Universidade Federal de São Carlos

Centro de Ciências Biológicas e da Saúde

Programa de Pós-Graduação em Ecologia e Recursos Naturais

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ECOLOGIA DA INVASORA *HEDYCHIUM CORONARIUM* J. KÖNIG (ZINGIBERACEAE)

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São Carlos

Dezembro de 2014

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais, do Centro de Ciências Biológicas e da Saúde, da Universidade Federal de São Carlos, sob a orientação da Profa. Dra. Dalva Maria da Silva Matos.

São Carlos

Dezembro de 2014

Ficha catalográfica elaborada pelo DePT da
Biblioteca Comunitária/UFSCar

C532ei

Chiba, Wagner Antonio de Castro.
Ecologia da invasora *Hedychium coronarium* J. König (Zingiberaceae) / Wagner Antonio Chiba de Castro. -- São Carlos : UFSCar, 2014.
87 f.

Tese (Doutorado) -- Universidade Federal de São Carlos, 2014.

1. Ecologia. 2. Macrófitas aquáticas. 3. *Hedychium coronarium*. 4. Invasão biológica. 5. Decomposição. I. Título.

CDD: 574.5 (20ª)

UNIVERSIDADE FEDERAL DE SÃO CARLOS

Centro de Ciências Biológicas e da Saúde
Programa de Pós-Graduação em Ecologia e Recursos Naturais

Folha de Aprovação

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Dedico este trabalho aos meus pais Marcia e Wagner,
meu irmão Lucas e minha noiva Alessandra, partes
indissociáveis do que sou.

"Meu caminho pelo mundo, eu mesmo traço. A Bahia já me deu,
régua e compasso. Quem sabe de mim sou eu, aquele abraço!"

Gilberto Gil

Agradecimentos

À Dalva, pela orientação, amizade quase maternal e acima de tudo, por acreditar na minha ciência;

Aos meus pais, Marcia e Wagner e meu irmão Lucas, por tudo, pelo sempre;

À minha noiva (e em breve esposa) Alessandra, companheira de todas as horas, não importando às distâncias literais, cujo amor me constitui à cada dia;

À Fundação de Amparo à Pesquisa do Estado de São Paulo, ao Conselho Nacional de Pesquisa e à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, pelas bolsas concedidas;

À Renata Almeida, pela ajuda incondicional e por ser minha força de vontade em inúmeras situações;

Ao Rob, pela orientação em terras inglesas e aprendizado que fez expandir minhas fronteiras;

Ao Irineu e à Marcela, por manterem suas portas abertas para mim e meu trabalho;

Ao Evaldo, pela solicitude e por me mostrar que nem sempre CX (XCS!);

Ao Leite, Rafael e Pavel, pelas ajudas no delineamento, montagem dos experimentos, coletas, identificações, análises, amizade de sempre;

Ao Marcos Arduin pelas análises e ensinamentos histológicos;

Ao Hamilton, Rosane, Natasha, Marcel, Mari, Mariane, Déia, Will, Rafael, Laranja, Luiz, Gabi, Rayane, Hugo, Paola, pelas indispensáveis ajudas em campo;

Resumo

Devido à importância das espécies invasoras vegetais na diminuição de diversidade biológica e depreciação da qualidade ambiental, existe grande necessidade de estudos que abordem o desenvolvimento destes organismos, seu potencial de invasão e seus impactos ecológicos nas áreas invadidas. Nós avaliamos o desenvolvimento, invasividade e aporte de detritos de *Hedychium coronarium*, invasora herbácea agressiva de ambientes úmidos, assim como a invasibilidade das comunidades das áreas ripárias invadidas. O estudo de dois anos da dinâmica populacional constatou maior mortalidade e natalidade de rametas durante o período de inverno, indicando estratégia de efeito prioritário para recrutamentos dos rametas. Os experimentos de decomposição *in situ* e *in vitro* demonstraram baixas taxas de mineralização de detritos dos rametas, comparadas com outras macrófitas de mesmo hábito e nicho. Os modelos senoidais e exponenciais demonstram a estocasticidade dos eventos de desenvolvimento e acumulo de detritos de *H. coronarim* nas áreas invadidas. Os rizomas apresentaram respostas histológicas para diferentes umidades do solo. Em solos com alta umidade, constatamos grande desenvolvimento de aerênquimas. Já em baixa umidade, o rizoma apresentou grande acúmulo de grânulos de amido. Os experimentos de remoção demonstraram que a invasora alterna o investimento preferencial entre os crescimentos vegetativo e o reprodutivo segundo a umidade do solo e hábitos das competidoras. Constatamos também a utilização dos seus rizomas como recurso alimentar de capivaras durante o período de inverno.

Palavras-chave: Lírio- do- brejo; dinâmica populacional; biomassa; decomposição; adaptação fenotípica; competição.

Abstract

Because the importance of invasive plant species in biological diversity reduction and environmental quality depreciation, there is great studies need addressing these organisms development, invasive potential and changes in nutrient cycling at invaded areas. We evaluate the development, invasiveness and debris input of *Hedychium coronarium*, aggressive herbaceous weed of wetlands, as well as the invasiveness of riparian communities. The two-year population dynamics study found increased ramets mortality and births during the winter season, indicating primary effect strategy for ramets recruitment. The *in situ* and *in vitro* decomposition experiments demonstrated low mineralization rates comparing with others same habit and niche of macrophytes. Sinusoid and exponential models demonstrates stochasticity of development and debris accumulation of *H. coronarim* in invaded areas. Rhizomes showed histological responses to different soil moistures. In high moisture soils, we found great aerenchyma development. Under low moisture, rhizomes showed greater starch granules accumulation. Removal experiments presented alternations in the preferential vegetative or reproductive investments according to soil moisture and habits of competitors. We also noted the use of rhizomes as food resource by capybaras during the winter season.

Keywords: butterfly ginger; population dynamics; biomass; decomposition; phenotypic adaptation; competition.

Sumário

I - Introdução Geral

Invasão biológica é um processo de degradação dos ecossistemas causado pela proliferação descontrolada de espécies exóticas ao ambiente, sendo hoje considerada entre as principais de perda da diversidade biológica (Simberloff & Rejmánek 2011). Uma espécie é considerada invasora quando adquire vantagem competitiva perante a comunidade invadida concomitante ao desaparecimento de obstáculos naturais à sua proliferação, permitindo rápida expansão e a conquista de novas áreas, nas quais se torna a população dominante (Valéry et al., 2008). Esta vantagem competitiva adquirida é traduzida na invasividade da espécie, ou seja, sua capacidade de se reproduzir e dispersar a partir do local de origem e se estabelecer em um novo local (Simberloff & Rejmánek 2011). Já os obstáculos ao seu estabelecimento se caracterizam pela invasibilidade dos ambientes, ou seja, a susceptibilidade (1) das diferentes comunidades a serem invadidas por espécies não nativas e (2) das condições abióticas que propiciariam a invasão. Esta susceptibilidade considera a resistência biótica oferecida pela diversidade de espécies, bem como a resistência abiótica oferecida pela distância até a fonte de propágulos das invasoras e o grau de perturbação e condições edafo-climáticas das comunidades invadidas (Fridley 2011).

A comunidade de plantas (ou macrófitas) aquáticas compreende um grupo diversificado de organismos, desde macroalgas até angiospermas, que ocorrem em ambientes sazonalmente ou permanentemente alagados (Chambers et al., 2008). São altamente produtivas e apresentam grande importância na estruturação dos ambientes aquáticos (Wetzel, 2001). Possuem características que lhes permitem rápida dispersão, crescimento e reprodução, mesmo em condições subótimas, como sob intensa competição com outras espécies (Spencer e Bowes, 1990) ou em ambientes naturalmente diversificados abioticamente, como as áreas riparias (Richardson et al. 2007). Assim, devido à esta grande capacidade de adaptação e plasticidade, algumas macrófitas aquáticas são potencialmente invasoras (Pieterse e Murphy, 1990), podendo comprometer a biodiversidade e processos ecossistêmicos em ambientes aquáticos (Simberloff e Rejmánek, 2011).

As macrófitas aquáticas tendem a ser mais amplamente distribuídas que as plantas terrestres (Santamaría, 2002). Isto se deve principalmente ao fluxo de água (Sculthorpe, 1967). O fluxo de água é o principal vetor na dispersão de plantas aquáticas, agindo no sentido de propagação de propágulos da montante à jusante dos corpos de água (Barrat-Segretain, 1996). Os baixos níveis de diferenciação genética observada nas comunidades de plantas aquáticas indicam que esta modalidade de reprodução clonal é a principal estratégia de dispersão entre as macrófitas aquáticas (Simberloff 2009). Existem várias vantagens na expansão clonal da população em plantas aquáticas (Lambrecht-McDowell e Radosevich, 2005): (1) aumenta o sucesso na disputa pelos recursos limitantes, tais como luz e superfície do substrato (Stuefer, 1996), (2) aumenta a capacidade de superar estresse, como desfolha, (3) eleva a velocidade de estabelecimento e dominância de uma área, excluindo competitivamente outras espécies (Elberse et al., 2003). Assim, a distribuição espacial das macrófitas aquáticas se correlaciona à conectividade hidrológica de habitats ao nível de paisagem (Thomas et al., 2006) e com a modalidade de reprodução primordialmente assexuada (Simberloff 2009).

A heterogeneidade espacial nos regimes hidrodinâmicos das áreas alagáveis podem induzir diferentes formas de desenvolvimento das macrófitas aquáticas (Pollux et al., 2007). Em habitats lóticos, forças hidráulicas têm grande impacto sobre a morfologia das plantas. Estas plantas respondem ao aumento da velocidade da água através da plasticidade fenotípica, no sentido de diminuir danos mecânicos (e.g. redução do tamanho da planta e biomassa, aumento da densidade das plantas através do decréscimo do espaçamento entre os indivíduos, incremento do pecíolo e da flexibilidade das folhas, reduzindo rigidez e áreas de contato direto) (Puijalon et al. 2005). Já em ambientes lênticos, a dinâmica cíclica de inundações sazonais obriga adaptações da vegetação ripária no sentido de suportar as alternâncias num ambiente ora aquático, ora terrestre (Richardson et al. 2007). Desta forma, a plasticidade fenotípica é um dos mais importantes mecanismos de adaptação das espécies ripárias (Ren & Zhang 2009) e desempenha um papel fundamental nas invasões vegetais (Rejmánek 2011). Esta adaptação morfo ou fenotípica permite a manutenção da espécie invasora em locais diversificados, fornecendo vantagens competitivas em uma ampla variedade ambiental (Richards et al. 2006).

O crescimento excessivo de macrófitas aquáticas ocasiona um aumento da biomassa e consequente aumento nas taxas de decomposição de detritos (Bianchini Jr. et al., 2010). Segundo Wetzel (2001), detrito pode ser definido como a matéria orgânica oriunda da perda não predatória de carbono orgânico proveniente de qualquer nível trófico (incluindo egestão, excreção, secreção, etc.) ou como sendo a entrada de carbono orgânico a partir de fontes externas ao ecossistema. Estes resíduos podem ser encontrados em duas formas distintas: (i) matéria orgânica particulada (MOP) e (ii) matéria orgânica dissolvida (MOD). Em geral, para ecossistemas lacustres, uma das principais fontes de energia e carbono encontra-se na forma de detrito orgânico (Mann, 1988). As macrófitas aquáticas ocupam um papel de destaque na ciclagem de nutrientes, uma vez que estas se constituem, usualmente, na principal fonte autóctone de detritos nesta região (Pieczynska, 1993), podendo ser responsáveis por até 50% do aporte de matéria orgânica e nutrientes para o sistema (Benner et al., 1986). Dessa forma, a maioria dos detritos da zona litorânea, tanto particulados quanto dissolvidos, se constitui principalmente de compostos residuais provenientes de material vegetal. Desta forma, o aumento no aporte de detritos em áreas ripárias invadidas ocasiona alterações na ciclagem de nutrientes destes ambientes. Dentre as principais consequências destas alterações estão (1) as diminuições das concentrações de oxigênio dissolvido da água (Rose e Crumpton, 1996), (2) alteração do potencial redox (van der Putten et al., 1997), (3) aumento das taxas de colmatação (Rooth et al., 2003) e (4) alterações nos ciclos biogeoquímicos. A grande quantidade de detritos também podem influenciar (5) na diminuição da diversidade vegetal (Meyerson et al., 2000), (6) no aumento da produtividade primária (Jordan et al., 1990) e (7) em alterações nas relações tróficas (Batzer, 1998) destes ecossistemas.

Embora processos de invasão por macrófitas aquáticas sejam relativamente bem descritos em outros continentes (Cushman et al. 2010; Larkin et al. 2012; Turner et al. 2014), estudos desta ordem são escassos na região Neotropical (Michelan et al., 2010). Tendo em vista a importância das espécies invasoras na diminuição de diversidade biológica e depreciação da qualidade ambiental, existe grande necessidade de estudos que abordem o desenvolvimento destes organismos, potencial de invasão e aporte de matéria orgânica para os ecossistemas. Em específico, *Hedychium coronarium*, muito popular no Brasil como objeto de ornamentação, é considerada na categoria II da Resolução SMA (2009). Esta categoria refere- se às espécies cuja criação ou cultivo sob condições controladas, com restrições estabelecidas por normas específicas de acordo com o resultado da análise de risco, deverão ser permitidas na forma da lei. Desta forma, estudos que abordem seu potencial invasor e outros possíveis riscos ao ambiente são essenciais para o enquadramento da sua utilização ou como argumentação para seu controle.

Caracterização da espécie estudada

Hedychium coronarium: *Hedychium coronarium* J. König (Zingiberaceae) é uma macrófita perene de ambientes úmidos como sub-bosques (Instituto Hórus, 2011). Conhecida popularmente como lírio-do-brejo, mariazinha-do-brejo, gengibre-branco ou lírio-borboleta, é nativa da Ásia Tropical e extensamente utilizada com fins ornamentais (Kissmann & Groth 1991). Caracteriza-se por ser uma planta herbácea rizomatosa e perene, podendo atingir até 2 m de altura (Macedo, 1997). Possuem caule cilíndrico avermelhado na base, folhas coriáceas, lanceoladas, com distribuição alternada e lígula (Santos et al., 2005). Inflorescências são terminais, com flores brancas, trímeras, zigomorfas e bastante perfumadas (Kissmann & Groth 1991). Bem adaptada às Américas, principalmente no Brasil (Lorenzi & Souza, 2001) sendo comum em toda zona litorânea (Kissmann & Groth, 1991), principalmente em regiões de brejo (Couto & Cordeiro, 2005). Devido ao seu rápido crescimento e dispersão, é considerada invasora, invadindo agressivamente baixadas úmidas e pantanosas, margens de lagos, riachos e canais de drenagem, formando densas populações (Lorenzi, 1991) e substituindo a vegetação original (Lorenzi & Souza, 2001; Santos, 2005) desde os Estados Unidos até a Argentina (Kissmann & Groth 1991). Apresenta difícil controle devido à sua reprodução vegetativa extremamente eficiente, através de fragmentos de rizomas dispersos pela água (Stone et. al., 1992) originando novas plantas facilmente (Kissmann & Groth, 1991).

Caracterização das áreas de estudo

Os experimentos foram realizados no município de São Carlos, na represa formada pelas águas do córrego do Espraiado ao lado de uma área de cerrado dentro do Campus da Universidade Federal de São Carlos (área semi-natural), no córrego Santa Maria do Leme, localizado na área urbana de São Carlos, no Rio Monjolinho, localizado no Horto municipal de São Carlos, e na sua zona rural do município. O município está localizado na região central do estado de São Paulo, entre as coordenadas 47°30’ e 48°30’ Longitude Oeste e 21°30’e 22°30’ Latitude Sul. A área é de 1.132 km^2. A população total é de aproximadamente 240 mil habitantes, dos quais 95,1% são de assentamento urbano (IBGE, 2014). O clima é classificado como úmido subtropical (Tolentino, 1967) ou mesotérmico brando (Nimer, 1972), com verão quente e úmido, de outubro a março, e inverno seco, de abril a setembro. A drenagem tem um padrão dendrítico, refletindo a geologia regional. O Rio Monjolinho, responsável pela principal drenagem urbana, atravessa a cidade no sentido leste-oeste. Tem como afluentes o córrego do Gregório, Tijuco Preto, Santa Maria do Leme e Espraiado.

Objetivo

Avaliar o desenvolvimento, invasividade e aporte de detritos de *Hedychium coronarium* assim como a invasibilidade de áreas ripárias.

Objetivos específicos:

- Descrever o desenvolvimento *in situ* de populações invasoras de *H. coronarium*;

- Quantificar a produção e decomposição *in situ* e *in vitro* de detritos da invasora, assim como avaliar sua perenidade nas áreas invadidas;

- Quantificar a influência competitiva da invasora sobre o desenvolvimento de espécies vegetais nativas em experimentos de manipulação *in situ*;

- Determinar a estratégia de desenvolvimento e reprodução da invasora submetida à diferentes umidades do solo;

- Desenvolver modelos descritores e preditores do seu desenvolvimento.

Figuras

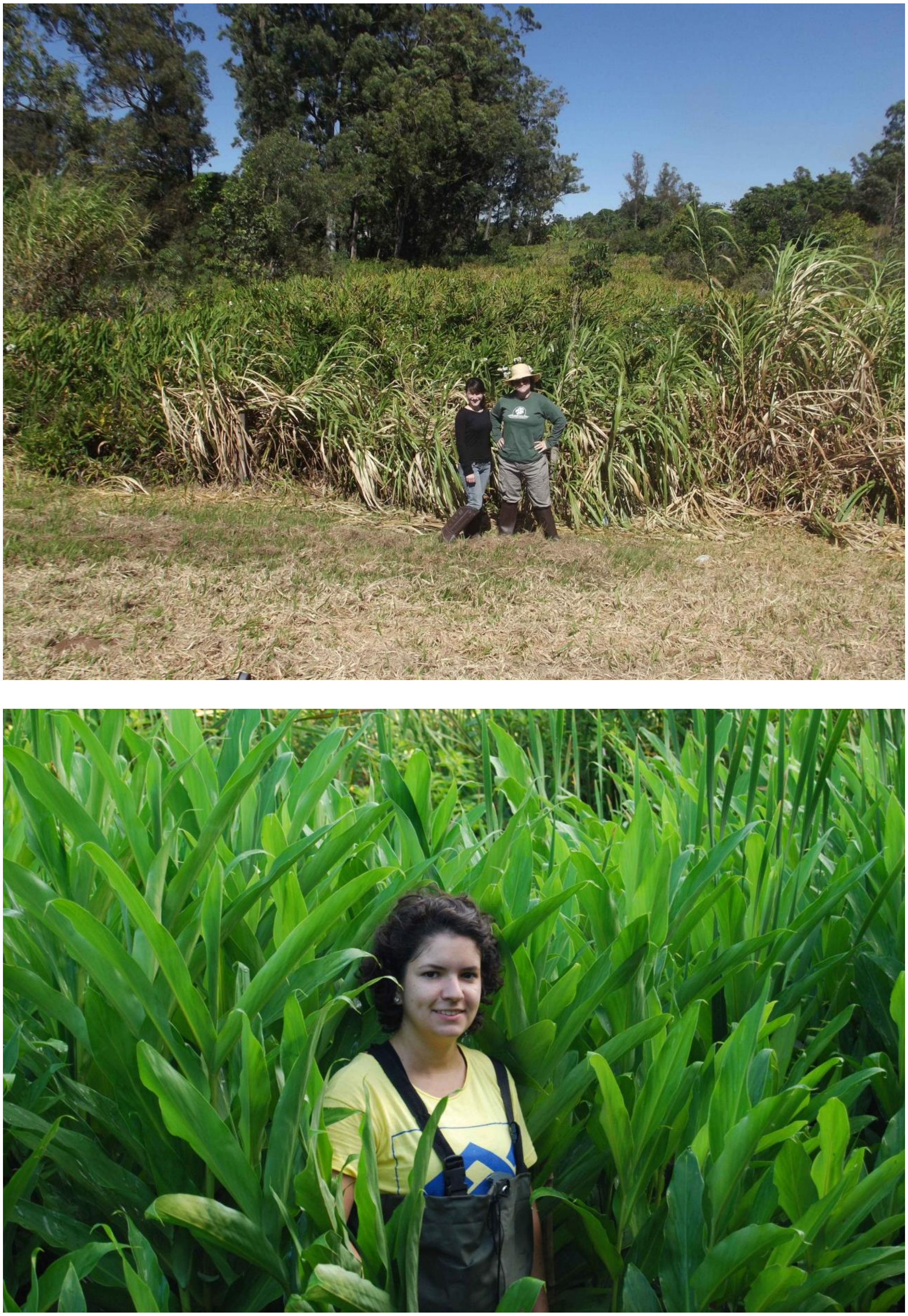

Figura A. Área invadida por *H. coronarium*.

Figura B. Detalhe da inflorescência de *H. coronarium*.

FIGURA C. Evento de frutificação de *H. coronarium*.

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II - Capítulo 1

Dinâmica da biomassa de *Hedychium coronarium* J. König invasiva (Zingiberaceae)

Biomass dynamics of the invasive *Hedychium coronarium* J. König (Zingiberaceae)

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Abstract

Some invasive wetland plants (with large stature, dense growth, abundant litter) promotes dominance outcompeting other species for resources and modifying habitat conditions with a large debris amount. These biotic and abiotic changes in invaded environments should be seen as a fetched mechanisms by which aggressive invasive plant species displace native plants. We simulate the biomass dynamics of *H. coronarium* ramets to estimate the debris accumulation in invaded sites over the time. During two years, we measure the total number, height, regeneration and mortality of *H. coronarium* ramets in three different landscapes. We quantified the ramets debris decomposition *in situ* and *in vitro* using litterbags. Through sinusoid model, we estimated the average height fluctuation. To increase the accuracy of results, we used exponential models to simulate the debris decay, mineralization and debris accumulation applied to live and dead ramets data. The highest ramets mortality occurred during the winter as for the highest ramets recruitment, indicating a priority effects strategy. *H. coronarium* presents very low mineralization rates comparing with other macrophytes of the same life forms due to refractory and allelopathic debris proprieties. Model results present a seasonal dependent debris accumulation in invaded environments. The dominant live biomass, high debris contribution and low debris mineralization observed can cause native plants suppression and changes in nutrient cycling. Seasonal dependence of invasive species should be considered to prioritize and coordinate landscape-scale management.

Keywords: debris accumulation, decomposition processes, wetlands, population dynamics, seasonality.

1. Introduction

Elevated temperatures and solar radiation in tropical ecosystems enable herbaceous to exhibit high primary production rates over the entire year (Silva et al., 2009). Thus, various species of aquatic macrophytes cover extensive riparian areas (Richardson et al. 2007), becoming invaders in both natural and artificial freshwater ecosystems (Michelan et al., 2010). Among the macrophytes with higher invasive potential in riparian zones, white ginger lily *Hedychium coronarium* J. König (Zingiberaceae) is one of the most aggressive rhizomatous herbaceous weeds (Lorenzi 1991). It invades wetlands and marshes, lake banks, streams, and drainage channels, spreading dense populations and replacing native vegetation (Lorenzi & Souza 2001). The functional traits shared by *H. coronarium* and other invasive wetland plants (large stature, dense growth, abundant litter) promote dominance through two pathways according to Larkin et al. (2011): (1) live plants outcompeting other species for resources such as space, light, and nutrients (Farrer and Goldberg 2009) and (2) debris modifying habitat conditions (e.g., reduced light, soil temperature, and space availability) (Vaccaro et al. 2009).

Plant debris is the main organic matter source in soils, being an integral part of nutrient cycling in all ecosystems (Couteaux et al., 1995). Debris decomposition rates influence nutrient availability and thereby other biotic processes (Vitousek and Howarth 1991). At the community level, decomposition rates are controlled by species or functional type composition (Quested et al. 2005). Therefore, invasive species can cause profound changes in litter decomposition and nutrient cycling via altered quality of litter inputs (Ehrenfeld et al., 2010). Kourtev et al. (2003) assigned alterations in nitrogen dynamics, soil pH and enzyme activity patterns of microbial community in invaded areas to exotic plant debris. So altered debris quality can provoke profound changes in structure and function of decomposer communities (Kolar and Lodge 2001), influencing the abundance, identity and activity rates of soil biota (Wolf and Klironomos, 2005). Consequently, nutrient cycling at ecosystem scale may be slowed down by exotic invasions (Godoy et al., 2010).

Plant debris accumulation in ecosystems mediates the relationship between soil nutrients, primary productivity and plant species diversity (Berendse 1999). Habitats with litter may provide ideal micro-sites for invasive species to establish because of greater soil water availability, higher soil fertility that enhance plant growth (Betes et al., 2006) and inhibition of native plants (Callaway and Ridenour, 2004). Invasion at elevated nutrient availability and a dominance based in high primary productivity levels involves the physical effects of development of a massive litter layer that could indeed inhibit the growth of native plants (Currie et al., 2014). For example, the invasive *Typha × glauca* produces more than ten times the litter found in native communities in invades sites of the Great Lakes, Canada. This great amounts of plant litter provides strong reduction in light availability at the soil surface, inhibition of regeneration from seed of most plants and consequent native species density decrease (Tuchman et al., 2009). Thus, changes in community level, soil conditions, or both caused by invasion processes may feedback or moderate the decomposition patterns, slowing down nutrient cycling (Godoy et al, 2010) and providing a positive feedback to the exotic plant species (Farrer and Goldberg, 2009). These environmental changes should be seen as a mechanisms by which aggressive invasive plant species displace native plant species (Larkin et al., 2011).

Given the importance of studies involving mechanisms of invasive plant species dominance and the ecosystem changes resulting (Levine et al., 2003), we aimed to simulate the interplay of *H. coronarium* ramets biomass dynamics, death biomass and decomposition processes to estimate the accumulation of *H. coronarium* debris in invaded sites by modeling approach.

2. Material and Methods

2.1. Ramet dynamics

We selected 3 invaded sites by *H. coronarium* in different landscapes (a robust spatial replication design): (1) a natural Cerrado reserve, (2) rural vegetation and (3) vegetation in an urban area. We established 20 plots of 0.25 m^2 along two transects of 30m length from the water body toward the native fragment vegetation adjacent to the invaded site in each landscape. For two years, bimonthly from March 2012 to January 2014 (12 collections), each ramet of *H. coronarium* was measured and marked with numbered tags to quantify production of new ramets, height growth, and ramet mortality. We considered each *H. coronarium* ramet as an individual.

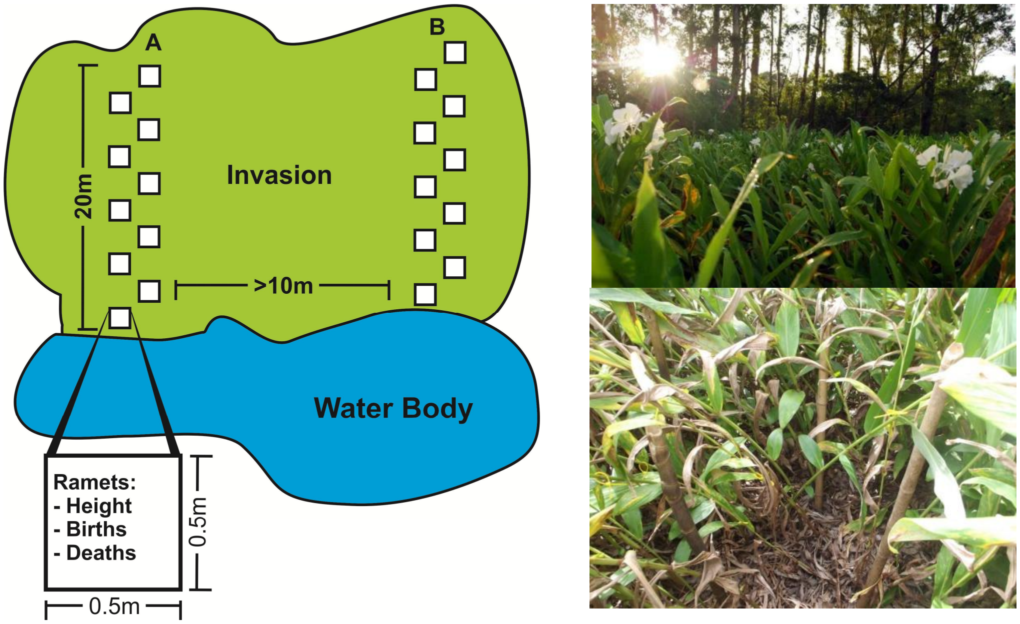

Figure A. Ramets dynamics experimental design.

2.2. Ramets debris decomposition

In July 2014, we collected 450 live ramets of *H. coronarium* randomly, 30L of water and 30kg of soil on the 3 invaded sites selected. The ramets and soil were dried at 60°C±5°C for 5 days. All dry ramets were cut in 10cm pieces approximately and mixed together regardless leaves, stem or flowers (dry biomass). The dry soils of each site was macerated and mixed together. The collected water of each site was stored and mixed together.

2.2.1. In situ experiment: We prepared 90 litterbags (20 × 20 cm; ϕ pore = 0,5 cm) with 15g of *H. coronarium* dry biomass and marked with numbered tags. In August 2014, we disposed 30 litterbags in each invaded site. On the collection days (1, 3, 5, 10, 15, 20, 30, 40, 50 and 60), we took three litterbags in each site and washed carefully to remove macroinvertebrates and other particulate materials. Then we dried the litterbags at 60°C±5°C for 5 days and measured the remaining particulate organic matter (POM) of each one gravimetrically.

Figure B. *In situ* litterbags.

2.2.2. In vitro experiment: we prepared 30 incubations (18.5 × 11.5cm pot with 1.5L) with 50g of dry soil, 10g of dry biomass and 300mL of collected water to simulate the invaded sites substratum. In each incubation we disposed 30 little litterbags (10 × 10 cm; ф pore = 0,5 cm) with 2g of *H. coronarium* dry biomass and marked with numbered tags. Then, we watered each incubation with 200mL of collected water (until saturate the substratum) and disposed the incubations in a photoperiod (12/12h) incubator at 25°C±2°C. On the same collection days of the *in situ* experiment, we took 3 little litterbags of the incubations. Then we dried the little litterbags at 60°C±5°C to constant weight and weighted the remaining POM of each one.

Figure C. *In vitro* incubations with litterbags.

2.3. Height x biomass relationship

To estimate the biomass in function of ramets height, we collected 100 ramets of *H. coronarium* from the 3 invaded sites . Each ramet was measured in height, marked with numbered tags, washed and dried at 60°C±5°C to constant weight .Then, we weighted each ramet. All the weights measuremets were taken through an analytical balance (Boeco; 0.0001g precision).

2.4. Data analysis

We considered the height data of dead ramets (ramets whose fronds were dry and without any apparent chlorophyll) as the last ramet height value measured before found a ramet dead. We adjusted the temporal variation in the height of living and dead ramets (RH) values of the three sites to a sinusoid model (Equation 1) (Batschelet, 1978).

$$RH = A + (B \times \cos((\frac{2\pi}{365}) \times (t - t_{max}))) \qquad (1)$$

where: A = average height of ramets (cm); B = standard deviation (cm); t = time (day) and t_{max} = time with highest height value (day).

The temporal variation of debris decay (DD) *in situ* and *in vitro* (Experiment 2.2) were adjusted to an exponential model (Equation 2). To compare the *in situ* and *in vitro* decomposition processes, we confronted each other through an linear regression.

$$DD = A \times e^{-k \times t} \qquad (2)$$

where: A = initial debris mass (g); k = mass loss coefficient (day^{-1}); t = time (day)

The half-life (t ½) of the debris in *in situ* and *in vitro* experiments was calculated using Equation 3:

$$t_{½} = \frac{\ln(0.5)}{-\mathrm{k}} \qquad (3)$$

where: k = mass loss coefficient of each experiment

We fitted a power model to the data of the Experient 2.3. We used the model resulted to estimate the average biomass of living and dead ramets through the values obtained from the Equation 2. We estimated the living and dead biomass per m² (BM) through the results generated for the power model multiplied by the median of ramets per m² (both for the living and for the dead ramets over the Experiment 2.1) (Equation 4).

$$BM = (A \times \mathrm{x}^{\mathrm{b}}) \times N \qquad (4)$$

where: A = ramets biomass when height is equal to zero (g), b = increment coefficient and N = number of ramets (individuals.m^{-2})

We derived the results of Equation 4 to estimate the production of daily debris per m² to the living and the death biomass data. For the death biomass data, we considered the positive values of the derivation results as debris production and the negative data (negative debris contribution) as zero debris production. On the other hand, for the living biomass data, we considered the positive values of the derivation results as ramets growth exclusively (and zero debris production) and the negative data (negative living biomass production) as the debris production. We adjusted these two different daily debris production data to an exponential model (Equation 5) according Olson (1963). The Equation 5 results are the daily debris accumulated (DA) of *H. coronarium* ramets per m².

$$DA = (\frac{dBM}{dt} + DR_{t-1}) \times \mathrm{e}^{-\mathrm{k}} \qquad (5)$$

where: $\frac{dBM}{dt}$ = daily debris production; and k = mass loss coefficient

The mineralized debris per m².day^{-1} is the difference between the sum of the daily debris production data and the daily debris accumulated. All the simulations were realized at the software OriginPro 8 SR0 (v8.0724(B724).

3. Results

Over the two years, we monitored 3070 ramets of which 2465 new ramets (recruitments) and 2344 death events. Figure 1 shows the total number of ramets, divided in remaining ramets, recruitments and deaths over this period. Mortality and number of new ramets were higher between July and August (indicated by September data, for both experimental years). The average values of individuals per m² during the experiment was 45.54 (SD = 7.71) for the living and 14.21 (SD = 4.28) for the dead ramets. Figure 2 shows the fit at the sinusoid model (Equation 1) of the living (Average Height = 93.23cm, SD = 17.69cm) and height of dead ramets (AH = 99.98cm, SD = 8,23cm) over the time.

The first exponential model (Equation 2) showed robust fittings for the mass loss process (Figure 3), with determination coefficients (r^2) obtained by kinetic fittings were 0.97 for *in situ* experiment and 0.88 for *in vitro* experiment. The linear regression (Figure 3C.) shows faster mineralization process *in situ* (2.13 times higher) than *in vitro*. The t½ regarding the mineralization process was 152 days for *in situ* and 492 days for *in vitro* experiment. According the best adjustment, we utilized the mass loss coefficient (k) from the *in situ* experiment (0.00459) for the daily debris accumulation model.

Figure 4A presents the ratio between the height and ramets biomass in the Experiment 2.3 and the adjustmet to the power model ($r^2 = 0.903$). The power model adjusted to the living average ramets height values generated by the sinusoid models (Equation 4) presented the highest living ramets biomass in March 7 (649.48g.m^{-2}) and the lowest ramets biomass in September 5 (287.31g.m^{-2}). To the dead ramets adjustment, the power model presented the highest detritus contribution in July 21 (192.24g.m^{-2}) and the lowest contribution in January 20 (135.41g.m^{-2}) (Figure 4B).

Figure 5A presents the highest ramets debris accumulated values (g.m^{-2}) for winter seasons (living model: 314g.m^{-2}; death model: 50g.m^{-2}) and the lowest values for summer seasons (living model: 123g.m^{-2}; death model: 20g.m^{-2}). The living model (362g.year^{-1}) presented a 6.35 times higher mineralization process than death model (57g.year^{-1}) (Figure 5B).

4. Discussion

H. coronarium ramets are very susceptible to seasonality. The highest mortality of ramets occurred during the winter season. Similar result was presented by Santos et al. (2005) and this seasonal pattern may be explayned by low rainfall (i.e. lower soil moisture) (Volaire et al., 1998) low temperature and high wind speed (Rich et al., 2008) during winter. Our results showed that the establishment of new ramets are mediated by (1) massive death ramets events and (2) the beginning of spring season. In nonnative ranges, *H. coronarium* forms dense crops with strong intraspecific competition (Chiba et al., unpublished data; Chapter III of this thesis). In invasive populations, mature plants decreases light and space availability, important resources to new recruitments (Bosdorf et al., 2004). So the massive death events of mature ramets during winter season allowed the highest emergence of new *H. coronarium* ramets during July and August (measured in September of both experimental years). Besides, the recruits establishment was only possible with the subsequent mild climate of spring season (i.e. rainfall resumption, rising temperatures and low wind velocity).

Seasonal recruitment assimilation is recognized as an invasive strategy for rhizomatous plants. The spread of *Arundo donax L.* (Poaceae), a vigorous invasive species of warm riparian habitats, is delayed until spring due mild climate conditions (Decruyenaere and Holt, 2005). However our results shows the main *H. coronarium* recruitment occurring before the spring season and consequently before the main native plants recruitment. This early recruitment could provide competitive advantages before the native plants. The priority effects, or the impacts of early-arriving species on those arriving later in a system, can allow exotic species to colonize when they establish first and subsequently pre-empt resources (Wainwright et al., 2012). Priority effects can operate seasonally, as invasive species filling a "vacant phenological niche" by being active earlier than native species (Wolkovich & Cleland 2011). Nevertheless further studies are needed to confirm the seasonal priority effects operating in *H. coronarium* because we do not have information on native species recruitment.

The faster mineralization of the *in situ* comparing the *in vitro* decomposition experiment is assigned to the effects of losses by smaller detritus particles sedimentation, abrasion, action of macro and micro decomposer organisms (e.g., fragmentation and enzymatic attack) and synergy among these factors (Silva et al., 2011). So the environmental significance of the *in situ* experiment is higher than the *in vitro* experiment due to procedures carried out under standardized conditions being very different from natural field settings (Vignati et al., 2007). However, laboratory-based mechanistic investigations are the ideal tool to establish causal links between selected variables and chemical or biological responses (Silva et al., 2011). The parameterization of mathematical models utilized in the description of broad phenomena in decomposition processes can only be defined under controlled conditions (Peret & Bianchini, 2004). In this study, the *in situ* experiment measures the specific microbiota and chemical oxidation contribution in the mineralization process, once the photodegradation in this conditions can be disregarded (Santos et al., 2006). The chemical oxidation in aerobic incubations is responsible by 1 to 5% of all oxygen consumption in different macrophyte debris decay (Nunes et al., 2007). Thus our results allowed to estimate the specific microbial contribution in the overall decomposition process, being responsible by 42% to 46% of all *H. coronarium* debris decay.

Our decomposition results demonstrated very low mineralization rates, represented by high half-life times of debris for both *in situ* and *in vitro* experiments. Comparing with others same habit and niche macrophytes (i.e. herbaceous, emergent, rizomathous), *H. coronarium* presents 1.4 times higher half-life time debris than *Typha latifolia* L. (Typhaceae) (Schnitzer et al., 2000) and at least 2.4 times higher than *Typha* × *glauca* Godr. (Typhaceae) (Nelson et al., 1990), all in *in situ* experiments. For *in vitro* experiments, this macrophyte presents 3 times higher half-life time debris than *Typha domingensis* Pers. (Typhaceae) (Cunha-santino et al., 2006) and at least 10.9 times higher than *Cyperus giganteus* Vahl (Cyperaceae) and *Oxycaryum cubense* Poepp. & Kunth (Cyperaceae) (Bianchini Jr et al., 2006).

Temperature is one of the most important factors that influence the organic matter decomposition rate (Wetzel 2001). Usually when temperature increases, organisms metabolism and enzymatic production intensity increase (Piontek et al.

2009). Our *in vitro* experiments were carried out at 25°C, while all the others *in vitro* experiments compared, were carried out at 20°C. Thus, its expected lower mineralization rates and consequent higher half- life time of *H. coronarium* debris in a 20°C condition when compared with the current experiment.

The low mineralization rates of *H. coronarium* can be explained by the quality of debris. The composition of the substances found in different species changes the metabolism and composition of the decomposing microbiota (Harner et al., 2009). Besides presenting high fiber content, with 43% of cellulose (Anonymous, 1912), *H. coronarium* ramets also presents polyphenolic compounds and terpenoids as the antimicrobial substances caryophyllene and myrcene (Martins et al., 2010), the larvicide linalol (Prakash et al., 2010) and sesquiterpenoids against herbivory attack (Lan et al., 2013). These refractory and allelopathic proprieties can decrease the biota debris consumption of *H. coronarium*.

The sinusoid models explained successfully all the seasonal fluctuations exploring only mean data values for ramets height and ramets per m^2. Considerations of spatial heterogeneity of our experimental design (differences between each landscape) and intrinsic stochasticity processes of each experimental year (i.e. rates of ramets births and mortality) would complicate the model and emphasize noises (Van Nes and Scheffer, 2005). So we applied the concept of superindividuals (Scheffer et al., 1995), making all individuals and areas equal (mean values of each variable), without giving the field data.

Our debris accumulation model presents a wide seasonal variation in which the invaded ecosystem shows a positive net storage (production minus loss) of energy in the form of debris, unincorporated in mineral soil as described by Olson (1963). Still determinant to evidence this process overtime, simulation models are always somewhat uncertain (Van Nes and Scheffer, 2005). To increase the accuracy of our results we used two model conceptions to estimate the *H. coronarium* debris accumulation, but each model has weaknesses. The living ramets model overestimates the debris accumulation once consider all the live biomass reduction (Figure 4B) directly related to death ramets events. The biomass data comes from the average height data. In turn, the reduction in ramets average height is related to an indefinite wide number of stochastic processes (i.e. ramets births, growth rates, landscape influences). Applying the super-individuals concept and considering the robust relationship between height and biomass (Figure 4A), we can simplify this situation supposing all ramets height reductions resulting in ramets debris. On the other hand, the dead ramets model underestimates the debris accumulation. We estimate the dead ramets height as the last ramet height value measured before found its dead. However a ramet death is observed only 2 months after the last height measure, on the next collection. So the height values of each dead ramets can be underestimated according the precise death date over these two months. Therefore, we consider the accumulated debris value on the range between the overestimated and the underestimated model results.

Our results express quantitatively the real increase of particulate organic matter by *H. coronarium* debris overtime as well as the seasonal biomass dynamic of each fraction in terms of live, dead, mineralized and accumulated biomasses. The debris (or litter) accumulated is a fraction of the dead biomass in function of climate and decomposition processes (Aerts, 1997). There are others studies addressing invasive plants debris or litter accumulation as for *Typha* spp. (Typhaceae) (*T. orientalis* C.Presl in Pegman and Ogden, 2005; *T. angustifolia* and *T.* × *glauca* in Vaccaro et al., 2009) utilizing only harvesting method in invaded areas. This method is interesting for estimates the dead biomass of an invasive plant in a specific invaded site and time. However, the real particulate organic matter contribution of the invasion is not measured. In other study, Christensen et al. (2009) estimated the accumulation litter of the invasive *Phragmites australis* (Cav.) Trin. (Poaceae) between 267–526 g/m² in a mass-balance approach, utilizing experimental and literature data. Nevertheless they don´t explore the seasonal fluctuations in the debris contribution over the time.

The effects of a plant invasion occur across several levels of organization, from individual scale (growth and reproduction), to population–community interactions and ecosystem processes (i.e. litter production, N retention and recycling) (Currie et al., 2014). Therefore, identify and quantify the dynamics of different biomass fractions (live, dead, mineralized and accumulated) of *H. coronarium* invasions provides important tools to estimate its real impact according each organization level. The dominant live biomass, high debris contribution and low debris mineralization can cause native plant suppression and changes in nutrient cycling of invaded environments. Seasonal influence on the invasive species should be considered as an important ecologically based strategy to prioritize and coordinate landscape-scale management.

5. Acknowledgments

We thank the São Paulo Research Foundation (FAPESP, process 2012/09485-4) for funding our study through a scholarship to the first author. Marcelo B. Leite, Marcel L. Moitas, Pavel Dodonov, Hugo H. L. Saulino and Natasha S. Volcov assisted with field-work.

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Figures

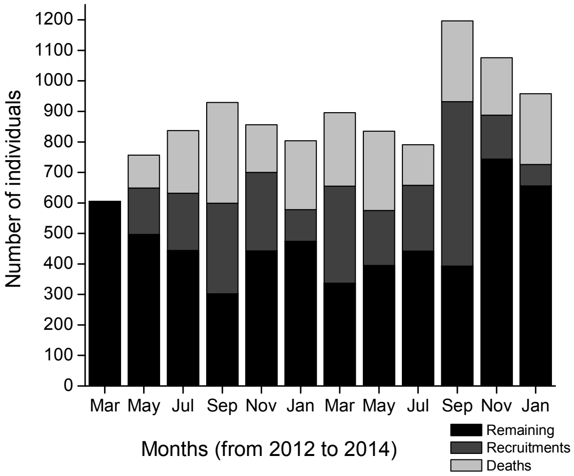

Figure 1. Population dynamics of *H. coronarium* and total number of ramets per class over the two experimental years.

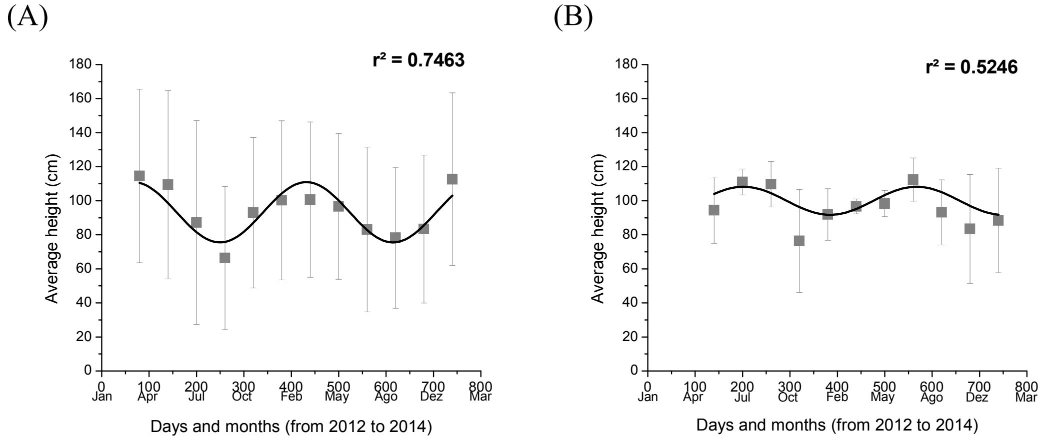

Figure 2. Sinusoid model applied to the live (A) and dead (B) average heights values of *H. coronarium* ramets over the two experimental years. Standard deviation bars and model adjust values (r^2) are expressed.

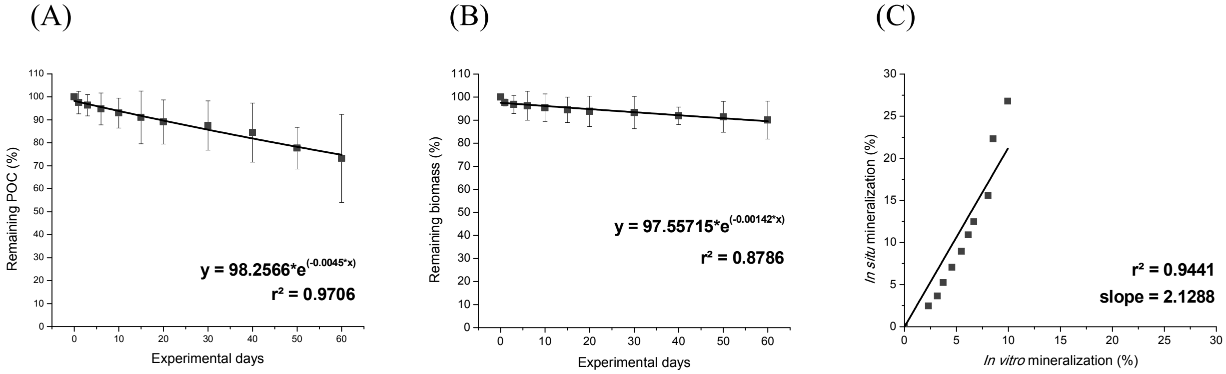

Figure 3. First exponential model (Equation 2) applied to the decomposition experiments *in situ* (A) and *in vitro* (B) for the debris decay values (in percentage) of *H. coronarium* ramets over the experimental days and respective equations resulted. (C) Linear regression between the debris decay values of the *in situ* and *in vitro* experiments and slope value. Standard deviation bars and model adjust values (r^2) are expressed.

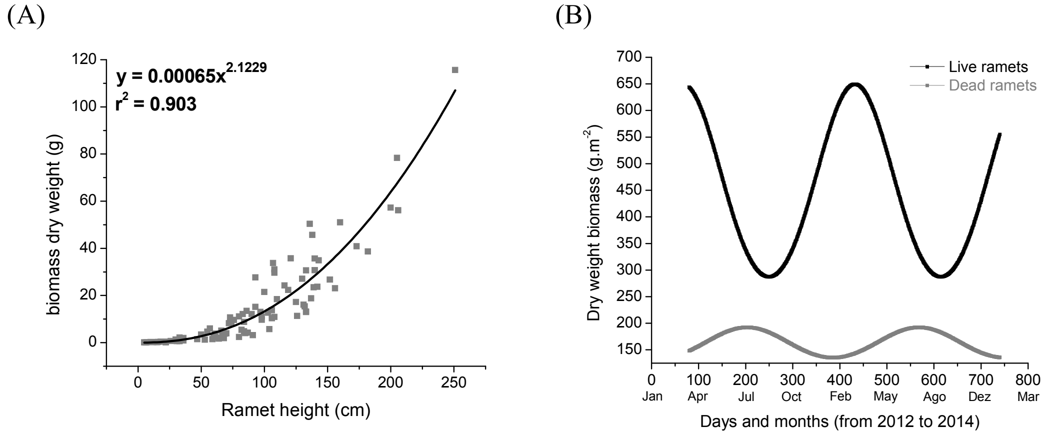

Figure 4. (A) Power model applied to establish the relationship between ramets biomass dry weight (in grams) and ramets height (in centimeters) of *H. coronarium* ramets and equation resulted with adjust value (r^2). (B) Biomass results of the live and dead sinusoid models values (Figure 2) fitted in the power model equation over the two experimental years.

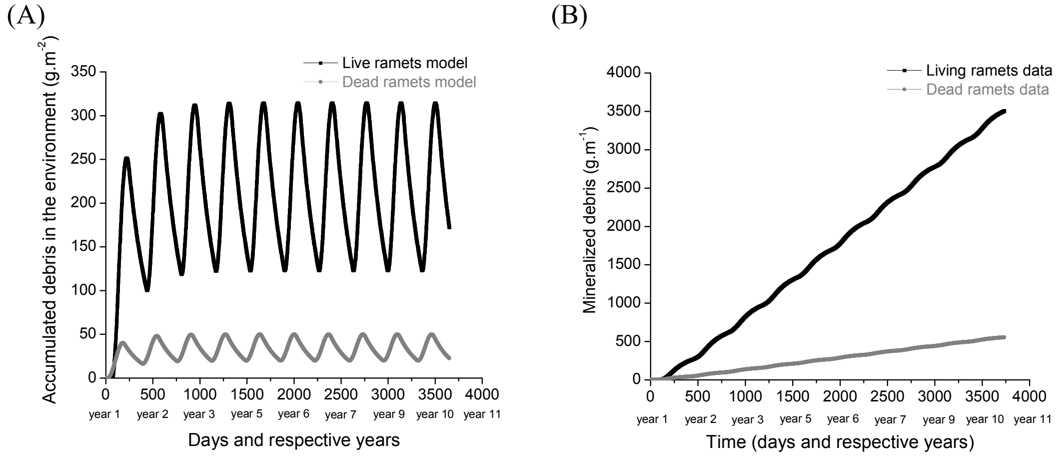

Figure 5. (A) Accumulated debris (in grams per square meter) in invaded areas of *H. coronarium* ramets generated by the live (Live ramets model) and dead (Dead ramets model) biomass results (Figure 4B) fitted in the second exponential model (Equation 5) in a 10 years projection. (B) Mineralized debris (in grams per square meter) in invaded areas of *H. coronarium* ramets for the live (Living ramets data) and dead (Dead ramets data) approach in a 10 years projection.

III - Capítulo 2

Estratégias de invasão do lírio- do- brejo *Hedychium coronarium* J. König (Zingiberaceae) em diferentes condições competitivas e ambientais

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 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 *H. coronarium* and native plants under different conditions of soil moisture in riparian areas, through removal experiments. We observed that *H. coronarium* exhibits different invasion strategies according to soil moisture, native species life form, and intensity of intra- and interspecific competition. In areas with high soil moisture and high competitive pressure, *H. coronarium* invests in vegetative rather than reproductive growth. In areas favorable to invasion, with drier soils and lower competitive pressure, *H. coronarium* colonizes the invaded area and expands its population. Our results suggest that *H. coronarium* has a negative influence on the recruitment of plants from the native community, with consequences to the biodiversity of invaded areas.

Keywords: plant invasion, competition, phenotypic plasticity, riparian areas, white ginger lily.

Introduction

Biological invasions represent a threat to the ecological balance and conservation of native plant communities (Simberloff 2005) due to the suppression of native species (Pyšek et al. 2012). One species is considered invasive when it acquires a competitive advantage concomitantly to the disappearance of natural obstacles to its proliferation, which allow fast dispersal and colonization of new areas where it becomes dominant (Valery et al. 2008). This competitive advantage is frequently related to high phenotypic plasticity, which allows the invasive species 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 broad environmental conditions or provides the invasive plant with competitive advantages in favorable environments (Richards et al. 2006). Hence, knowing the role of morphological and phenotypic adaptations in face of biotic (Burns and Winns 2006) and abiotic interactions (Williams et al. 2008) allows understanding the success of invasive species.

Among the environments under high risk of plant invasion are riparian ecosystems (Richardson et al. 2007). Riparian ecosystems are influenced by several human disturbances, which are related to process from local to global scale. Dams and flow regulation (Shafroth et al. 2002), land use in the coastal zone (Patten 1998), deforestation (Iwata et al. 2003), trampling and extensive livestock farming (Meeson et al. 2002), and water use for consumption (An et al. 2003) and leisure (Washitani 2001) alter the physical and chemical characteristics of water bodies, such as channel structure, drainage, sedimentation, and eutrophication. These disturbances, together with cyclic flood dynamics (Naiman & Décamps 1997) and the capacity of propagule dispersal of lotic environments (Planty-Tabacchi et al. 1996), lead to changes in the extension of the floodplain and its floristic composition, which makes riparian environments highly susceptible to biological invasion (Richardson et al. 2007). Conversely, invasive species not only respond to environmental conditions, but also modify the invaded sites (Wardle et al. 1998). Knowing the intrinsic functional characteristics of an exotic plant allows understanding its impact on the ecosystem, as plant characteristics affect environmental properties, such as luminosity, soil temperature, and nutrient cycling (Westoby & Wright 2006).

Understanding the dominance mechanisms of invasive species is a key to comprehend and mitigate their impacts (Byers et al. 2002). Testing experimentally the response of native plants to invasion, with a special focus on the first stages of development, can provide information on the degree of influence of the invasive plant on the community and how the systems responds to its reduction or removal (Cushman et al. 2010).

In this study, we assessed development in height and number of new individuals of the invasive white ginger lily *H. coronarium* J. König (Zingiberaceae) and other plants of the native community in riparian areas under different competitive and environmental conditions, through a removal experiment. Our hypothesis was that *H. coronarium* invests in vegetative or reproductive growth according to different (1) soil moisture levels, (2) removal treatments, and (3) life forms of the species present in the plant community. Different development strategies of *H. coronarium* may lead to different changes in the plant community.

Methods

Description of the problem invasive species

Hedychium coronarium is a perennial, rhizomatous, herbaceous macrophyte that occurs in wet environments and may reach up to 2 m in height (Macedo 1997). It is native to tropical Asia and is commonly used as an ornamental plant due to its white and fragrant flowers (Kissmann & Groth 1991). However, *H. coronarium* is considered a weed in many place because of its fast growth and rapid dispersal. It invades wetlands and marshes, lake banks, streams, and drainage channels, forming dense populations (Lorenzi 1991) and replacing native vegetation (Lorenzi & Souza 2001). *H. coronarium* is difficult to control because of its extremely efficient vegetative reproduction through rhizome fragments (Kissmann & Groth 1991).

Study area

The present study was carried out from September to December 2013, in four wet environments near São Carlos (47°30'-48°30'W; 21°30'-22°30'S), in São Paulo state, south-eastern Brazil; the sites were 10 km apart. The regional climate is classified as a transition between Cwa.i and Aw.i (Tolentino 1967), with a warm, humid summer, from October to March, and a dry winter from April to September.

Experiment of vegetation removal

In each area we delimited 1 transect with 2 experimental sub-blocks, each containing between 50 and 80% of *H. coronarium* cover (Figure A). One sub-block was close to the margin of the main water body (denoted the Wet treatment), which was very susceptible to flooding, and the other was separated by 20 m from the main water body (the Dry treatment). In each block we delimited three 1.5 x 1.5 m plots and allocated each one a vegetation management treatment randomly. The three treatments applied were:

(1) The untreated control (denoted Ctr) where no plants were removed, not even *H. coronarium* ramets.

(2) Plots where all *H. coronarium* ramets were removed leaving all individuals of other plant species (denoted Nat). This assessed the regeneration capacity of the plant community in the absence of *H. coronarium*.

(3) Plots where all plants were removed at the start of the experiment (Month, Year) (denoted All). This assessed the regeneration capacity of both *H. coronarium* and native species.

We considered native plant community all plant species found in the area, except *H. coronarium*. At the beginning of the experiment (September, 2013), we marked all plants found in the plots with numbered plates. In the removal experiments, we cut the plants at ground level, taking care to minimize soil disturbance and removed the material from the plots. At fortnightly intervals, we monitored the survival, recruitment, and height of all marked individuals. We considered each *H. coronarium* ramet as an individual. We also classified all individuals according to life-form: herbaceous or arboreal/shrubby. We assessed the percentage of soil moisture based on 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 and growth of all plants, 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 their entire life.

Statistical analysis

To test for significant differences between treatments, we used a split plot analysis of variance (function 'aov' within the R statistical environment (R Development Core Team, 2013). We used the height of the individuals on the last day of the experiment as the response variable, management treatment (Ctr, Nat, All), moisture content (dry versus wet sites) and their interaction as fixed factors and a nested error structure (Blocks/Moisture/Treatment). We used a T- Student test (TS) to test for differences between soil moisture between sub-blocks. To test which treatments in each sub-blocks showed differences between the height of *H. coronarium* and other plants of the community, we used an Analysis of Variance test (ANOVA) with a post hoc Tukey test. We then analyzed the height data of new individuals of *H. coronarium*, and of the plant community that regenerated during the experiment, using a generalized linear mixed model (GLMM) to test for differences between (1) treatments and control within the same sub-block, and (2) treatments and control of different sub-blocks. All analyses were run in either Past 2.17c or the lme4 packages within the R statistical environment (R Development Core Team, 2013).

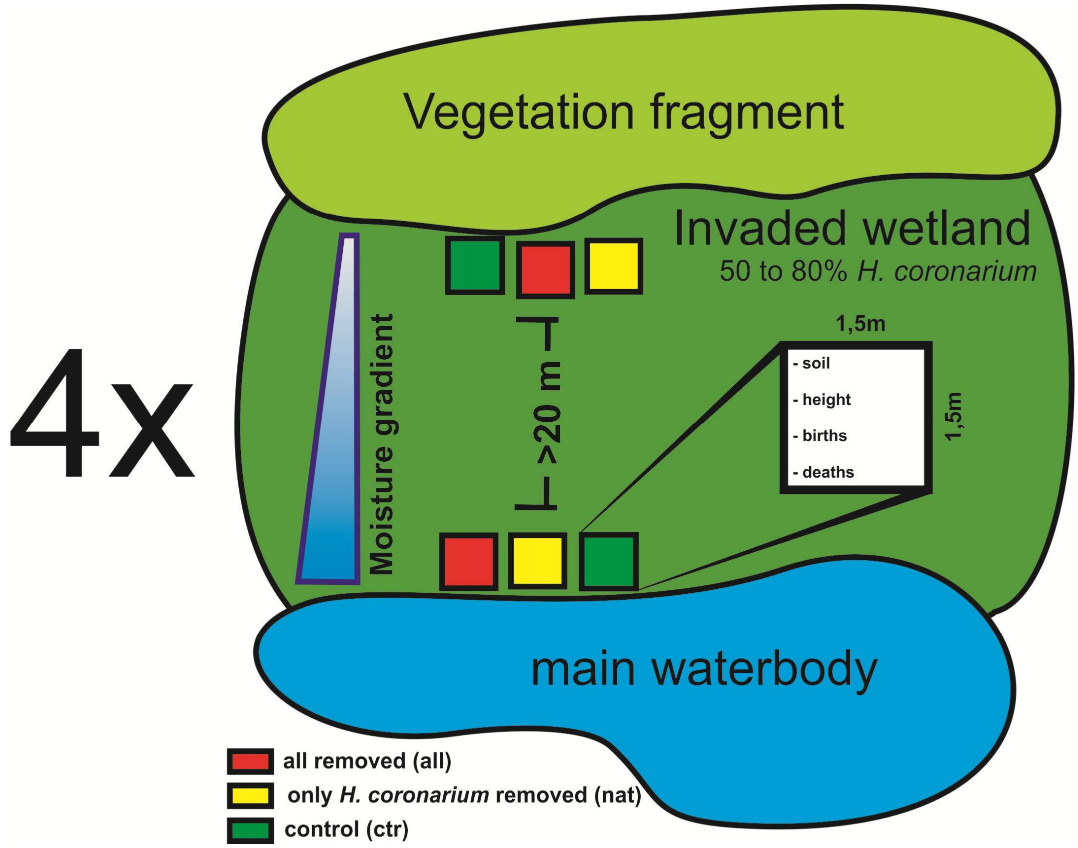

FIGURE A. Experiment of vegetation removal

Results

The wet sub-blocks (close to water bodies) had a greater average soil moisture content (Figure 1) than dry sub-blocks (TS; p<0.001). Over the four months, we monitored 2,932 individual plants of which 2,497 plants regenerated or sprouted: 2,069 *H. coronarium* ramets and 428 seedlings of native plants (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).

The treatments of removal differed from each other, and also the dry and wet sub-blocks were considered separately only for *H. coronarium* (Table 2). The average height was lower and the number of ramets of *H. coronarium* was larger in dry sub-blocks than in wet sub-blocks (Table 3 and Figure 3). The average height of ramets of *H. coronarium* in dry sub-blocks showed the following ranking: all < nat < ctr. The average height of native plants in the dry sub-blocks showed the following ranking: all > nat > ctr. The average height of ramets of *H. coronarium* in wet sub-blocks under different removal treatments showed the following ranking: all = ctr > nat. The average height of native plants in the wet sub-blocks under different removal treatments showed the following ranking: all > nat = ctr.

We did not detect significant differences between removal and control treatments in the same sub-block either for *H. coronarium* or for native plants (GLMM; dry sub-block: $p = 0.356$; wet sub-block: $p = 0.195$). There were significant differences, though, between removal treatments of wet sub-blocks and the control of dry sub-blocks (GLMM; $p < 0.001$), as well as in removal treatments of dry sub-blocks and the control of wet sub-blocks (GLMM; $p < 0.001$) for both *H. coronarium* and native plants. Figure 4 shows differences in vegetation growth patterns between treatments of soil moisture throughout time.

Discussion

Our results suggest that the white ginger lily shows different development strategies in response to soil moisture and presence of native plants of the native community. In the dry sub-blocks, the growth strategy of both *H. coronarium* and the native plants varied with removal treatment. In the treatment in which all plants were removed (all) *H. coronarium* showed the lowest growth in height, but a higher production of ramets. Hence, this invasive plant prefers to invest in new sprouts to quickly expand its cover.

Conversely, plants of the native community showed lower recruitment, but higher average height. This may be interpreted as evidence of a competitive pressure of *H. coronarium* on the native plant community, whose individuals invest in growth in height to overgrow the dense foliage of this invasive plant.

In the control (ctr), the new ramets of *H. coronarium* may be subjected to higher intra- and interspecific competition, with the presence of already established individuals both of the native plant community and *H. coronarium*. Hence, the control (ctr) had a smaller number of ramets, but their average height was the highest among the treatments of removal in dry sub-blocks, evidencing the aggressiveness of *H. coronarium*. The regeneration of the native plant community was higher in this treatment, probably due to a lower competitive pressure exerted by *H. coronarium*, with a proportionally smaller number of individuals, and a higher amount of adult individuals initially present in the experiment. In the experiment of exclusive removal of *H. coronarium* (nat), we obtained intermediate values both of number of new ramets and average height for *H. coronarium* and plants of the native community. We believe that the relationship among resource availability (e.g., light and space), lack of intraspecific competition, and presence of interspecific competition allowed higher production of new ramets compared to the control (ctr). We observed higher recruitment in the native plant community in the treatment with native plants (nat) than in the treatment of removal of all plants (all), due to the presence of adult plants in the beginning of the experiment. However, we observed lower recruitment of native plants in treatment native (nat) than in the control (ctr), probably related to a fast occupation of space by new ramets of *H. coronarium*, which suppressed the development of seedlings of native plants. These results point to a trade-off between investment in height and investment in new ramets in *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). These characteristics may contribute to fast dissemination and growth of the invasive population, overlapping evolutionarily the invaded community (Turner et al. 2014). However, we did not find other studies that assessed the trade-off between vegetative and reproductive growth in the context of plant invasions.

The treatments located in wet sub-blocks differed from the treatments located in dry sub-blocks in growth and number of ramets. The average height of *H. coronarium* in all wet treatments was higher than in the dry treatments, but the number of new ramets was smaller. These results can be associated with higher competition with native plants and with rhizome adaptability to anaerobic stress.

Differences in life form between native and exotic species play an important role in the process of invasion and establishment (Scharfy et al. 2011). Exotic species have higher invasion success in areas with fewer morphologically and functionally similar plants. Pyšek et al. (2009) observed that the best-succeeded invasive plants in Central Europe are herbaceous species in areas dominated by perennial grasses. In our experiment, the plant community associated with wet areas is composed mainly of herbaceous plants (Figure 2). These plants have higher metabolism compared to arboreal and S plants (Grime et al. 1997), which dominated the plant community in the dry areas of our experiment. Hence, we believe that 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 et al. (2011), the impact of the invasive plant *Melilotus alba* Medik. (Fabacea) 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 competition, an increase in allochthonous nutrient input (White & Jentsch 2001), and disturbances in trophic structure (McCann 2007). It is likely that a high percentage of water in the soil may be unfavorable to the development of *H. coronarium*. High soil moisture is stressful for the rhizome and stimulates metabolic processes associated with anaerobic sediments, such as fermentation (Chen et al 2003). The use of fermentation in the metabolism of glucose is less efficient than cellular respiration and increases the need for soluble sugars. Consequently, it decreases the starch content of rhizomes in situations of anaerobic stress, such as long floods (Chen et al 2005). Some unpublished data collected by us evidenced lower amounts of amyloplasts in the rhizomes of *H. coronarium* in wet areas than in dry areas. Hence, we believe that floodable areas are unfavorable to the development of the rhizomes of *H. coronarium*, whereas the establishment of other species is favored, especially herbaceous species, and aquatic or semi-aquatic plants (Table 1).

Our results corroborate the trade-off proposed by Grime (1977), 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).

The recruitment and spatial distribution of native plants in marshes are driven mainly by abiotic factors (Viereck et al. 1993). Seasonal peaks of flood 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 of arboreal (Chapin et al. 2006). However, our experiments of removal showed that the establishment of new ramets of *H. coronarium* had a negative influence on the regeneration of native plants, which corroborates Blaine et al. (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.

Acknowledgments

We thank the São Paulo Research Foundation (FAPESP, process 2012/09485-4) for funding our study through a scholarship to the first author. Marcel Rejmánek helped in experimental design, Rafael O. Xavier in plans identification, Helton G. Carvalho advised on the statistical analysis and Hamilton M. Moya and Natasha S. Volcov assisted with field-work.

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Tables

Table 1. List of species and life-forms recorded within the species-removal experiment between in both the low and high moisture regimes, dry and wet sites respectively in the four months between September to December 2013. Key to: H = herbaceous, S = shrubs and T= trees

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

Table 2. Results of a split-plot analysis of variance testing for the effects of removal treatment (Treatment) and plot moisture content (Moisture, wet *versus* dry) in the height of both recruits of *H. coronarium* and native species the end of the experiment. Significant differences are denoted: ns = not significant (P>0.05), *** = P <0.001.

Error stratum	Factor	df	*H. coronarium*				Native species			
			Sums of Squares	Mean Square	F	P	Sums of Squares	Mean Square	F	P
Error: Block	Treatment	2	3177	1588	-	-	2224.3	1112.1	-	-
	Moisture	1	11128	11128	-	-	2.8	2.8	-	-
Error: Block x Moisture	Treatment	2	151715	75858	-	-	1024.2	512.1	-	-
	Moisture	1	1174	1174	0.1	ns	2299.9	2299.9	0.6	ns
	Treatment x Moisture	1	12	12	-	-	159.6	159.6	-	-
Error: Block x Moisture x Treatment	Treatment	2	36350	18175	15.7	***	8391	4196	3.2	ns
	Treatment x moisture	2	22367	11184	9.6	***	665	332	0.2	ns
	Residuals	12	13920	1160	-	-	15875	1323	-	-

Table 3. Results of an analysis of variance (ANOVA) testing for the different removal treatments according soil moisture of both recruits of *H. coronarium* and native species at the end of the experiment. Significant differences is denoted: *** = P <0.001.

Sub-block	*H. coronarium*					Native species				
	df	Sums of Squares	Mean square	F	P	df	Sums of Squares	Mean square	F	P
Dry	2	43706,4	21853,2	44.6	***	2	2,16081	1,08041	13,85	***
Wet	2	23863,1	11931,5	17.7	***	2	0,5002	0,25014	3,348	0,03

Figures

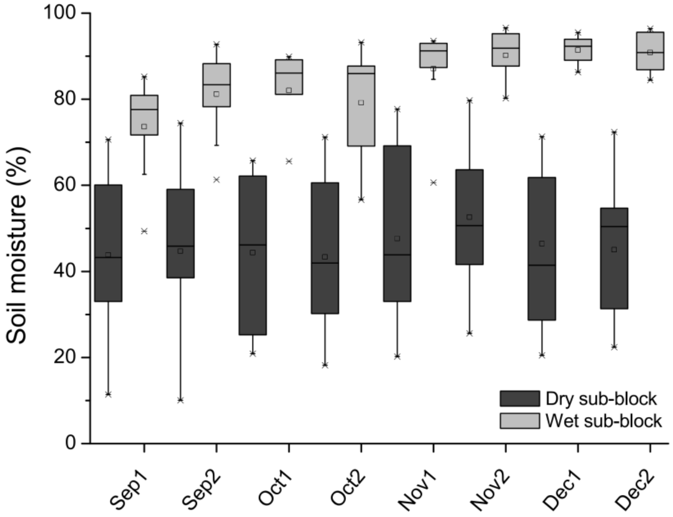

FIGURE 1. Moisture content of soils in the dry and wet sub-blocks within the species-removal experiment.

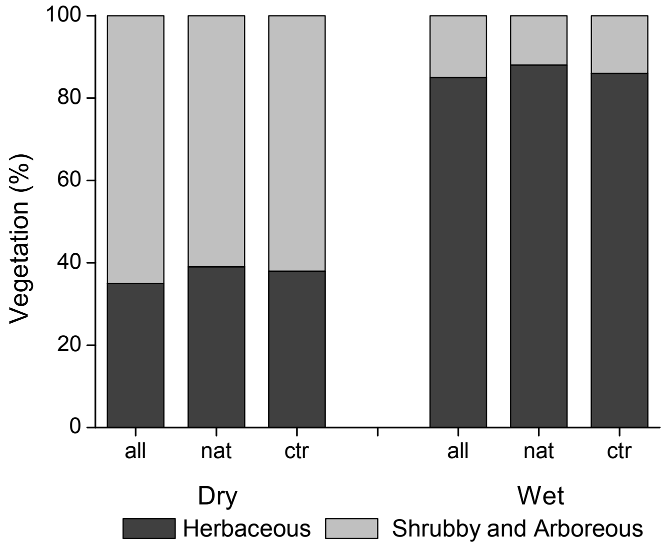

FIGURE 2. Proportion of recruits with different life-forms into the plant community following removal treatment at the end of the species-removal experiment in both dry and wet areas. Key to treatments: Ctr = control – no removal; Nat = only *H. coronarium* removed; All = all species removed.

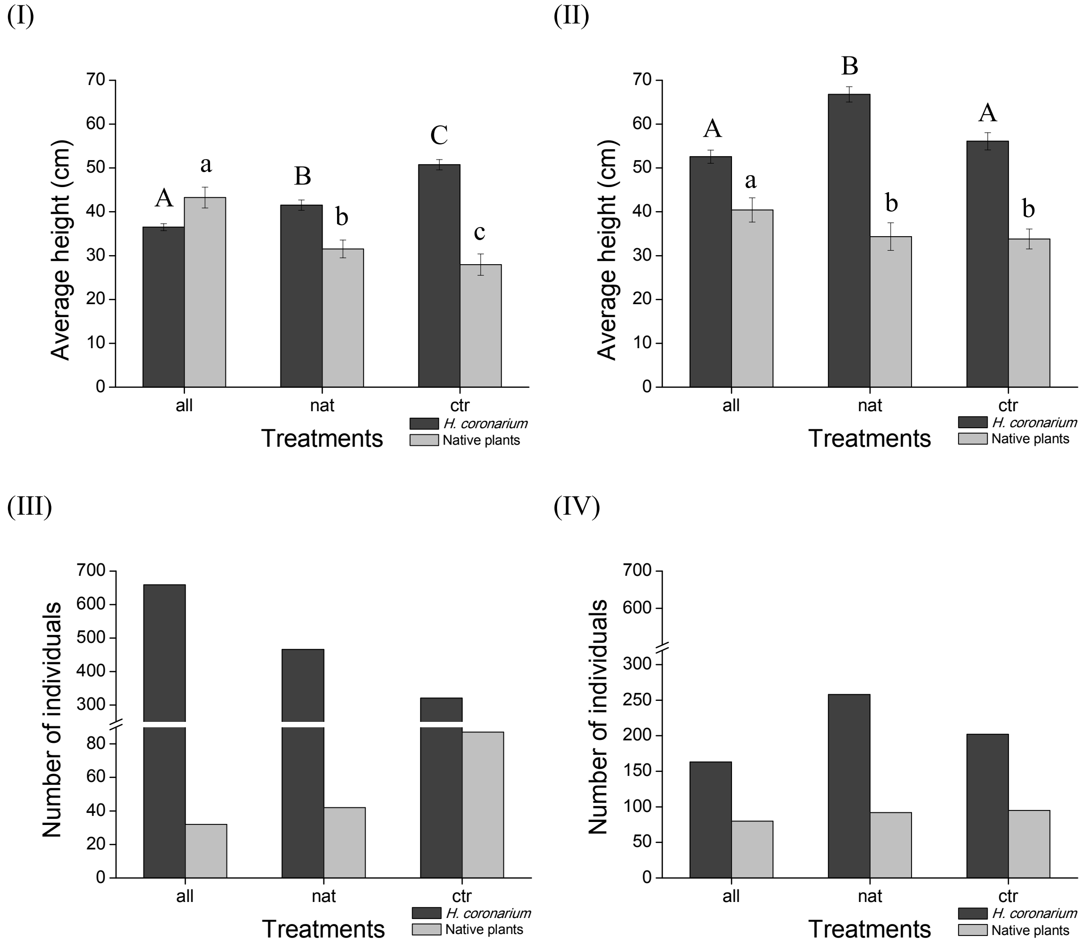

FIGURE 3. Average height (I and II) and number of recruits (III and IV) of *H. coronarium* and native plant species in sub-blocks with low (I and III) and high (II and IV) soil moisture. Different letters indicate significant differences (ANOVA with a post hoc Tukey test; $p<0.05$) between treatments.

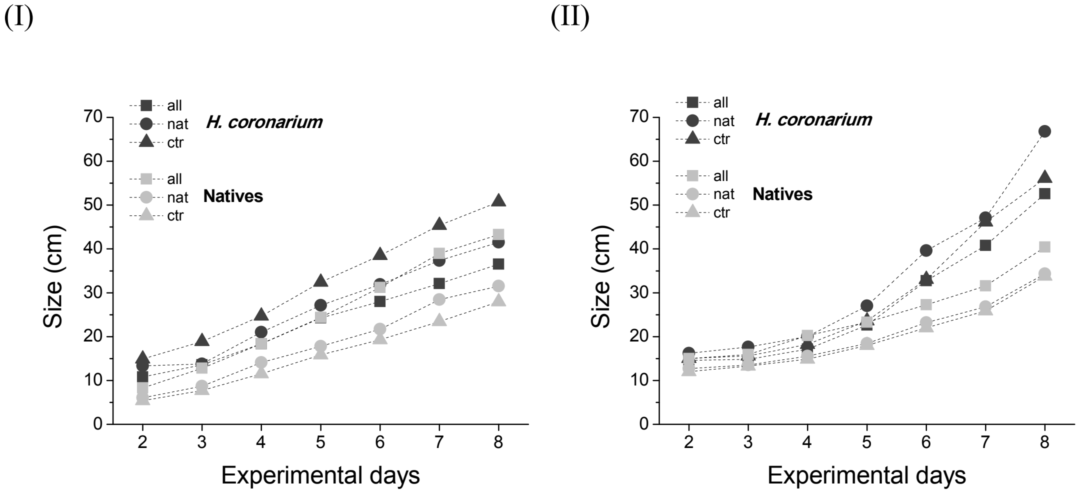

FIGURE 4. Average height of new ramets of *H. coronarium* and native plant species in different treatments and in sub-blocks with low (I) and high (II) soil moisture, which were born during the experiment.

IV - Capítulo 3

Primeiro registro de herbivoria da macrófita invasora *Hedychium coronarium* J. König (Zingiberaceae)[1]

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[1] Trabalho publicado na revista Biota Neotropica Jul/Sep 2013 vol.13, no. 3 endereço eletrônico. ISSN 1676-0603

First record on the herbivory of the invasive macrophyte *Hedychium coronarium* J. König (Zingiberaceae)

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Abstract

Invasive species can cause structural and functional changes in their non-native habitats, such as changes in the trophic chain. We describe the first register of ramet herbivory of butterfly ginger, an aggressive aquatic weed in Brazil, by capybaras in a floodplain area of a Cerrado reserve. This is the first record on the herbivory of *H. coronarium* in invaded areas. Capybaras could be using the butterfly ginger as habitat and as food resource, which could cause changes on the apparent competition between these invasive and native macrophytes.

Key words: Butterfly ginger, aquatic weed, capybaras

Resumo

Espécies invasoras podem causar alterações estruturais e funcionais nos ecossistemas invadidos, tais como alterações na cadeia trófica. Neste trabalho, descrevemos o primeiro registro de herbivoria de rametas de lírio-do-brejo, erva daninha aquática agressiva no Brasil, por capivaras em uma área de várzea de uma reserva de Cerrado. Este é o primeiro registro de herbivoria de rametas de *H. coronarium* em áreas invadidas. As capivaras desta região podem estar se utilizando dos bancos de lírio-do-brejo como habitat e como recurso alimentar, o que poderia ocasionar alterações na competição aparente entre esta invasora e as macrófitas nativas.

Palavras-chave: Lírio-do-brejo, erva daninha aquática, capivaras

One species is considered invasive when acquiring a competitive advantage, in addition to the disappearance of natural obstacles to spread, allowing its rapid dispersal and dominance in a new habitat (Valery et al. 2008). This dominance causes structural and functional changes in these ecosystems (Mack & D'Antonio 1998). Nowadays, biological invasion is considered the second biggest cause of global biodiversity loss (Wilcove et al. 1998, McGeoch et al. 2010). Changes in ecological processes as in food webs are important impacts of invasive species (Vitousek 1990, Mack et al. 2000).

Aquatic macrophytes are among the most important global invasives, threatening biodiversity and ecosystem processes in aquatic environments (Pieterse and Murphy 1990; Santamaria 2002). They spread rapidly, are able to grow and reproduce in sub-optimal conditions such as under intense competition (Spencer and Bowes 1990) and present a rapid metabolism and large biomass in eutrophic ecosystems (Pieterse and Murphy 1990). In Brazil, *Hedychium coronarium* J. König, Zingiberaceae, is an aggressive weed, invading floodplains, lake shores, streams and drainage channels, where it establishes dense populations (Couto & Cordeiro 2005, Lorenzi 1991). It can reach up to 2.0 m tall, also named as butterfly ginger (Macedo 1997, Santos et al. 2005, Instituto Hórus, 2012). It is native in tropical Asia and widely used for ornamental purposes (Kissmann & Groth 1991). Due to its rapid growth and dispersal, it is considered an important weed and replaces the native vegetation (Santos et al. 2005). Our objective is to describe the first record on the herbivory of these invasive macrophyte by capybara (*Hydrochoerus hydrochaeris* Linnaeus 1766).

From October 2011 to April 2013, we followed every two months a population of *H. coronarium* in 20 plots of 0.5 m^2 located a floodplain area of ca. 0.8 ha, within the forest reserve of the Federal University of São Carlos (21° 58'15.00" S and

47°53'16.45" W). Each ramet of *H. coronarium* found was measured and marked with numbered tags to evaluate the population dynamics.

From June to August 2012, we found in 7 plots, grazed ramets associated with the disappearance or fragmentation of numbered plastic tags (Figure 1). Grazed ramets were smaller than 25 cm height. No adult ramets were damaged or had tags missing or broken. In these plots, we found footprints and feces of *H. hydrochaeris*, a very common herbivore in this region. The fragments of the tags showed signals of *H. hydrochaeris* dental arcade.

H. hydrochaeris is a wild herbivore and the largest Brazilian rodent. Adults consume approximately 3Kg/day of fresh forage. Capybaras are selective grazers, and choose plants with high protein content (González - Jiménez 1978). According to Ferraz et al. (2007), capybaras are commonly found in large banks of *H. coronarium*, using them only as shelter from predators. Although rhizomes of these species have high quality nutritional content (Clippel et al. 2008), no signs of herbivory were observed, such as impression of dental arcade or revolving the sediments near the plants. The preference for *H. coronarium* ramets in early stages of development suggests that these plants have greater palatability and fewer secondary compounds than adult ramets (Bowers & Stamp 1993).

The preferential herbivory of new ramets of *H. coronarium* could be attributed to a lower availability of other resources during the winter, when capybaras can present more opportunistic behavior than in periods of high resource abundance, as in spring (Borges & Colares 2007). This is the first record of *H. coronarium* herbivory by capybaras and also the first record of herbivory of this macrophyte outside its native range. This record reinforces the need for further studies on the relationship between herbivory and invasive plants. Besides using the stands of *H. coronarium* as habitat (Ferraz et al. 2007) we observed that capybaras can also feed on them. This could affect the competitive capacity and the apparent competition (Dangremond et al. 2010) between these invasive and native macrophytes. In this case, *H. coronarium* could benefit capybaras by offering favorable habitat from predators, adverse microclimatic situations besides serving as abundant food resource. These benefits would provide changes in the abundance and / or distribution of populations (Holt 1977, Holt & Kotler 1987) of capybara. As a result, these changes in capybara populations could change the rate of predation and affect the population dynamics of native species used primarily as it´s resource. Thus, these could be allow the expansion of *H. coronarium*.

Acknowledges

We thanks the National Council of Technological and Scientific Development (CNPq), and São Paulo Research Foundation (FAPESP) process number 2012/09485-4, at scientific support in the form of a scholarship to the first author.

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Figure

FIGURE 1. Numbered plastic tags bitten by capybara

V - Conclusão Geral

H. coronarium é uma invasora agressiva de ambientes ripários, impactando todas as escalas do ecossistema. Apresenta alta produtividade e baixas taxas de mineralização dos detritos, propiciando grande acumulo de material orgânico particulado nas áreas invadidas. Possui larga adaptabilidade no seu desenvolvimento em diferentes umidades do solo. É altamente competitiva, reduzindo recrutamento e influenciando no crescimento de comunidades nativas. Por se desenvolver durante todo o ano, serve de recurso alimentar para capivaras durante o inverno, o que pode ocasionar alterações nas relações de predação e competição aparente de plantas nativas.

Acredito que sejam necessários mais estudos sobre a plasticidade fenotípica de *H. coronarium*, principalmente quanto à disponibilidade hídrica. O seu padrão de ocupação abrange desde a zona litorânea de corpos d´água avançando adentro à mata ripária e por vezes encontrada a mais de 100m dos limites de inundação. Assim esta invasora expõe capacidade adaptativa morfológica refinada do rizoma quanto às suas relações hídricas assim como fisiológicas, da planta como um todo, que devem ser aprofundadas.

Estudos de competição ao nível específico devem ser explorados. Em nossas observações de campo, verificamos vários exemplos das relações hídricas mediando os limites de dominância da taboa (*Thypha* spp.) e do lírio- do- brejo. Quando ambas estão presentes nas regiões litorâneas, a taboa domina emergindo da água, enquanto o lírio é mais abundante nas regiões não inundadas. Experimentos abordando estas relações hídricas com espécies nativas abundantes devem ser explorados para o entendimento dos mecanismos de dominância desta invasora.

A alta recalcitrância dos seus rametas também levantam perguntas sobre a qualidade dos seus detritos, tanto no conteúdo de compostos lignino- celulolíticos quanto na influência de compostos secundários, ou até mesmo alelopáticos, nos processos de mineralização da matéria orgânica particulada. O levantamento da biota decompositora, tanto micro quanto macro, deve ser realizado para áreas invadidas por lírio comparado com as de áreas controle. O estudo dos efeitos desta serrapilheira exótica na comunidade detritívora é essencial no entendimento dos seus impactos sobre a biota e nas alterações da ciclagem de nutrientes nestes ambientes.

As relações de *H. coronarium* e capivaras devem ser cuidadosamente exploradas. O pisoteio destes roedores pode propiciar maior fragmentação dos rizomas e portanto, aumentar o potencial de propagação da invasora. Como verificado por literatura e pelas nossas observações, as capivaras se aproveitam das invasões de lírio tanto como habitat quanto recurso alimentar. Inclusive em algumas oportunidades, avistamos a presença destes animais com filhotes em invasões urbanas de lírio. As conquistas territoriais de capivaras diretamente associadas às áreas invadidas por *H. coronarium* traz preocupações epidemiológicas. A febre maculosa (Proteobacteria *Rickettsia rickettsii*), transmitida por carrapato- estrela (*Amblyomma cajennense*) é um importante parasita de capivara. Desta forma, a expansão territorial de capivaras, associada à novas invasões de lírio, pode ocasionar o aumento da propagação de certas doenças prejudiciais ao homem.

A estruturação e desenvolvimento de seus rizomas devem ser extensivamente estudadas como elemento chave num possível manejo das áreas invadidas. No entanto, por apresentar frutos zoocóricos e cores vibrantes, a difusão desta invasora por aves deve ser objeto de futuros estudos.