, whereas the establishment of other species is favored especially herbaceous species, and aquatic or semi-aquatic plants. Our results fit the trade-off hypothesis proposed by Grime (1979), in which a species is unable to be highly tolerant to stressful environmental conditions and simultaneously have high reproductive potential. However, the different strategies of growth and ramet expansion evidenced in the treatments of removal allow us to conclude that *H. coronarium* has high phenotypic plasticity, and, hence, optimal adaptation to the different situations created. This plasticity contributes to the invasion success in marsh areas and allows the invasive plant to optimize its reproductive potential under different environmental conditions (Richards et al., 2006), expressed by different soil moisture and intra- and interspecific competitive conditions (Burns and Winn, 2006). Therefore, our results point to a trade-off between investment in height and investment in new ramets of *H. coronarium* under different competition and colonization conditions. High growth rates and reproductive capacity are frequently reported in studies on invasive species (van Kleunen et al., 2010), and those characteristics provide invasive species with competitive advantages related to the use of light, nutrients, and space (Larkin et al., 2012). However, we have not found other studies that have assessed trade-off between vegetative and clonal reproductive growth in the context of plant invasions.

The recruitment and spatial distribution of native plants in marshes are driven mainly by abiotic factors (Viereck et al., 1993). Seasonal flood peaks help seed dispersal (Stella et al., 2006) and prevent native seedlings to compete with annual invasive grasses (Richardson et al., 2007). Biotic pressures, such as competition, influence recruitment in marsh communities with an established canopy (Chapin et al., 2006). However, our experiments of removal showed the establishment of new ramets of *H. coronarium* had a negative influence on the regeneration of the plant community, which corroborates Blaine and Tricia (2011), who studied invasions by *M. alba* in flooded areas of Alaska. Hence, even in recently- invaded areas, *H. coronarium* has a negative influence on the recruitment of native plants, and so affects community structure in the short term and decreases biodiversity in the long term.

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