



UNIVERSIDADE DE BRASÍLIA  
INSTITUTO DE CIÊNCIAS BIOLÓGICAS  
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

Mecanismo(s) de interferência de *Guilandina bonduc* L. em  
populações de *Cyperus atlanticus* Hemsl. na Ilha da Trindade,  
Brasil.

TESE DE DOUTORADO

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Orientador: Prof. Dr. Fabian Borghetti

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**ANABELE STEFÂNIA GOMES**

Tese apresentada ao Programa de Pós-graduação em Botânica da Universidade de Brasília, como parte dos requisitos para obtenção do título de Doutora em Botânica sob a orientação do Prof. Dr. Fabian Borghetti

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*“Todo fruto é vontade da semente”*

Antônio Arnaut

Dedico esse trabalho:

Aos meus pais, especialmente ao meu pai, meu maior incentivador, minha maior paixão.

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## **Mecanismo(s) de interferência de *Guilandina bonduc* L. em populações de *Cyperus atlanticus* Hemsl. na Ilha da Trindade, Brasil.**

### **Introdução Geral**

O desempenho da planta, que pode ser categorizado em crescimento, sobrevivência e reprodução, depende do acesso de um indivíduo ao espaço e aos recursos (Trautz et al, 2017). Esse acesso está condicionado à presença de outros indivíduos que também requerem espaço e recursos, tornando o desempenho das plantas em comunidades muito diferente daquele que seria como indivíduos solitários. Dessa forma, o papel das interações intra e interespecíficas deve ser considerado fator essencial da composição e dinâmica de comunidades vegetais (Callaway et al, 2002; Maestre et al, 2009).

A coexistência, entendida como a persistência de longo prazo de numerosas espécies dentro de uma dada região, é uma das questões ecológicas mais fundamentais nos estudos de comunidades animais e vegetais. Um fator que contribui no entendimento de coexistência é a diferença nas habilidades das espécies para o uso de recursos ambientais, de tal forma que cada espécie é um concorrente superior para um recurso limitador diferente (Tilman, 1986, 1987, 1988). Essas diferenças interespecíficas fazem com que combinações de espécies levem a um equilíbrio na biomassa vegetal de acordo com a disponibilidade de recursos (Tilman et al, 1997b). A abundância relativa das espécies não é somente afetada pelas mudanças nas razões de recursos limitantes. Perturbações no habitat também podem gerar desequilíbrios, propagando-se por toda a comunidade e tendo efeitos profundos e por longo prazo (Tilman, 1988; Tilman et al, 1997a).

As espécies vegetais estão sujeitas a um complexo conjunto de interações inter e intraespecíficas, tais interações são mediadas por diversos fatores ou recursos, bióticos e abióticos, que podem ser restritivos ou abundantes dependendo das características de cada habitat (Tilman, 1999; Callaway; Walker 1997; Gurevitch et al, 2009; Butterfield; Callaway, 2013). O que mais comumente é visto é que, devido a flutuações periódicas na oferta dos recursos, as comunidades de plantas raramente estão em equilíbrio (Tilman et al, 1987). As flutuações no regime de coexistência podem ser mais pronunciadas em ambientes sujeitos a pulsos de disponibilidade de recursos, como ambiente com sazonalidade e regimes de pluviosidade e seca bem determinados. Ou ainda, em ambientes

com diferenças espaciais na disponibilidade dos recursos (Davis et al, 2000; Schwinning; Kelly, 2013).

Assim, em estudos sobre interações entre espécies deve se considerar a disponibilidade dos recursos, o papel desses na fisiologia das plantas, a variabilidade temporal e espacial na sua oferta (Craine; Dybzinski, 2013). Alguns fatores importantes incluem as propriedades físicas e/ou químicas do recurso, a distribuição do recurso no espaço (se recurso é distribuído de forma homogênea ou irregularmente), a dinâmica de renovação de recursos, e se são distribuídos ao longo de um gradiente (Schwinning; Weiner, 1998). Adicionalmente, a disponibilidade de recursos também é fortemente dependente do padrão de distribuição de plantas (Trautz et al, 2017). Em geral, investigar a interação das espécies em resposta ao suprimento de recursos torna-se complexo pelas características únicas de cada um dos diferentes recursos envolvidos no processo (Craine; Dybzinski, 2013).

Um recurso é considerado limitante quando o aumento da sua disponibilidade acarreta no aumento da taxa de crescimento da espécie (Tilman, 1986), indicando que sua oferta é inferior em relação à demanda no ambiente (Craine; Dybzinski, 2013). Em geral, água, nutrientes e luz são os principais recursos que limitam o crescimento das plantas e são considerados recursos pelos quais as plantas individuais competem (Craine; Dybzinski, 2013).

O suprimento não suficiente de água é um dos mais importantes fatores limitantes da produtividade. Embora o regime de fogo, a intensidade de pastoreio e especialmente a disponibilidade de nutrientes estejam entre fatores que também influenciam ecossistemas, é comumente aceito que se a água for limitada, ela se torna o principal recurso que afeta a estrutura e organização da vegetação (Rodriguez-Iturbe et al, 1999). As espécies apresentam diferentes graus de susceptibilidade aos padrões de flutuação de umidade e aos regimes estresse hídrico e, mesmo tendo adaptações para enfrentar períodos de seca, todas as espécies sofrem perdas de biomassa durante períodos de estresse hídrico (Schwinning; Kelly, 2013).

Na grande maioria dos ecossistemas a água está disponível de forma heterogênea no tempo e no espaço (Gurevitch et al, 2009; Craine; Dybzinski, 2013). Fatores como propriedades físicas do solo, incluindo quantidade de matéria orgânica, profundidade e cobertura vegetal atuam na manutenção da água no solo. Adicionalmente, deve se considerar os efeitos da redistribuição da água no solo pelas plantas, influenciando os padrões de umidade do solo em nível de comunidade e ecossistema (Scholz et al, 2002;

Prieto et al, 2012). A redistribuição de água para camadas superficiais do solo favorece a absorção de nutrientes e a manutenção da microbiota do solo. Por outro lado, maior quantidade de água que esteja superficialmente alocada pode ocasionar maior perda por evaporação ou consumo por outras espécies, especialmente herbáceas. Em outro contexto, estratégia oposta, mas também efetiva é a redistribuição hídrica para camadas mais profundas do solo como forma de armazenamento para momentos de maior estresse (Hultine et al 2004). Todos esses fatores, bióticos e abióticos atuam nas flutuações diárias e sazonais, de tal forma que em certos intervalos a água pode estar completamente ou parcialmente disponível, ou mesmo restrita (Rodríguez-Iturbe et al, 1999; Gurevitch et al, 2009; Craine; Dybzinski, 2013). Além da disponibilidade de recursos, as plantas presentes em determinados habitats têm características anatômicas, morfológicas e/ou fisiológicas que resultam em diferentes estratégias para persistirem em tais ambientes (Tilman, 1987; Schwinning; Kelly, 2013).

Dessa forma, as plantas têm evoluído com inúmeras estratégias distintas para que possam lidar com a heterogeneidade e flutuações de recursos nos ambientes (Schwinning; Kelly, 2013). Para cada habitat, definido pela sua taxa de fornecimento de recursos e sua taxa de perturbação, são encontradas plantas com morfologia e aspectos fisiológicos associados a essas condições (Tilman, 1988; Tilman, 1999; Schwinning; Kelly, 2013; Lynch et al, 2014). Em ambientes com restrições hídricas, características e estratégias como ajuste osmótico, controle estomático, morfologia e anatomia radicular para maior absorção e eficiência do uso de água podem trazer vantagens às espécies relacionadas a melhor habilidade competitiva ou à tolerância a estresses (Nilsen et al, 1983; Schwinning; Kelly, 2013).

As espécies interagem de maneiras variadas que resultam em efeitos recíprocos positivos e/ou negativos, sendo que a maioria dessas interações ocorre por meio da modificação direta ou indireta de meio ambiente local (Tilman, 1999; Callaway e Walker 1997; Gurevitch et al, 2009; Butterfield e Callaway, 2013). As interações podem ter balanços diferentes de acordo com o nível e o tipo de estresse a que as plantas estão sendo submetidas. Portanto, a importância de interações positivas e negativas na estruturação de comunidades é mais bem compreendida quando são analisadas ao longo de diferentes gradientes ambientais, fases da vida, tamanhos e densidades das espécies (Callaway e Walker 1997).

A competição é um tipo de interação que pode ser definida como uma redução no desempenho fisiológico de uma planta devido ao uso compartilhado de determinado(s)

recurso(s) com suprimento limitado. Logo, é considerada uma interação negativa, ao passo que reduz as taxas de crescimento populacional de um ou ambos os competidores (Gurevitch et al, 2009). A competição por recursos tem sido considerada uma força determinante da estruturação de comunidades de plantas e seleção natural (Craine; Dybzinski, 2013).

A zona de influência da espécie também deve ser considerada em estudos de competição entre espécies. Nesse sentido, uma planta cresce utilizando recursos ocorrentes em sua zona de influência, os recursos são utilizados para o crescimento da população, resultando no aumento da sua área de influência. Conseqüentemente, as plantas passam a competir quando suas zonas de influência se sobrepõem, mostrando que as relações espaciais também influenciam as interações competitivas (Schwinning; Weiner, 1998).

A disputa de um par de espécies por um mesmo recurso pode resultar em redução da concentração de recursos de maneira que ocasiona a exclusão da espécie menos competitiva (Tilman, 1986; Huston e De Angelis, 1994). Invariavelmente em interações competitivas em pares há co-variância negativa porque um aumento na abundância de uma espécie geralmente leva a uma diminuição na abundância de outra (Tilman, 1999). A abundância relativa de espécies muda em resposta às mudanças nas razões de recursos limitantes e o resultado da competição interespecífica varia dependendo de qual recurso é limitante (Tilman, 1988).

Quando se incorpora níveis de estresse do ambiente às interações entre espécies significativa parte dos estudos levam à ‘hipótese do gradiente de estresse’ (HGE) (Bertness e Callaway, 1994). De acordo com a teoria, em comunidades em desenvolvimento sob alto nível de estresse a facilitação deve ser particularmente comum (Bertness e Callaway, 1994). Entretanto, em comunidades onde o ambiente físico não é limitante e a pressão dos consumidores é menos severa, as interações competitivas devem ser dominantes (Bertness e Callaway, 1994; Maestre et al, 2009). Resumidamente a facilitação deverá aumentar conforme aumenta o estresse abiótico e diminui a produtividade, enquanto a competição tende a ser atenuada (Callaway et al, 2002).

O denominador comum da maior parte dos estudos de HGE é que eles têm sido feitos em habitats com fortes níveis de estresse e potencialmente letais, onde interações facilitadoras expandem o nicho das espécies alvo (He & Bertness, 2014). Além disso, grande parte dos testes para a hipótese estudou a interação entre um único par ou alguns pares de espécies e avaliaram mudanças na magnitude e direção das interações de pares ao longo de gradientes de estresse (Maestre et al, 2009).

Os muitos trabalhos relativos a HGE nos últimos 20 anos levaram a um refinamento do modelo original de hipótese de gradiente de estresse (Maestre et al, 2009). Tal progresso se deu à medida que outras variáveis passaram a ser consideradas, como característica das espécies que interagem, o estágio ontogênico, os indicadores utilizados para avaliar o desempenho da planta, o tipo de fator de estresse e a magnitude do estresse imposto (Michalet et al, 2006; Maestre et al, 2009). Diferentes estudos sugerem que efeitos facilitadores dos benfeitores são visíveis quando os beneficiários são jovens e de menor porte. Quando os beneficiários são mais velhos e de maior porte, interações competitivas podem predominar, justificando padrões de mortalidade das plantas facilitadoras observados em vários sistemas. Ou seja, espécies podem começar seu ciclo de vida como beneficiários, mas tornam-se concorrentes significativos com seus antigos benfeitores à medida que crescem (Callaway, 1995; Callaway e Walker, 1997).

Estudos sugerem que a relação entre estresse e facilitação pode não ser estritamente crescente (Michalet et al, 2006; Maestre et al, 2009; Smit *et al*, 2009) e que o aumento da facilitação se esgotaria quando sob alto nível de estresse, quando a tolerância máxima das espécies beneficiárias e benfeitoras é atingida (Tielborger & Kadmon, 2000; Pugnaire & Luque, 2001; Holmgren et al, 2012). Mesmo em situações onde o papel relativo da facilitação aumenta com o estresse, o efeito absoluto deve em princípio ser maior em condições intermediárias de estresse (Maestre et al, 2009).

No entanto, He & Bertness (2014) sugerem que a maior parte dos trabalhos que contestam a teoria não se enquadra nos requisitos para que seja considerado um estudo de gradiente de estresse. Para testes experimentais do HGE, se recomenda os seguintes critérios: a) que se quantifique o nicho fundamental (sem vizinhos) e o nicho realizado (com vizinhos) de uma espécie ao longo de um gradiente de estresse do estudo, b) ter preferencialmente ao menos quatro níveis de estresse, c) manter o estágio ontogenético das espécies constantes em todos os níveis de estresse.

Modelos teóricos simples em ecologia têm desempenhado papel-chave como catalisadores no avanço da nossa compreensão e estimuladores da pesquisa. Dessa forma a hipótese do gradiente de estresse tem despertado o interesse do balanço de interações positivas e negativas em resposta a recursos limitantes. Todavia, como qualquer teoria científica, o HGE tem sido questionado e refinado, de maneira que esta hipótese tem sido apurada no sentido de prever o papel das interações na dinâmica e estabelecimento de comunidades e até paisagens vegetais (Maestre et al, 2009). Assim, abordagens teóricas

juntamente com experimentais são necessárias para investigar como a disponibilidade dos recursos podem reger as interações entre espécies.

### **Ambientes Insulares**

Ilhas podem ser classificadas em continentais ou oceânicas. O que as diferencia é que ilhas oceânicas são aquelas que surgiram do fundo do oceano e que nunca foram conectadas a um continente, diferentemente das ilhas continentais. As ilhas oceânicas podem ser ilhas derivadas a partir de corais ou de atividades vulcânicas (Mueller-Dombois, 2002). A principal diferença biológica entre uma ilha continental e uma ilha oceânica é que ilhas continentais já tem uma diversidade de espécies proveniente do continente da qual a ilha era conectada. Em contraste, as ilhas oceânicas são formadas sem vida e o número de espécies tende a aumentar a uma taxa que irá depender do seu isolamento (Nunn, 2003).

Ambientes insulares diferem entre si principalmente no que tange a formação geológica, a natureza e das fontes renováveis dos recursos. No obstante, em regra as ilhas têm características comuns como tamanho pequeno, limitação de recursos naturais, distância relativa dos continentes, o que pode promover endemismo, vulnerabilidade ecológica e tendência à instabilidade ecológica (Imamura & Towle, 1987; Nunn, 2003; Gillespie, 2007).

A forma, tamanho e geologia das ilhas determinam, em grande parte, as comunidades naturais que se desenvolvem sobre elas (Imamura & Towle, 1987). Elevação e tipo de substrato são os principais determinantes dos tipos de ilhas, e esses dois parâmetros físicos, juntamente com níveis de precipitação, também são determinantes da riqueza florística (Mueller-Dombois, 2002). Mesmo em uma ilha de pequeno tamanho se pode observar diferenças climáticas, inclusive de regimes de pluviosidade, de forma que diversos autores afirmam que em determinadas ilhas, especialmente aquelas com maior gradiente de elevação, podem ser constituídas por diversos “biomas” (Imamura & Towle, 1987; Mueller-Dombois, 2002). Tal conceito pode ser especialmente aplicado às ilhas vulcânicas que, em função de uma maior altitude que lhes é característica, apresentam uma diversidade maior de ambientes, o que reflete na sua maior riqueza florística quando comparadas às ilhas continentais (Imamura & Towle, 1987; Mueller-Dombois, 2002).

Inúmeras ilhas têm passado por alterações e destruição de seus habitats naturais, redução de populações e extinção de espécies nativas, com frequência ocasionadas pela introdução de espécies exóticas de animais e vegetais (Caujape-Castells et al, 2010). Mudanças na densidade populacional de uma espécie podem afetar a disponibilidade de

vários recursos, tais como nutrientes, água, luminosidade e, conseqüentemente, influenciar indiretamente o estabelecimento, crescimento e reprodução de espécies próximas (Tilman, 1986; Callaway e Walker 1997; Gurevitch et al, 2009).

Provavelmente devido ao seu isolamento, espécies nativas e especialmente as endêmicas de ilhas oceânicas são consideradas menos competitivas que espécies de origem continental. De maneira geral, as espécies insulares têm poucas defesas adaptativas e estão mais suscetíveis às mudanças em seus habitats naturais e mais sensíveis a condições estressantes (Brookie et al, 1988; Coblentz 1990).

Em contrapartida, o isolamento das ilhas oceânicas as torna “laboratórios vivos” para compreensão da adaptação e da evolução das espécies, como as faz extremamente vulneráveis a espécies invasoras e outras tensões (Imamura & Towle, 1987; Gillespie, 2007). A instabilidade dos ambientes insulares tem impulsionado estudos de interações entre espécies, focando na competição entre espécies exóticas e espécies nativas (Schofield, 1989; Vila e Muñoz, 1999; Schindler et al, 2016). No que tange ao impacto da introdução de espécies exóticas, a maior parte dos estudos se concentra na perda de biodiversidade, mas os efeitos sobre todo o ambiente, mesmo após a retirada das espécies introduzidas, são de igual importância (Nunn, 2003).

Estudos sobre a biodiversidade e interações entre as espécies nativas e exóticas em resposta a variações climáticas em ilhas também tem ganhado espaço, especialmente aqueles relacionados a ilhas de maior altitude. Estudos como de Arévalo et al (2005) e Birnbaum et al (2015) analisaram interações entre espécies introduzidas e nativas no que tange à distribuição de suas populações em resposta aos gradientes altitudinais. Entretanto há uma lacuna de estudos sobre as interações de espécies nativas a gradientes de estresse em ambientes insulares.

#### Ilha da Trindade

A Ilha da Trindade e o Arquipélago Martin Vaz formam o grupo insular mais afastado da costa brasileira, distante 1.160 km do estado do Espírito Santo. A Ilha da Trindade é parte de uma grande cadeia vulcânica submarina orientada no sentido leste-oeste, conhecido como lineamento Vitória-Trindade (Alves, 1998; Clemente, et al, 2009; Serafini et al, 2010). A Ilha está sob domínio da Marinha do Brasil e possui uma área total de 9,28 km<sup>2</sup>, a parte emersa chega aos 620 m de altitude e sua porção imersa tem profundidade de 5.800 m (Alves, 1998; Serafini et al, 2010). O clima é classificado conforme Koppen como tropical sem estação seca (Af). A temperatura média anual é de 25,3°C (Figura1), sendo os meses de fevereiro e março os mais quentes do ano (27,7 °C) e

o mês de agosto o mais frio (22,9°C) (Pedroso et al, 2017). Quanto a pluviosidade (Figural1), a média anual é de 1476 mm, é maior nos meses de outubro e novembro, com índice de chuvas entre 180 e 215 mm/mês, e menor em janeiro e fevereiro com 64 mm/mês (Pedroso et al, 2017).

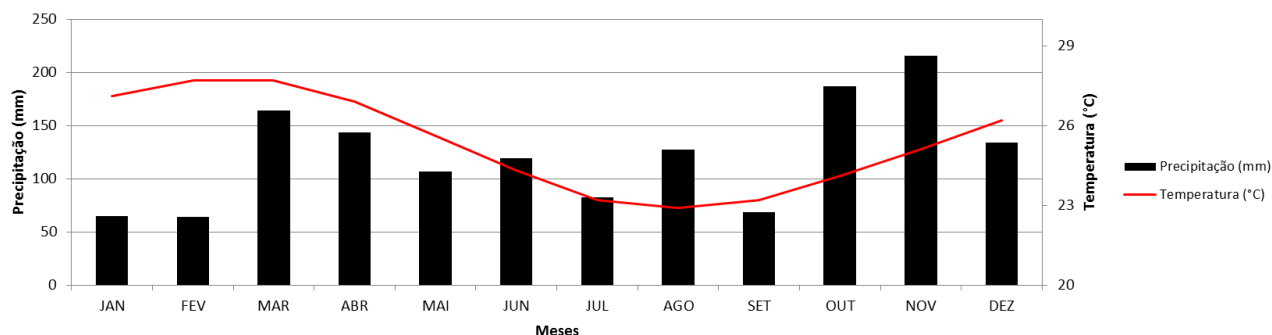


Figure 0-1. Pluviosidade e temperatura média mensal na Ilha da Trindade com base nos anos de 1962 a 2010 fornecidos pelo Banco Nacional de Dados Oceanográficos da Marinha do Brasil

Dentre as ilhas oceânicas brasileiras, Fernando de Noronha e Trindade foram as ilhas que mais sofreram alterações de sua biodiversidade, passando por profundas modificações nas características naturais da sua biota (Serafini et al, 2010).

A história natural da Ilha da Trindade, bem como a descrição de espécies e das mudanças na vegetação durante mais de 200 anos, são relatadas com detalhes por Alves (1998) e Alves e Martins (2006). Um fato marcante é a introdução de animais exóticos em 1770, por Edmund Halley. Relatos dão conta de que Halley ainda pode ver a exuberante floresta que recobria quase toda superfície da ilha, que foi praticamente extinta pela ação de cabras (*Capra hircus*) e exploração madeireira (Lobo, 1918; Alves, 1998; Martins & Alves, 2007; Alves & Silva 2016). Ao menos duas espécies arbóreas constituíam a floresta de Trindade *Colubrina glandulosa* Perkins (Rhamnaceae) e *Paratecoma peroba* (Record & Mell) Kuhl. (Bignoniaceae) (Witovisk, et al 2017). Com a introdução dos animais ocorreu a supressão da vegetação nativa e o desaparecimento de grande parte dos cursos de água que foram observados até o começo do século XX (Lobo, 1918; Barth, 1958; Alves et al, 2011, Silva et al 2013). Com a remoção da cobertura vegetal, o solo também se degradou rapidamente e o processo de erosão se agravou, levando a diminuição do horizonte orgânico (Alves 1998). Em 1994, a Marinha do Brasil começou a empreender esforços para que as cabras fossem retiradas da Ilha, e em em 2004 as últimas cabras puderam ser removidas. A retirada dos animais exóticos possibilitou a regeneração da flora nativa e, concomitantemente, dos cursos de água doce (Martins & Alves, 2007; Alves et al, 2011, Silva & Alves, 2011).



Neste processo de re-vegetação da Ilha, em áreas como o Pico do Desejado, o ponto mais alto da ilha com 620 m de altitude, foram ressurgindo formações compostas por samambaias gigantes (*Cyathea delgadii*) e a arbórea *Sideroxylon obtusifolium* (Roem. & Schult.) T.D. Penn (Barth, 1958; Alves, 1998; Silva & Alves, 2011; Carvalho-Silva et al, 2013). Os demais pontos da ilha passaram a contar com a dominância de espécies herbáceo-arbustivas e tem como espécies mais abundantes *Cyperus atlanticus* e *Bulbostilis nesiotis* (Clemente et al, 2009; Faria et al, 2012).

Apoiado no crescente interesse de pesquisas na Ilha, na sua alta biodiversidade marinha e terrestre e na necessidade de conservação das espécies, foi publicado, em 20 de março de 2018 o Decreto 9.312, que criou a Área de Proteção Ambiental do Arquipélago de Trindade e Martim Vaz e o Monumento Natural das Ilhas de Trindade e Martim Vaz e do Monte Columbia.

### **Interação entre *Guilandina bonduc* e *Cyperus atlanticus***

Mesmo com a existência atual de vegetação recobrando o solo antes desnudo, Alves e colaboradores (2011) identificaram a presença de halos de solo nu, caracterizado pela mortalidade de *Cyperus atlanticus*, ao redor de plantas em vários pontos da Ilha da Trindade. Primeiramente, se verificou a formação desses halos ao redor da espécie exótica *Syzygium cumini* (L.) Skeels. Posteriormente, foi constatada a expansão dos halos mais acentuada ao redor de *Guilandina bonduc* L. (Carvalho-Silva et al, 2013). Destaca-se, no entanto, que observações mais recentes indicaram que no Pico do Desejado as duas espécies (*C. atlanticus* e *G. bonduc*) convivem sem a formação de halos de mortalidade (figura 2.).



Figure 0-2. Halos de mortalidade de *Cyperus atlanticus* ao redor de agrupamentos de *Guilandina bonduc* em vários pontos da Ilha da Trindade. Agrupamentos de *Guilandina bonduc* L. ocorrem na parte interna e populações de *Cyperus atlanticus* Hemsl se distribuem na parte externa.

A leguminosa *Guilandina bonduc* que tem como sinonímia *Guilandina bonducella* L. e *Caesalpinia bonducella*, possui distribuição pantropical e é comum nas ilhas do Atlântico sul. A espécie pode ser dispersa por aves marinhas, como as fragatas, mas também por meio de hidrocoria. Também conhecidas como “*drift seeds*” ou “sementes de deriva”,

sementes de *G. bonduc* têm viabilidade de pelo menos 2 anos e podem flutuar por mais de 30 anos em águas marinhas, o que explica a sua distribuição em praias em várias partes do mundo (Hamann, 1984; Gunn & Dennis, 1999; Perry & Dennis, 2003). O primeiro registro desta espécie em Trindade foi em 1916 (Lobo 1919; Alves 1998). Em Galápagos ela é considerada uma planta invasora, presumidamente introduzida, mas sem relatos de como isso possa ter ocorrido. Nesta ilha a espécie é reportada por causar significativas mudanças ecológicas nas áreas onde se estabeleceu, devido à substituição de comunidades vegetais nativas por um estrato arbustivo monoespecífico (Eckhardt, 1972; Schofield, 1989).

Em Trindade, Alves (1998) e Carvalho-Silva e colaboradores (2013) relatam que *G. bonduc* vinha servindo como alimento a cabras, o que provavelmente manteve suas populações sob controle. A erradicação das cabras provavelmente permitiu que populações de *G. bonduc* voltassem a se proliferar, causando a supressão de populações nativas, como a endêmica *C. atlanticus*.

*Cyperus atlanticus* foi descrita por Hemsley em 1884, como uma espécie endêmica da Ilha da Trindade e Martin Vaz. Relativo a interação das duas espécies, o cenário que se vê atualmente na Ilha é um gradual padrão de invasão por *Guilandina bonduc* de áreas antes ocupadas por populações de *Cyperus atlanticus*.

Este trabalho visa investigar a causa desses padrões distintos e apresenta como hipótese central a disponibilidade de recursos. Tem como escopo ainda, investigar interações entre estas espécies submetidas a gradientes ambientais gerados pela altitude em um ambiente com clima tropical úmido, aparentemente pouco estressante, mas que pode exercer influência significativa na dinâmica da comunidade. Nesse sentido, se contrapõe a maior parte dos estudos sobre interações entre espécies, especialmente os realizados em ambientes insulares, uma vez que estes se concentram em espécies exóticas; e estudos realizados em ambientes não insulares, mas que geralmente, se concentram em locais de condições ambientais bastante estressantes. Finalmente, acredita-se que o entendimento das interações após perturbações pode servir de base para ações futuras de conservação e manejo de ambientes insulares, em particular a Ilha da Trindade.

Visamos à publicação do manuscrito proveniente desse estudo em revistas de qualis A1, como a Oecologia, OIKOS ou Ecology.

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## **From coexistence to competition for water between two native species in a no dry environment: a study case on Trindade Island.**

### **Abstract**

Habitats are spatially and temporally heterogeneous in respect to resources available for plants, different species diverge in their responses to this heterogeneity. In periods or areas of resource scarcity, more tolerant species may become more abundant, suppressing and/or excluding others with which they previously coexisted. Volcanic islands frequently consist of several habitats within a small area, representing an opportunity to verify the interaction between species under different microclimatic regimes. On Trindade Island, a Brazilian volcanic island subjected to a tropical no dry season climate (Koppen Af), differences in the interactions between two native species, *Guilandina bonduc* and *Cyperus atlanticus*, were observed. In that way, the aim of this study was to analyze factors that may influence the interaction between these two species in different types of microhabitat of the island. Water potential, temperature and nutrients of the soil, leaf water potential, specific leaf area and root distribution of both species, and recolonization potential of *C. atlanticus* were investigated in four areas. We found that in areas with higher water availability and milder temperatures the two species coexist, but in areas subjected to more intense water deficit *G. bonduc* suppressed and displaced *C. atlanticus*. All the analyzed sites have large amounts of macro and micro nutrients. The presence of *G. bonduc* decreases the leaf water potential of *C. atlanticus*. The experimental removal of *G. bonduc* stands allowed the Cyperaceae to recolonize, even under the most water restrictive conditions. Thus, in environments with favorable conditions, especially with respect to water availability, the two species coexist. As resources become more limiting the interaction becomes competitive, *G. bonduc* suppresses populations of *C. atlanticus*. Evaluations of interactions among species after disturbances in insular environments are necessary in order to understand the resilience of these and other environments to disturbance events. In addition, it might be used as a basis for the planning of conservation and management actions in these areas.

Key words: plant interaction, water availability, spatial heterogeneity, *Guilandina bonduc*, *Cyperus atlanticus*, volcanic island

## **Introduction**

Coexistence can be understood as the long-term persistence of numerous species within an area. It is one of the most fundamental ecological issues addressed in animal and plant community studies. One way that coexistence can be explained is the different abilities of species to use environmental resources, like water and nutrients (Tilman, 1980, 1988). Plant communities are rarely in balance with resources due to periodic fluctuations in supply (Tilman et al, 1987). Several observational and experimental studies indicate that even though species persist in a region, their relative abundances are subject to oscillations in response to changes in resource-constraining ratios (Tilman et al., 1987; Davis et al., 2000). Changes in resource availability are also caused by weather variations and specific events at sites.

These fluctuations in coexistence may be more pronounced in environments with resource availability pulses, such as the environment with seasonality and well-defined rainfall patterns, as well, in environments with spatial differences in resource availability (Schwinning; Kelly, 2013). In periods or areas of resource scarcity, species more tolerant to eventual stresses might become more abundant, suppressing or even excluding the other species with which they previously coexisted (Davis et al., 2000, Schwinning; Kelly, 2013).

When dealing with resources, it is important to define that a resource is considered limiting when the increased availability of the resources causes an increase in the growth rate of the species (Tilman, 1986). In general, the main classes of limiting resources are nutrients, water, and light (Craine; Dybzinski, 2013). When analyzing the behavior of plants in response to the limitation of these resources, it is crucial to analyze characteristics that might influence the availability of these resources in the environment, such as physical or chemical properties, distribution in space, dynamics of renewal and whether they are distributed along a gradient (Schwinning; Weiner, 1998).

In the last two decades, especially after ‘stress-gradient hypothesis’ (SGH) several researches has been investigate the behavior of species in response to different levels of stress and how this influences the coexistence or balance between competitive and facilitative interactions. One way that the theory might be explained are the interactions between species changing from competition to facilitation with increasing of stress (Bertness and Callaway, 1994). In addition, other researchers, who studied stress levels, support or disagree with the theory (Tielborger & Kadmon, 2000; Pugnaire

& Luque, 2001; Michalet et al., 2006; Maestre et al., 2009; Holmgren et al, 2012; O'Brien et al, 2017).

Water supply is one of the most important limiting factors of plant productivity, playing a key role in the balance between species interactions (Rodriguez-Iturbe et al, 1999; Craine; Dybzinski, 2013; Schwinning; Kelly, 2013). In most ecosystems, water is freely available for short periods of time, with periods that water is partially or completely unavailable (Gurevitch et al, 2009). In addition to the water provided by precipitation, soil characteristics (physical and chemical) and soil depth influence the water availability to plants (Gurevitch et al, 2009). The interaction of roots with soil can also be a determinant. The root system, at certain levels of humidity, can both absorb and redistribute water in the soil, thus affecting water and vegetation dynamics (Scholz et al., 2002; Prieto et al. al, 2012).

The availability of resources, the ability of plants to capture them or tolerate periods of stress are some of the decisive factors for populations to maintain themselves in environments. Plants present in certain habitats have anatomical, morphological and/or physiological characteristics that result in different strategies to persist in such environments (Tilman, 1987; Schwinning; Kelly, 2013). In this way, plants have been evolving with innumerable distinct strategies to deal with heterogeneity and resource fluctuations in environments (Schwinning; Kelly, 2013). In environments with water restrictions, characteristics and strategies such low leaf water content, osmotic adjustment, stomatal control, along with root morphology and anatomy for greater water absorption bring advantages to the species with better competitive ability or higher tolerance to stresses (Nilsen et al., 1983; Schwinning; Kelly, 2013). Better competitive ability and/or greater stress tolerance might be representative characteristics of invasive behavior by some species, which result in the reduction of other populations or even the competitive exclusion of others less resistant to stress (Esquivias et al, 2014). In short, invasive species may have a higher plasticity in responding to environmental changes caused by disturbances (Alpert et al, 2000).

Invasive behavior may occur with both exotic and native species (Alpert et al., 2000; Valéry et al., 2009). An invasive species is defined as that which spreads in space and has negative effects on species that were already present where it occupies (Alpert et al., 2000). In addition, Valéry and collaborators (2009) argue that both native and exotic species that spread in a region can be called invasive, because in both cases the same basic mechanism acts, interspecific competition. Native species are considered

invasive when they increase in abundance due to changes, especially caused by humans, in their natural habitats (Alpert et al., 2000).

### **Insular environments**

Insular environments, especially oceanic islands, are highly susceptible to invasion of exotic species, which leads to interest in research related to interactions between exotic and native species (Brockie et al., 1988; Caujape-Castells et al., 2010). Similarly, studies about native species with invasive behavior have also growing (Shiflett et al, 2014; Thompson et at, 2017). One of the factors that has supported the growth of research on species interactions in insular environments is that the behavior of species can be analyzed in response to different levels of resources within a small area. The difference of microclimatic on Islands is due to the fact that environments are generally geographically isolated, have smaller sizes, when compared to continental environments, and differentiated topography (Imamura & Towle 1987; Groombridge, 1992). Due to the above, even on a small island, climatic differences might be observed, including different rainfall patterns, causing some authors to state that on certain islands, especially those with higher elevations, several biomes might be considered (Mueller-Dombois, 2002).

Elevation, type of substrate and rainfall are quite variable depending on the kind of oceanic island (volcanic or derived from corals) and these factors are also determinants of floristic richness (Mueller-Dombois, 2002). Even islands with high levels of rainfall are not necessarily exempt from water scarcity. The topography and geology of an island largely determine where rain accumulates and how long the water will remain available (Imamura & Towle 1987). Oceanic islands of volcanic origin have higher altitude and may have higher rainfall levels due to the orographic effect, however, this precipitation are concentrated more strongly at the higher elevations, resulting in different water availability throughout the area of the island (Imamura & Towle 1987).

Among the Brazilian oceanic islands, Fernando de Noronha and Trindade were the ones that suffered the most changes in their biodiversity due to human influence, undergoing profound changes in the natural characteristics of their terrestrial biota (Serafini et al, 2010). On the Trindade Island, a volcanic island, about 1200 km from the mainland, changes in soil, native vegetation and creeks were due to the introduction of

exotic animals in 1770, especially goats (*Capra hircus*). Only in 2004, the last goats were eradicated, thus allowing the regeneration of native flora and, concurrently, creeks (Martins & Alves, 2007; Alves et al, 2011, Silva & Alves, 2011).

Trindade Island exhibited at least three types of soil and precipitation is not uniform, being more concentrated on the highest areas where the upper horizons of the soil absorb and store rain water (Alves et al. al., 1998, Clemente et al. 2009). As expected, such conditions result in differences between vegetation on the peaks of the Island when compared to that of the lower parts. These differences point to interaction between the species *Cyperus atlanticus* Hemsl (endemic) and *Guilandina bonduc* L. (pantropical). On its main Peak (Desejado) the species coexist and, at lower parts of the island, *G.bonduc* has expanded, apparently leading to the suppression of populations of *C. atlanticus*.

The aim of this study is to understand the interactions between an endemic and a pantropical species, in locations of different abiotic characteristics and stress levels. In addition, this study, on Trindade Island, can represent a greater understanding about resilience of these and other environments to disturbance events.

### **Hypotheses:**

1. The populations dynamics of *Guilandina bonduc* and *Cyperus atlanticus* is correlated to the rainfall pattern on Trindade Island. NOS HALOS
2. The peculiar topography might leads to both different abiotic conditions, on different locations of the Island and interactions among the species are affected by abiotic factors.
3. The mortality of *C. atlanticus* is related to the presence of the *Guilandina bonduc*.

### **Materials and Methods**

#### Study area

The study was conducted on Trindade Island (20°29'32 "S / 29°17'21" W), which along with the Martin Vaz Archipelago form the insular group farthest from the Brazilian coast, 1,160 km off of the shore of the state of Espírito Santo. Trindade Island has a total area of 9.28 km<sup>2</sup>. The emerged part has a height of 620 m and its immersed portion a depth of 5,800 m. Its climate is tropical no dry season (Koppen Af) having an average annual temperature of 25.3 °C (Pedroso et al, 2017). Characteristic of places

with this climatic pattern, rainfall well distributed throughout the year. The average annual rainfall is 1476 mm, with the months of October and November having higher monthly rainfall, between 180 and 215 mm/month, and less rainfall, January and February with 64 mm of rain/month (data based on the years 1961 to 2010 provided by the National Oceanographic Data Bank of the Brazilian Navy).

Nearly 5% of the plant composition corresponds to forest vegetation, which occurs almost exclusively on the top of the Island, herbaceous-shrub vegetation composes the rest of the cover, with *Cyperus atlanticus* and *Bulbostilis nesiotis* Hemsl being the most predominant species (Alves, 1998, Clemente et al. al, 2009).

### Study Species

The suppression of populations of the endemic *C. atlanticus* was observed due to the expansion of the exotic *Syzygium cumini* (L.) Skeels, by Alves et al. (2011). The most pronounced suppression occurred in response to the expansion of native shrub *G. bonduc* (Carvalho-Silva et al, 2013). Usually, the *Guilandina* populations are found in circular formation surrounded by bare soil, previously occupied by Cyperaceae populations. This formation, in this study is entitled halo. In more recent personal observations, it has been observed that in Desejado Peak, at 604 m altitude, both species (*C. atlanticus* and *G. bonduc*) coexist without the formation of halos.

### *Cyperus atlanticus*

It is a species endemic of Trindade Island and Martin Vaz, described by Hemsley in 1884, being the main specie in the communities of the lower sites on the Island. It is an herbaceous plant, a perennial, with terminal inflorescence, rhizomatous, C4 with Kranz anatomy of the Chlorociperoid type (Alves 1998). In Brazil, there are 653 species of Cyperaceae, of which 181 are endemic. The family has representatives in all six Brazilian biomes. The genus *Cyperus* is the second most abundant, having representatives in diverse habitats that include forests, high plains, wetlands, savannas, sandy areas and lagoons (Alves et al. 2009; Arruda & Neves 2005; Martins et al. 2007, 2008; Leite et al. 2009). On Trindade Island, the principal way of reproduction is by seeds.

### *Guilandina bonduc*

The first record of the species on Trindade Island was in 1916 (Lobo 1919, Alves 1998). It is a woody species, C3. *Guilandina bonducella* L. is synonymous with *Caesalpinia bonducella*, having a pantropical distribution. It is common in the islands

of the South Atlantic. It can be dispersed by seabirds, such as frigates or by sea currents, referred to as having "drift seeds", and may float for more than 30 years, having a viability of at least two years, with physical dormancy (Hamann, 1984; Gunn & Dennis, 1999; Perry and Dennis, 2003; Hessou et al 2009). On Trindade Island, the most common reproduction is asexual by resprouting.

### **Methodology**

The experiment was conducted from June 2013 to February 2016, during 10 expeditions ranging from periods from two days up to three months of permanence on the Island. In order to understand the mechanisms of interaction between the *G.bonduc* shrub and the endemic *C. atlanticus*, measurements were taken of the expansion and retraction of populations of both species. Abiotic parameters that may influence interaction in different locations of the Island was also measured, along with functional characteristics of the leaves and of root distribution of both species and also experiments of removal of the shrub.

### **Dynamics of halos**

In order to verify whether the shrub was actually expanding and suppressing the populations of *C. atlanticus*, 10 representative halos were measured. From these halos the perimeter of the inner circles (surface covered by *G.bonduc*) and external (the bare surface that it was covered by individuals of *C. atlanticus*) of the halos were measured. Measurements were made by marking points, every two meters, in the GPS (global positioning system) (60CSx Garmin<sup>®</sup>). Having such information made it possible to calculate the area in square meters, using the free software EasyGps<sup>®</sup> for geographic information system.

The measurements were made between July 2013 and December 2015 and divided into four intervals: July/13 to April/14, May/14 to October/14, November/14 to June/15 and July/15 to Dec/15. These measures were compared to cumulative rainfall of each period ranging from 325 to 724 mm.

### **Experimental Design**

At different locations on the island (figure 1-2) different levels of interaction between the species can be verified. Thus, the area where the species interacted was divided into four levels: Null invasion (NULL) 20°30'41" S – 29°19'28,8" W (604 m), where there is no mortality of *Cyperus*; Initial (INI) 20°31'9,71" S – 29°18'12,14" W (60 m), with well-defined halos; Intermediate (INT) 20°30'52,45" S – 29°18'36,65" W



(103 m), where halos begin to interconnect, and Advanced (ADV) 20°30'46,57" S – 29°18'35,08" W (75 m), where there are few populations of *Cyperus*, according to figure 1-1. In the areas covered by *Guilandina* (GUI), by *Cyperus* (CYP) and uncovered soil previously occupied by the populations of *Cyperus* (BARE SOIL), representative halos were selected and sampled.

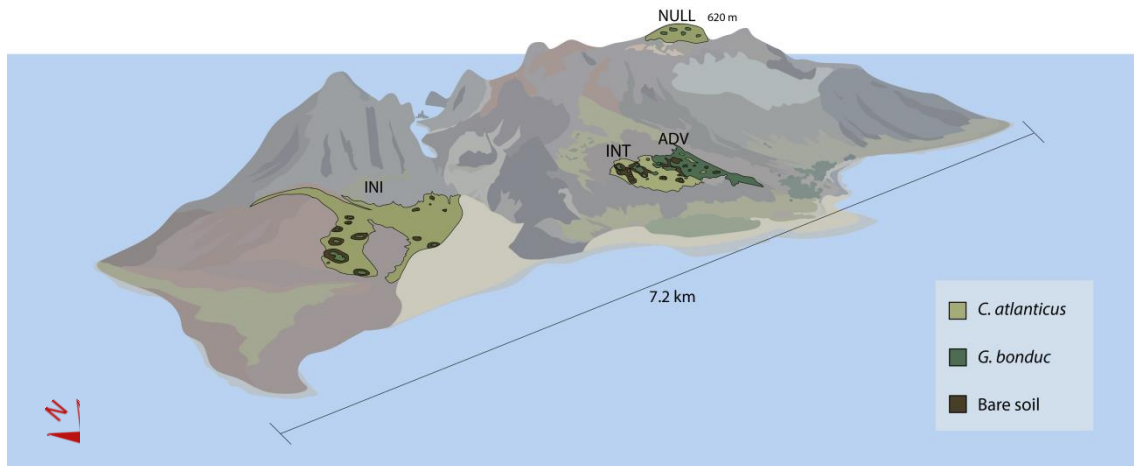


Figure 1-1. Scheme of Trindade Island showing the four areas studied: Null, where there is no mortality of *Cyperus*; Initial (INI), with well-defined halos; Intermediate (INT), where halos begin to interconnect, and Advanced (ADV) where there are few populations of *Cyperus*.

### Abiotic conditions of study area

#### Water potential ( $\psi^{ws}$ ) and temperature of soil

For the purpose of verifying whether microclimatic differences of the areas interfere in the interaction between the species, during three months, soil water potential and soil temperature were measured in the different areas.

The measurements were made between the months of December 2015 and February 2016. At each of the areas these measurements of soil water potential and temperature were made in three different soil coverages (*Guilandina*, *Cyperus* and bare soil). These measurements were made at 4 different times of the day, 9:00 am; noon; 2:30 pm and at midnight at two different depths: 4-5 cm and 9-10 cm. Eight repetitions to each area were made. Temperature measurements were made using the geothermometer Incoterm<sup>®</sup>. For measurements of  $\psi^{ws}$  two replicates were made for each sampling. The soil collected was stored in hermetically sealed capsules and transported in a thermal box to the laboratory of the scientific station where the  $\psi^{ws}$  measurements were made by the WP4C Decagon Water Potential Meter.

### Nutrients

In order to analyze the physical characteristics of the soil, soil pH and nutrients were measured from samples collected in the areas subjected to different levels of invasiveness. Soil samples were collected within sites of monospecific populations of each species, and where bare soil previously covered by Cyperaceae.

At each site four soil samples were collected, between 0 and 10 cm of depth. The four samples were joined in a mixed sample. These samples were sent to a specialized company to analyze physical characteristics, macro and micronutrients, pH and organic matter. Were used the protocol of Mehlich (1953) to extract P, K, Na, Zn, Fe, Mn and Cu, to S were used mono-calcium-phosphate, to B were used hot water and to the colorimetric determination to organic matter.

### Biotic responses of species

Species may have different biotic responses according to the stress level they are under and to the species they must interact with. Therefore, we measured different biotic responses including the leaf water potential of both species, the specific leaf area (SLA), and the distribution of roots of the species at different levels of invasion.

#### Leaf water potential ( $\psi^{wl}$ )

To investigate a strategy that could possibly confer tolerance to water stress to species, leaf water potential of both monospecific populations of species were measured and compared. In addition, to inquire whether the presence of *G.bonduc* interferes with *C. atlanticus*, comparisons of leaf water potential of monospecific populations of *Cyperus* were made along with *Cyperus* populations having interference of *Guilandina* in each of four different invasion areas.

Four samples of mature leaves were carried out during the months of December 2015 and February 2016. The samples were done during two periods of the day, at noon and midnight and for each sample, four replicates were measured. To measurements of *G. bonduc* were used leaflets and to *C. atlanticus* were used parts of leaves. Collected leaves were stored in hermetically sealed capsules and transported inside a thermal box to the laboratory of the Trindade Island Scientific Station, where measurements of  $\psi^{wl}$  were made with a Water Potential Meter (WP4C - Decagon). Each measurement was taken in approximately three minutes.

#### Specific leaf area (SLA)

To obtain the specific leaf area, 11 leaflets of *G.bonduc* were collected from the populations of representative halos on each of the four invasion areas. The leaflets were

fully unfolded and photographed and using the Image J<sup>®</sup> free program, their area was obtained. After that, the leaflets were dried at 50°C for 72 h to obtain the dry biomass. The ratio of leaflets area and dry biomass was calculated, representing the specific leaf area.

#### Root distribution

Concerning root distribution, this response was verified in all areas of invasion. Soil samples were collected with cylindrical metal tubes (40 cm length and 10 cm diameter). Four soil samples were collected from within the monospecific species populations (*G. bonduc* and *C. atlanticus*) in addition to that of bare soil previously taken from Cyperaceae (bare soil).

Each sample was subdivided into sub-samples 10 cm long. The soil was sieved and all the roots from the *Guilandina* or *Cyperus* were identified. The roots were dried at 50 °C for 72 h to obtain the dry biomass.

#### Removal experiment

To verify the potential of recolonization by *C. atlanticus*, and whether the presence of *G. bonduc* is determinant of this, we experimentally removed *G. bonduc* shrub populations.

Considering that at “Null” areas, the interactions between species were not resulting in the suppression of *C. atlanticus*, this area was not included in this experiment. In the other areas, two representative halos were selected, of which the entire aerial part of *G. bonduc* was removed in November 2014.

Six and 12 months after removal, measurements of area (m<sup>2</sup>) were made in locations previously without vegetation or covered by *Guilandina* to determine the potential of revegetation by Cyperaceae. In addition, in areas where *Guilandina* populations regrown measurements of coverage were made.

#### Statistical analysis

For all the statistical analyses the statistical software RStudio<sup>®</sup> version.1.0.136 was used (Packages car, lsmeans, lme4, multcomp).

The period of water potential sampling coincided with a non-normal period of rainfall, with almost 270 mm in January, the month in which most of the samples were collected. This irregular index of rain caused many soil samples to reach their saturation point with values of  $\psi^{wS}$  equal to 0. As a result, we had an inflation of zeros and it was necessary to use hurdle models for the statistical analysis, where the analysis was

divided in two models, a binomial model and a continuous model (Zuur et al, 2009; Zuur & Ieno, 2016).

The first model consisted of analyzing the probability of events of soil water-saturated, occurring in the different areas, coverage, and depths used as independent variables. For this, a binomial linear generalized mixed model (GLMM) was used, classifying the response variable ( $\psi^{wS}$ ) in: zero, the value that represents the water-saturated soils; and any other value than zero, which was considered unsaturated soil, being transformed to 1.

In the second model, the objective was to verify the water stress intensity in the same areas, coverage and depths as those used in the previous model, however, zero values that were saturated soil were removed. Thus, the values of  $\psi^{wS}$ , different of zero, were used in a generalized linear mixed model (GLMM) with the continuous data  $\log_{10}$  transformed.

In both models, the different days and times of sampling, as well as replicates were used as random variables. The selection of models, from the model filled with all interactions was done by AIC and the post hoc test used was Tukey. The significance value used was 5%.

For the temperature data, the aim was to analyze the differences between Areas, Coverage, and Depths. For that, a generalized linear mixed model (GLMM) was used with continuous data, which consisted of temperature values  $\log_{10}$  transformed. Similarly, for the  $\psi^{wS}$  models, the variables days and sampling times were used at random and the selection of models was done by AIC. The post hoc test used was Tukey (5%).

For the analysis of leaf water potential, mixed linear generalized models (GLMM) were used. Leaf water potential was used as continuous response variable while the different areas, the different sampling times and the types of soil cover were categorical independent variables. The replicates and repetitions of the samplings were used as random variables. The selection of the best model from the full model was done by AIC.

Even though samples were taken at all areas and soil cover patterns, not all sites and areas reached the desired depths (40 cm). Most of the samples did not reach more than 20 cm, when cylindrical tube found rocks. Then, it did not have sufficient variability for to run statistical analysis.

For SLA analysis, ANOVA was used. The different areas were used as non-dependent variables and the transformed log of index values of specific leaf area were used as the response variable, with post hoc test being Tukey (5%).

For the analysis of the *G.bonduc* removal experiment, the transformed log of measurements of the areas (m<sup>2</sup>) of cover by the legume and the bare soil (GUI and BARE SOIL) were considered the continuous response variable. For analysis, GLMM was used with the interactions between Invasion (INI, INT, ADV), Coverage (GUI and BARE SOIL) and cut time (Before, 6 mth and 12 mth). The best model was chosen by AIC and the post hoc test was Tukey (5%).

### Results

We found that the expansion and retraction of populations of both species coincided with the cumulative rainfall of each period (Figure 1-2).

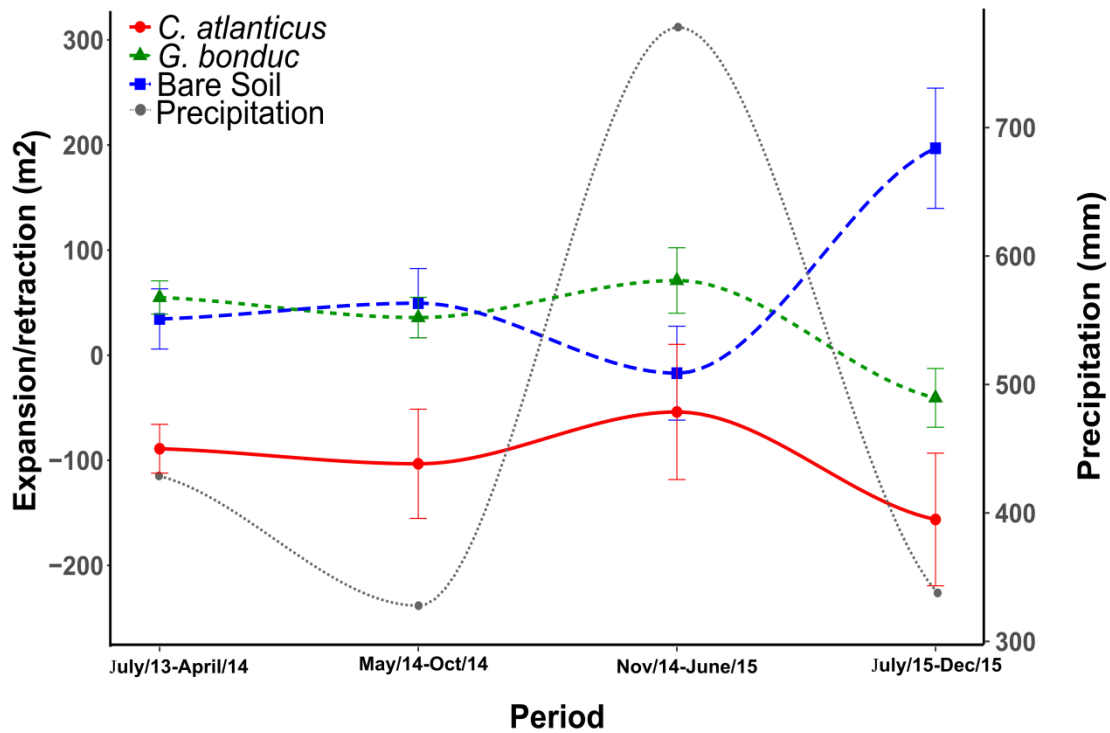


Figure 1-2. Expansion /retraction (m<sup>2</sup>) of populations of *Guilandina bonduc* L., *Cyperus atlanticus* Hemsl and bare soil, in four periods and cumulative rainfall (mm) in the same periods.

The fluctuations in the populations of both species are strongly related to the accumulated rainfall in the periods analyzed. *Guilandina* showed just no expansion of its populations in the fourth period in which there was low rainfall preceded by the highest rainfall regime. Similarly, in the last period analyzed, *Cyperus* had the greatest decrease of its populations, however, in contrast with *Guilandina*, the species suffered suppression at all the periods, being the smaller loss in response to the highest index of

rain. This constant suppression, independent of water availability, suggests that the permanence of the *Cyperus* populations in the analyzed areas may be strongly linked to the presence of *Guilandina*.

The expansion of bare soil area is inversely related to the level of rainfall. In all other periods except for third, areas without vegetation cover expanded. In third period analyzed, there was a slight retraction of the bare soil area.

When were analyzed the decrease in coverage of Cyperaceae populations during all periods of the study period it exceeds 3,000 m<sup>2</sup> considering 10 halos.

Microclimatic factors mediating the interaction between species

Water potential and temperature soil

Table 1. Independent variables which were chosen by the Akaike criterion for the binomial and continuous model of water potential ( $\psi^{ws}$ ) and soil temperature, based on a general model considering the variables: area, coverage, depth and the interaction between them. Significant results were by analysis of variance for variables and interactions selected for each model (\*\*0.001, \*\*0.01, \*0.05).

$\psi^{ws}$	
Binomial model – probability of stress	
Variables	P
Area (NULL, INI, INT, ADV)	< 2.2e-16 ***
Coverage (CYP, GUI, BARE SOIL)	2.761e-08 ***
Depth (5, 10 cm)	0.0184 *
$\psi^{ws}$	
Continuous model – intensity of stress	
Variables	P
Area (NULL, INI, INT, ADV)	< 2.2e-16 ***
Coverage (CYP, GUI, BARE SOIL)	1.588e-06 ***
Depth (5, 10 cm)	< 2.2e-16 ***
Area: Coverage	3.568e-14 ***
Depth: Coverage	0.001299 **
Temperature	
Continuous model	
Variables	P
Area (NULL, INI, INT, ADV)	< 2.2e-16 ***
Coverage (CYP, GUI, BARE SOIL)	< 2.2e-16 ***
Depth (5, 10 cm)	1.261e-12 ***
Area: Coverage	< 2.2e-16 ***
Depth: Coverage	0.00288 **

From a general model that considered the independent variables, ‘Area’, ‘Coverage’, ‘Depth’ and interaction between variables, the selection of the best model of the explanatory variables was generated by AICc according to table 1.

For the binomial model, the significant variables were ‘Area’, ‘Coverage’ and ‘Depth’. No interaction between the variables was found. For the continuous models of  $\psi^{ws}$  and soil temperature the explanatory variables were ‘Area’, ‘Coverage’ and ‘Depth’ and there was interaction between ‘Area’ and ‘Coverage’ in addition to ‘Depth’ and ‘Coverage’.

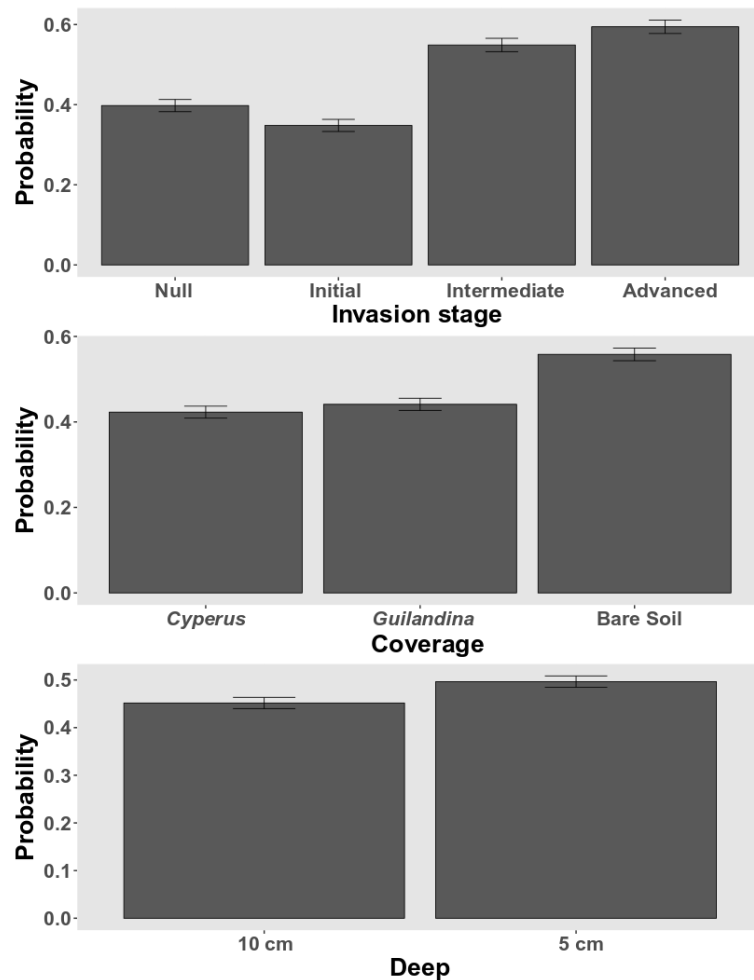


Figure 1-3. Probability of soil being non-water saturated in the different Areas - Null, where there is no mortality of *Cyperus*; Initial, with well-defined halos; Intermediate, where halos begin to interconnect, and Advanced where there are few populations of *Cyperus*; Soil Coverages: *Guilandina*, *Cyperus* and Bare soil, previously occupied by the populations of *Cyperus*; and depths 10 cm and 5 cm. Larger values represent greater probabilities of the non-water saturated happens.

For the binomial model for  $\psi^{ws}$ , the probability of the presence or absence of soil saturation was analyzed. Regarding the different areas, it was evident that the highest probability of soil saturation occurred in the Initial Invasion followed by the Null Invasion. The Advanced and Intermediate invasions are the least probable for occurrence of saturation, respectively, however they are not statistically different from each other (Figure 1-3).

As expected, bare soil presents the greatest chance of no occurrence of soil saturation. Both types of vegetation cover (*Guilandina* or *Cyperus*) are equally as effective in maintaining soil moisture, and the two differ from uncovered soil. When analyzing the depths, there is a statistical difference between 10 and 5 cm, with a lower chance of saturation occurrence at 5 cm (Figure 1-3).

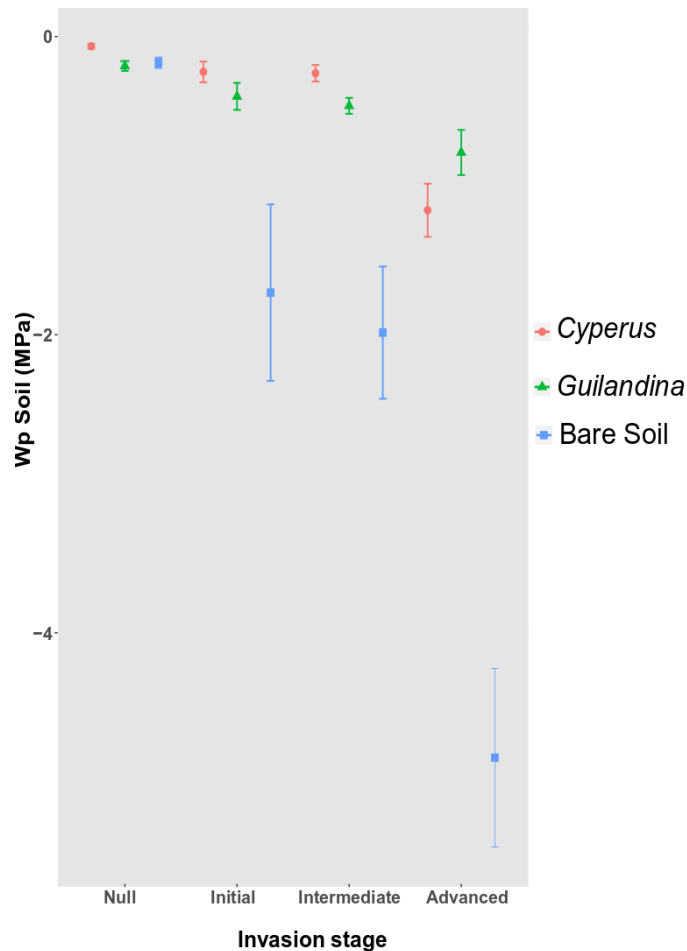


Figure 1-4. Average of soil water potential (MPa) showing the intensity of water stress in the different Areas: Null, where there is no mortality of *Cyperus*; Initial, with well-defined halos; Intermediate, where halos begin to interconnect, and Advanced where there are few populations of *Cyperus*; and Soil coverage by *Guilandina*, *Cyperus* and the Bare soil, uncovered areas previously occupied by the populations of *Cyperus*.

When analyzing differences in intensity, considering the interaction between areas and coverage, it can be seen that, regardless of the soil cover or the bare soil in comparison with those of more covered areas, the Null invasion presents the least intensity of stress. It is the only area where the  $\psi^{ws}$  of bare soil does not differ statistically from the vegetation cover, being close to the water-saturated point (0 MPa). Stress events become more severe as *Guilandina* invasion progresses, with more extreme water potentials appearing in Advanced Invasion (Figure 1-4).



In general, soil cover by *Cyperus* mostly avoids the loss of soil water. Considering all of the different soil covers (*Cyperus*, *Guilandina* and Bare soil), each one differs from the other. When there is an interaction between ‘Coverage’ and the ‘Area’ variables, *Guilandina* coverage is only more effective in Advanced invasion, because in this area the remaining populations of *Cyperus* are not dense enough, which decreases the effectiveness in maintaining moisture. The uncovered soils are those with the most negative potentials and the most stressful values are observed in the Advanced invasion area with an average of -4 Mpa (Figure 1-4).

The other interaction that explains the values of water potentials is that between different sites and depth. Soil covered by *Cyperus* or *Guilandina* do not differ statistically when compared at the same depths. However, the coverage of the two species differ from bare soil at 5 cm. Finally, at 10 cm only *Cyperus* covered soil differs from the soil without vegetation coverage (table 1).

Temperature

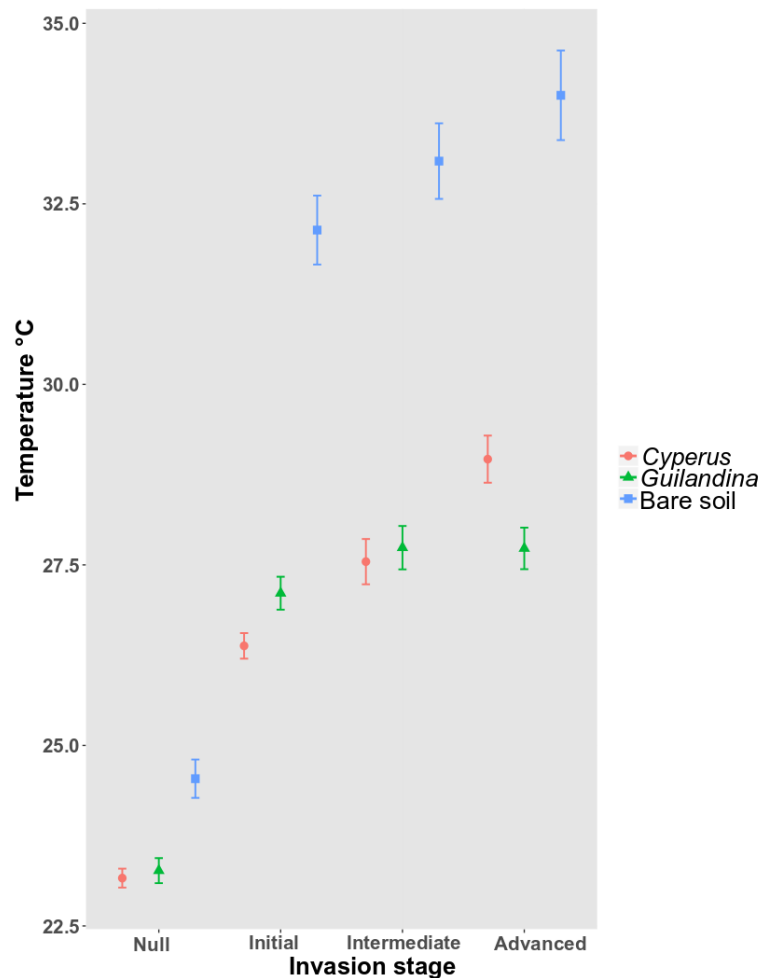


Figure 1-5. Average soil temperature (°C) in the different Areas: Null, where there is no mortality of *Cyperus*; Initial, with well-defined halos; Intermediate, where halos begin to interconnect, and Advanced

where there are few populations of *Cyperus*; and Soil coverage by *Guilandina*, *Cyperus* and the Bare soil, uncovered areas previously occupied by the populations of *Cyperus*.

With regard to temperature, the variables and the related interactions were the same as those selected for the water potential intensity model (Table 1). In this way, the NULL soil presented higher temperatures differing statistically from soil covered by both *Cyperus* and *Guilandina* (Figure 1-5).

With the exception of the Advanced invasion area, there was no significant difference when considering the effectiveness of the soil coverage by either of the species. As the result of water potential, at the most extreme level of invasion, *G. bonduc* was more effective than *C. atlanticus*, since the populations of Cyperaceae are less dense (Figure 1-5).

In the interaction between depth and coverage independent of depth, the temperatures of the soil covered by *Cyperus* did not differ from those covered by *Guilandina*, both of which differed from bare soil at all depths. Differences between the depths were only found in bare soil.

#### Soil characteristics

In general, all areas had high macronutrient values, and high total cation-exchange capacity (CEC) values, ranging from 26.1 to 43.6 cmolc/dm<sup>3</sup>. The values for the percent of base saturation, of H + Al at Desejado Peak, ranged from 81 to 89%, in contrast to the other areas for which this value was between 8 and 22%. Such values influence the values by base saturation of soil (BS) that in Null invasion is the lower value, from 11 to 15%, while in other areas this variation was from 78 to 92%. The pHs (in CaCl<sub>2</sub>) of soils on Desejado Peak were more acidic than other soils, varying from 3.8 to 5, values of which are classified as highly and very highly acidic. Values for other areas were between 5.6 and 6.5, considered low and very low acidity values. The most acidic values of most samples occurred in soil covered by *Guilandina* (Appendix).

#### Leaf water potential ( $\psi^{wl}$ )

The general model considered the independent variables, Area: Null, Initial, Intermediate and Advanced; Locations: *C. atlanticus* without influence of *Guilandina*, and under its influence, *G. bonduc* monospecific populations, the Period of the day: noon (Day) or midnight (Night) and the interaction between them. From this model, the selection of the best model containing the explanatory variables was generated by AIC according to table 2.

Table 2. Independent variables chosen by the Akaike criterion for analysis of the variable leaf water potential response ( $\psi_w$ ), from a general model considering the variables: Area, Location, Period of the day, and the interaction between them. Significance results were found by analysis of variance for variables and interactions selected for each model (\*\*\*0.001, \*\*0.01, \*0.05)

$\Psi_1$	
Comparisons between <i>Cyperus</i> with and without <i>Guilandina</i> Influence	
Variables	<i>P</i>
Location ( <i>Cyperus</i> no influenced and <i>Cyperus</i> with <i>Guilandina</i> )	1.807e-10 ***
Period (Day and Night)	3.051e-07 ***
Area:Location	0.01846 *
Period:Location	0.04234 *
$\Psi_1$	
Comparisons between <i>Cyperus</i> and <i>Guilandina</i> monospecific stands	
Variables	<i>P</i>
Area (Null, Initial, Intermediate and Advanced)	0.01282 *
Location ( <i>Cyperus</i> and <i>Guilandina</i> )	< 2.2e-16 ***
Period (Day e Night)	2.023e-07 ***
Area:Location	0.01460 *
Area: Period	0.01046 *

The general model considered the independent variables, Area: Null, Initial, Intermediate and Advanced; Locations: *C. atlanticus* without influence of *Guilandina*, and under its influence, *G. bonduc* monospecific populations, the Period of the day: noon (Day) or midnight (Night) and the interaction between them. From this model, the selection of the best model containing the explanatory variables was generated by AIC according to table 2.

The first model compared the leaf water potential of *C. atlanticus* populations under the influence of *G. bonduc* with that of monospecific populations without *Guilandina* influence. For this model, the explanatory variables chosen were the different Locations (*Cyperus* no influenced and *Cyperus* with *Guilandina*), Periods

(Day and Night) and the interactions between Area (Null, Initial, Intermediate and Advanced) and ‘Locations’ in addition to ‘Periods’ and ‘Locations’ (Table 2).

The second model compared the leaf water potential of monospecific populations of *C. atlanticus* and *G. bonduc*. In this model the explanatory variables selected were ‘Locations’ (*Cyperus* and *Guilandina* populations), ‘Periods’ (Day and Night), the ‘Areas’ (Null, Initial, Intermediate and Advanced) and the interactions between ‘Areas’ and ‘Locations’ along with ‘Areas’ and ‘Periods’ (Table 2).

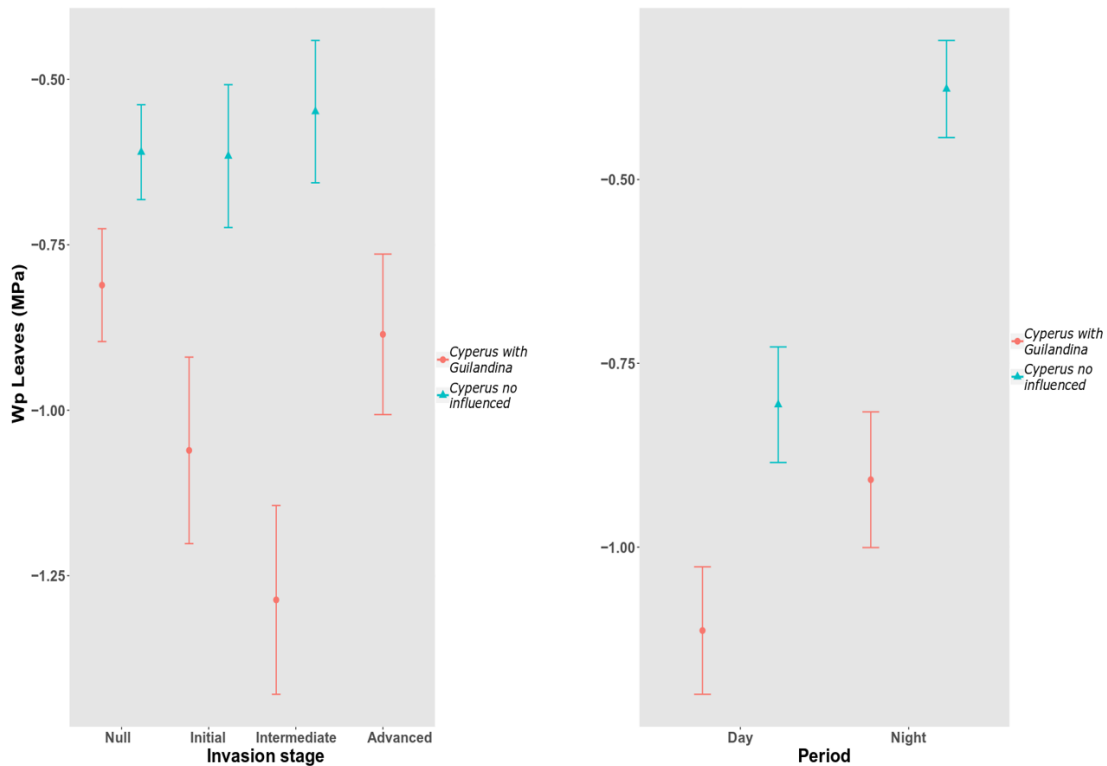


Figure 1-6. A) Average of leaves water potential (MPa) *Cyperus atlanticus* without *Guilandina bonduc* interference and *Cyperus* under *Guilandina* interference collected in areas: Areas: Null, where there is no mortality of *Cyperus*; Initial, with well-defined halos; Intermediate, where halos begin to interconnect, and Advanced, where there are few populations of *Cyperus*. We do not have *Cyperus* no influenced values in the Advanced because all the populations are already under the influence of *G. bonduc*.

In comparing the different populations of *C. atlanticus*, the variable 'Area' is not enough to influence leaf water potential, but when the different locations are also taken into account, significant changes can be seen in leaf water potential. On the other hand, ‘Locations’ and ‘Periods’ were variables that affected leaf water potential, both independently and interacting with other variables.

When analyzing the effect of ‘Areas’ and ‘Locations’ on leaf water potential, the populations of *C. atlanticus* under the influence of *G. bonduc* presented water potentials more negative than populations without such influence, independent of the ‘Area’ considered. This shows that the presence of *G. bonduc* causes additional stress to the Cyperaceae. Leaf water potentials measured during the day were always more negative than those measured at night (Figure 1-6A).

Regarding the interaction between the ‘Locations’ and ‘Periods’ (figure 1-6B), both *Cyperus* populations had the most negative potentials during at noon. Leaves collected from populations of *C. atlanticus* under the influence of *G. bonduc* had the most negative potentials. This difference was even more pronounced at night when *Cyperus* no influenced leaves had a  $\psi^{wl}$  of nearly zero. At night the leaves under the influence of the *Guilandina* show a  $\psi^{wl}$  statistically equal *Cyperus* no influenced presented by in the noon. This suggests that the presence of *Guilandina* conferred additional stress to the populations of *Cyperus*, compared to the stress that the climatic factors of the hours of higher daily temperatures confer (noon).

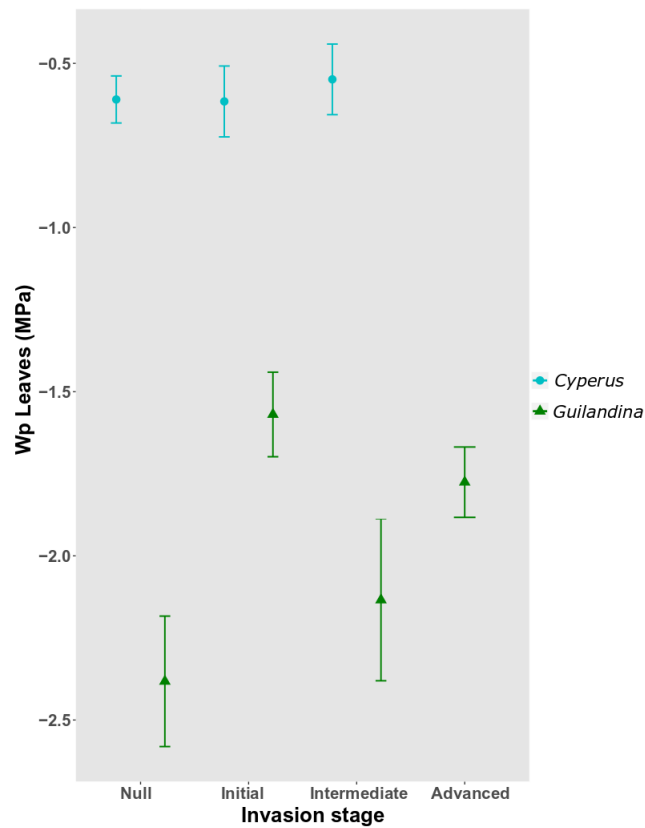


Figure 1-7. Average of leaves water potential (MPa) monospecific populations of *Cyperus atlanticus* and *Guilandina bonduc* collected in areas Areas: Null, where there is no mortality of *Cyperus*; Initial, with

well-defined halos; Intermediate, where halos begin to interconnect, and Advanced, where there are few populations of *Cyperus*. We do not have *Cyperus* no influenced values in the Advanced because all the populations are already under the influence of *G. bonduc*.

The second comparison made is between leaves of monospecific populations of both *Cyperus* and *Guilandina*. In this analysis, the largest differences are between species. Regardless of the areas or times of *Guilandina* sampling, its leaf water potential is significantly more negative than those of the Cyperaceae. While the  $\psi^{wl}$ s of *Cyperus* had less variation, are closer to zero and are independent of the areas in which the leaves were collected, the leaves of *Guilandina* presented potentials always below -1 MPa, with variations between the areas, and with the most negative potential being at the null level of invasion (Figure 1-7).

### Specific Leaf Area

Regarding the specific leaf Area (SLA) of *G. bonduc* in the four areas, there was no statistical difference between any of them (Appendix).

### Distribution of Roots

Table 3. Presence (X) or absence of roots of *Guilandina bonduc* and *Cyperus atlanticus* in soil with coverage of species (CYP or GUI) or without coverage (BARE SOIL) in different areas Null, Initial, Intermediate and Advanced invasions.

	Presence of roots of <i>G. bonduc</i>			Presence of roots of <i>C. atlanticus</i>		
	CYP	GUI	BARE	CYP	GUI	BARE
<b>Null</b>	X	X	X	X		X
<b>Initial</b>		X	X	X		
<b>Intermediate</b>		X	X	X		
<b>Advanced</b>	X	X	X	X		

Roots of *G. bonduc* were found in samples collected in all areas where it was present, as expected, but also in areas of bare soil and in areas dominated by *C. atlanticus* (table 3). These overlaps between *G. bonduc* roots and *C. atlanticus* occurred in particular in the ‘Null’ and in ‘Advanced’ areas. In the ‘Null’ invasion, however, the two species coexist, while in Advanced invasion, the presence of roots of *G. bonduc* suggests that this species is advancing over populations of *C. atlanticus* and causing its mortality (table 3).

The roots of *Cyperus*, were not found in any of the areas with *Guilandina* populations, except at bare soil in the ‘Null’ area, where both species coexist, reinforcing the predicted pattern of coexistence of the two species (table 3).

Regarding the biomass of the species, this factor was only analyzed at the depth of 10 cm, since the only samples that reached 40 cm were the ‘Null’ and ‘Initial invasion’ areas. In the other areas, most of the samples reached only the first depth.

As expected for both species the largest amount of roots was found below each species own population. Conversely, the lowest values for root biomass for both species occurred in the ‘Null invasion’. This may be due to the fact that the species have more depth so that the roots can penetrate or because there is more biodiversity in the area.

### Experimental Removal

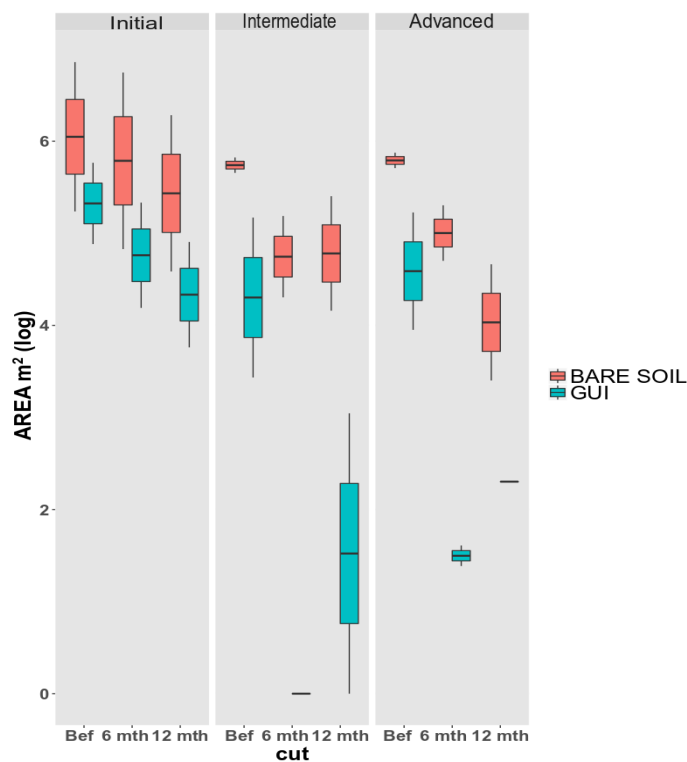


Figure 1-8. Measurements of bare soil and *Guilandina bonduc* populations before the removal and six and 12 months after the removal in the areas (INI), where there are well defined halos; (INT), where halos begin to interconnect, and Advanced (ADV) where there are few populations of *Cyperus atlanticus*.

Considering the variables of the general model, the explanatory variables according to the AIC were the different ‘Areas’ (INI, INT, ADV), the types of coverage (GUI and BARE SOIL) and time of removal (Before, 6 mth and 12 mth). Interactions of

this model were found between the 'Areas' and 'Coverage' in addition to 'Coverage' and 'Time of management'.

It should be emphasized that the decrease of the areas of bare soil after the removal of *Guilandina* populations results mostly from revegetation of these bare areas by the Cyperaceae. After the experimental removal of *G. bonduc* stands, only in the Initial invasion a consistent regrowth of their populations was observed, with several *G. bonduc* populations returning as fast as 6 months later. This return apparently led to a decrease of the bare soil which was not so expressive in the other areas (Figure 1-8). In the other areas, populations of *G. bonduc* returned slower, this allowed the establishment of populations of *Cyperus* over previously bare areas. In the Advanced invasion even after 12 months after the removal of *G. bonduc* the bare soils continued to decrease due to the expansion of *C. atlanticus*.

## **Discussion**

The present study focused on the suppression of a species in response to the population increase of a second one, both native, not including facilitation effects. The results showed that water stress gradient might be managing the interactions between the species at different portions of the Island. So far, our data reveals a relationship to the stress-gradient and interaction between *G. bonduc* and *C. atlanticus*.

The temperature and rainfall of Trindade Island can be categorized as a tropical ocean climate, characterized by well distributed rains during the year, without longer periods of drought. Even though the average annual rainfall is high (~ 1400 mm), the topography characteristics of Trindade Island support the significant differences found in the abiotic characteristics, mainly affecting soil water potential. At the macro level, considering the rainfall on the Island, the populations of the species in the present study vary in response to the amount of rain accumulated in each period (Figure 1-1). In microclimatic terms, a gradual increase of soil water stress and temperatures was verified, from the areas where the species coexist (Desejado Peack), to the areas where *G. bonduc* suppressed *C. atlanticus*. The later areas the plant populations showed more critical water potentials and higher soil temperatures. Supporting our data of higher water availability at Desejado Peak is the presence of greater floristic biodiversity and soil with more organic matter. The greater soil depths, found on Desejado Peak (Null),



when added to the greater amount of clay can also be favorable to the maintenance of soil humidity at highest parts.

In contrast, regarding nutrients, although very high CEC values were observed in all study areas, but the saturation by bases  $H^+$  and  $Al^{+3}$  in Null invasion may lead to the leaching other important bases such as  $K^+$ ,  $Na^+$ ,  $Ca^{++}$  and  $Mg^{++}$  which becomes not available for the plants (Ronquim, 2010). Another factor that influences the leaching of these cations is the acidity of the pH. Most acidic soils were found in Null invasion. As base saturation values below 50% indicate poor soils (Ronquim, 2010), the values found at the Peak (between 11 to 15%), indicated a poor soil in nutrients in this area. The soils of the other areas were less acidic with values of base saturation ranging from 78 to 92%, presenting high soil nutrient availability for the plants. When water potential decreases, soil impedance and amount of  $O_2$  increase, causing the flow of water (and dissolved nutrients) to the roots to decrease. Even if the soil contains adequate amounts of nutrients, without a suitable supply of water, they are not mobilized into the plants (Chapman et al, 2012). Despite high nutrient levels in almost all areas of the Island, they appear to be more available in areas other than 'Null', different from that found for soil moisture. Apparently, even with a low availability of nutrients in the Peak, these resources combined with great water availability are sufficient for the two species to coexist.

Even though the role of nutrients cannot be ignored, the *G. bonduc* invasion pattern and consequent suppression of Cyperaceae responds to the water stress gradient. Under less restrictive soil moisture conditions and milder temperatures, such as the conditions on the Desejado peak, the two species coexist. At the other extreme, in the area under advanced invasion, where the most negative soil water potentials and the highest temperatures were recorded, stands of *G. bonduc* suppress and outcompete populations of *C. atlanticus*. Considering a greater suppression of *Cyperus* populations with increasing stress conditions, the results contradict the reported 'stress-gradient hypothesis' (SGH), which in short, relates the increase of positive interactions with increased stress (Bertness and Callaway, 1994). Nevertheless, studies of refinement of this theory that demonstrate a variation in the responses depending on the level of stress, and considering that in extreme cases, the competition gains space and overcomes facilitation (Michalet, 2006; et al., 2009, Holmgren & Scheffer, 2010). The studies in which these responses were reported were mostly done in arid or semi-arid environments with a well-defined seasonality (eg Holzapfel et al., 2006; Michalet et al.,

2015; O'Brien et al., 2017; Pugnaire & Luque, 2001), in opposite of the climate of Trindade. Moreover, He & Bertness (2014) argue that the best evidence for the SGH has come from habitats with strong, potentially lethal stress gradients. They affirm that exceptions to the SGH often occur when analyzed weak stress gradients, or there is no limiting stresses environments. A strong seasonality condition does not occur on Trindade Island, with well distributed rainfall year round and no prolonged periods of drought. Even that the Island has different water supplies, on different locations, there are almost daily rains, it does not lead to environment with strong water stress. Then, it is possible that it is the way of SGH no works on our study.

According to the results found in our study, the efficiency of soil cover by the two species studied is evident, showing to be effective in microclimatic improvement affecting soil moisture and temperatures (figure 1-4 and 5). Comparing the interaction between two species, at high levels of stress, shading effects are considered to be an important facilitator effect between plants (Franco and Nobel, 1989; Holmgren & Scheffer, 2010). This facilitation process might be overcome, making space for competition, particularly in arid environments where the canopy may intercept the little rain that would be available to sub-canopy species. The net result of this interaction between species would be competition, in this case in the roots, because little water is available in the soil (Holmgren & Scheffer, 2010). However, in the present study microclimatic improvement by the shading of one species by another is not visually verified. Even in Desejado Peak (Null) where the species coexist, *G. bonduc* was found in monospecific populations at almost the same height of the populations of *C. atlanticus*. In other areas where the species do not coexist and even compete, this microclimatic amelioration could only be intra-specific because the populations were spatially separated by an extension of bare soil. In contrast to previous studies showing that water competition would be the predominant interaction in arid or semi-arid environments, this study found competition in a mesic environment.

When considering biotic characteristics of the species, the differences in leaf water potential for *C. atlanticus* under the influence of *G. bonduc* and populations without influence are compared. We found that the presence of the *G. bonduc* may represent an additional stress to the establishment of the Cyperaceae. This effect seems to be an indirect effect, since the leaves of *Cyperus* that were considered to be under influence of *Guilandina* were collected close to the halos, having the most negative values of  $\psi^{ws}$  (Bare Soil) in comparisons to leaves from populations far from *G. bonduc*.

It is important to mention that soil water availability influences in other biotic responses such as root plasticity, and mass flow (Chapman et al, 2012). However, a representative response of supply of soil water is leaf water potential, being considered by as a driving force for the movement of water through the plant (Jarvis, 1976). The lack of soil cover and the competition for water with roots of *Guilandina* may be inducing *Cyperus* to decrease its leaf water potential as a mechanism for absorption of water in the soil. Although, the differences in the areas under increasing influence of *G. bonduc* are not an explanatory variable for the decreasing of the leaf water potential of *C. atlanticus* (table 2). This is also an indication that the factor that might be definitive for the maintenance or not of *C. atlanticus* populations is the presence and, probably, competitive influence, of *G. bonduc*. In addition to this, at a macro level, in the Island, the decrease of *Cyperus* populations coverage is observed, independent of the water availability by rainfall (figure 1-1), indicating that the area covered by the endemic *C. atlanticus* might be strongly affected by the presence of *Guilandina*.

Our study showed that the leaf water potentials of *G. bonduc* were always lower than those of *C. atlanticus*, both during the day or at night, when individuals were in monospecific stands. The maintenance of the leaf potential of turgor, maintaining a low water content in the leaf at higher water deficits is a strategy for maintaining conductance and consequently growth, as verified for *Prosopis glandulosa* var. *torreyana* in the Sonoran Desert (Nilsen et al., 1983). Differences of the specific leaf area of *Guilandina* could not be found independent of the areas analyzed (Appendix). It showed that the species kept growing, and the low water potential of *Guilandina* leaves might be an important access contributing to the competitive performance showed by *G. bonduc*.

In the underground, we found roots of both species sharing the same area only in the two extremes, in the Desejado peak where they coexist, and in the advanced invasion, where *G. bonduc* roots go through the bare soil and reach the *Cyperus* populations. The presence of *Guilandina* roots in all bare soil sampled suggests that *Guilandina* expands initially belowground due its high capability for water absorption. When *G. bonduc* roots reach those soils sheltered by *C. atlanticus* populations, the higher soil water availability (figure 1-4) might promote higher growth due to its higher competitive capacity (figure 1-7). This process may be corroborated by the lower leaf water potential of individuals of *Cyperus* whenever it is in the presence of roots of *Guilandina* (figura 6 A-B).

The spread of *Guilandina* roots belowground allows the expansion of its populations and leads to the mortality of *C. atlanticus* and possibly other species. Petry (2015) tested the exudate and aqueous extract of *G. bonduc* roots on lettuce and radish growth, both increased the growth of the target plants compared to the control. Thus, it indicates that the interaction between *G. bonduc* and *C. atlanticus* probably is not allelopathic being representative of root competition. The interaction between woody and herbaceous plants is investigated, including the patterns of root distribution and water abstraction. The roots of shrubs have deeper access to the soil, which aims to explore a greater volume of water (Nilsen et al., 1983). However, Soyza and collaborators (1996), while analyzing the different sizes and depths at which the shrubs of *Prosopis glandulosa* use soil water, found that both large and small shrubs preferably access water from the superficial layers of the soil. Moreover, Pugnaire & Luque (2001) found that root competition between *Retama sphaerocarpa* and sub-canopy species was more intense in areas with higher stress. Furthermore, Callaway et al. (1991) found that interactions between *Quercus douglasii* and sub-canopy grasses depended on the root architecture of trees. Trees with high root biomass in the upper layers of the soil had stronger negative effects on the biomass of the understorey, a niche overlap causing root competition. Even though *C. atlanticus* it is not a grass, its root architecture accesses more superficial soils than the roots of *G. bonduc*. Even with this difference, when the roots were collected, we found that the areas of strongest suppression of *Cyperus* were in more shallow soils. Only in the Null invasion and Initial invasion areas showed all samples reaching 40 cm of depthless. This might be an indication that the two species are using water from the surface layers of the soil, areas of greater competition for resources by plants.

To address further the interactions between these two species, we conducted an experiment removing entire stands of *G. bonduc*. In all areas where the legume was removed, *C. atlanticus* returned, covering areas where the soil was covered by *Guilandina*. This included areas of advanced invasion, where the soil water potentials were found to be lowest and soil temperatures were the highest, indicating that these abiotic stresses were not so determining of *C. atlanticus* presence, and that the specie present a good tolerance to drought. Another study where two species of the *Cyperus* genus, *Cyperus brevifolius* (Rottb.) and *Cyperus kyllingia* Endl., were analyzed in different soil water regimes, showed the species were affected by water stress, but both maintained moderate growth, productivity and reproductive capacity even at soils with

of soil moisture as low as 14% (Rodiyati et al, 2005). *Cyperus atlanticus* was the species with the greatest expansion during the revegetation of an area degraded by goats, showing a great potential for recolonization (Martins & Alves, 2007). Thus, it seems that in areas of less water availability the greatest threat to this species is the presence of the *G. bonduc*.

Despite the fact that *Cyperus* has good tolerance to drought, *G. bonduc* seems to be a better competitor irrespective the stress level (figura ). On the Galapagos, *Guilandina*, presumably introduced, is considered an invasive plant and was reported to cause significant ecological changes by displacing native plant communities (Eckhardt, 1972; Schofield, 1989). It seems that *Guilandina* even presumably native of Trindade Island shows an invasive behavior. Another native shrub, *Morella cerifera* L., has expanded more than 400% in the last 50 years on Hog Island by moving into native pastures. The populations of the shrub changed the microclimate, and it has functional traits that allow for the maintenance of high photosynthetic and hydraulic efficiency, which are associated with the expansion of woody species (Thompson, et al 2017; Shiflett et al., 2014). Another example of native competitive shrub was showed by *Retama monosperma* (L.) Boiss, upon an endemic specie, *Thymus carnosus* Boiss (Esquivias et al. 2014). Such as *Guilandina*, the authors verified that the *R. monosperma* is well adapted to fluctuations in the rainfall. If an invasive species is defined as that which spreads in space and has negative effects on species that were already present where it occupies (Alpert et al., 2000). Thus, even though a native species in the Trindade Island, *G. bonduc* showed an aggressive invasive behavior outcompeting other native species growing on the surrounded areas of this species monospecific stands.

In short, we were able to verify the behavior of both species in microclimatic conditions that support the coexistence between both, and in other less favorable abiotic conditions that lead to competitive interactions that lead to suppression and causing the competitive exclusion of the species that showed less competitive ability. Species are able to respond to the heterogeneity of environments which they are exposed (Tilman, 1999). In addition, the performance of species into owns populations are very different from that when submitted to interactions with other species (Tilman, 1999). Supporting this idea, we verified that the permanence of a species in a habitat depends on the biotic and abiotic factors to which they are subjected. Trindade Island, even having a small area, presents abiotic variations, characterized by different microclimates that may govern the interactions between species. Furthermore, the possibility of what is

happening as a natural process of succession might not be excluded. However, in the areas where populations of *Guilandina* have expanded, the establishment of other species has not been verified. The changes of microclimatic that the shrub *M. cerifera* promoted provided own expansion across the Barrier Island (Thompson, et al 2017; Shiflett et al., 2014). Such as its, *Guilandina* might be using the same strategy and the microclimatic amelioration would be favoring only its own population's growth.

In conclusion, the present study showed a clear tolerance of *Cyperus atlanticus* to drought, however, our results also showed that *C. atlantics* has lower competitive abilities than *G. bonduc*. In water stress conditions, *Guilandina bonduc* showed greater competitive abilities, leading to out-competition and exclusion of *C. atlanticus* populations. The main limiting factor seems to be soil water availability. Even in an environment with almost daily rains, without a dry season, species might be subject to water competition, leading to the suppression of the species with lower competitive ability. This study showed that the increase of the populations of *G. bonduc* leads to decrease of the populations of *C. atlanticus* and increase of areas of bare soil. *C. atlanticus* is an endemic specie that has shown crucial importance in the process of revegetation of the Island. The areas with no vegetation cover are propense of erosion processes. This erosion process is quite pronounced on the Island. In events of storms, the erosive process is especially evident when there is a significant loss of soil. The soil is carried to the sea which prejudices the corals and marine life. Evaluations of interactions among species after disturbances in insular environments are necessary in order to understand the resilience of these and other environments to disturbance events. In addition, they serve as a basis for the planning of conservation and management actions in these areas.

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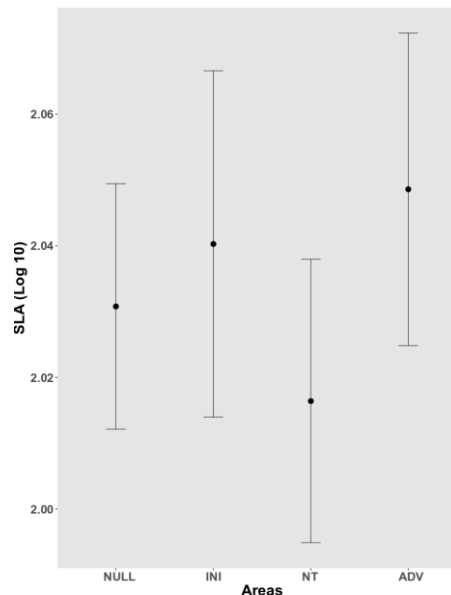
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## Appendix

Chemical and physical characteristics of the soil sampled in different areas Null, Initial, Intermediate and Advanced invasions, on locations of soil with coverage of *Cyperus atlanticus* or *Guilandina bonduc*, and without coverage.

	Null			Initial			Intermediate			Advanced		
	<i>Cyperus</i>	<i>Guilandina</i>	Bare Soil	<i>Cyperus</i>	<i>Guilandina</i>	Bare Soil	<i>Cyperus</i>	<i>Guilandina</i>	Bare Soil	<i>Cyperus</i>	<i>Guilandina</i>	Bare Soil
<b>Macronutrients</b>												
pH (CaCl <sub>2</sub> )	5	3,8	4,7	6,5	5,9	5,6	6,3	6	6,2	5,9	6	6,2
M.O (dag/Kg)	21,9	8,4	12,2	4,4	4,6	2,6	4,6	2,6	3,1	4,4	4,6	3,3
C org Total (%)	12,7	4,8	7,1	2,6	2,7	1,5	2,7	1,5	1,8	2,6	2,7	1,9
P (mg/dm <sup>3</sup> )	155,3	147,6	135,4	42,5	35,8	40,7	246,2	495,3	200,5	188,2	171,8	207,7
K (mg/dm <sup>3</sup> )	164,7	234	191,1	444	487	354	267	278	240	378	389	288
S (mg/dm <sup>3</sup> )	8	6,1	6,4	5,5	5,4	3,3	5,8	3,6	4	5,6	4,2	4,3
Ca (cmolc/dm <sup>3</sup> )	5,1	2,4	3,2	9,2	11,4	9,4	11,4	9,3	11,8	12,8	13,1	13,6
Mg (cmolc/dm <sup>3</sup> )	2,6	1,3	2	14,5	15,4	12,3	14,5	18,6	21,3	13,6	13,8	13,7
Al (cmolc/dm <sup>3</sup> )	1,1	2,7	2,6	0	0	0	0	0	0	0	0	0
H+Al (cmolc/dm <sup>3</sup> )	35,5	33,2	31,8	4,8	4,6	2,5	4	2,5	4,1	7,8	6,4	6,3
N total (%)	0,651	0,455	0,532	0,259	0,287	<0,05	0,217	0,028	0,091	0,175	<0,05	0,133
CTCt (cmolc/dm <sup>3</sup> )	43,6	37,5	37,5	29,6	32,6	26,1	30,6	31,1	37,8	35,2	34,3	34,4
V (%)	19	11	15	84	86	90	87	92	89	78	81	82
<b>Relationships</b>												
Ca/Mg	2	1,8	1,6	0,6	0,7	0,7	0,8	0,5	0,6	0,9	0,9	1
Ca/K	12,1	4	6,5	8,1	9,1	10,3	16,8	13,1	19,3	13,2	13,2	18,4
Mg/K	6,2	2,2	4,1	12,7	12,3	14,6	21,3	26,2	34,9	14	13,9	18,5
<b>Base saturation</b>												
K (%)	1	2	1	4	4	3	2	2	2	3	3	2
Ca (%)	12	6	9	31	35	36	37	30	31	36	38	40
Mg (%)	6	3	5	49	47	51	47	60	56	39	40	40
Na (%)	0	0	0	0	0	0	0	0	0	0	0	0
H + Al (%)	81	89	85	16	14	10	14	8	11	22	19	18
<b>Micronutrients</b>												
B (mg/dm <sup>3</sup> )	2	1,1	1,3	2	1,7	0,7	1,1	0,6	1	1,4	1	1,7
Zn (mg/dm <sup>3</sup> )	0,6	0,6	0,5	1,8	1,5	0,2	0,2	0,3	0,2	7,7	7,5	7,5
Fe (mg/dm <sup>3</sup> )	317,6	282,3	342,6	49,4	88,8	40,6	19	18,1	20,8	43,4	28,1	21,8
Mn (mg/dm <sup>3</sup> )	10,7	5,7	6,2	23	34,5	16,8	42,7	8,6	27,2	60,8	45,5	41,2
Cu (mg/dm <sup>3</sup> )	0,2	0,4	0,2	0,4	0,4	0,5	0,1	0,1	0,1	0,4	0,5	0,5
<b>Physical analysis</b>												
SILT (%)	55	51	60	54	56	21	40	27	43	50	49	48
CLAY (%)	30	26	26	18	20	6	20	16	26	34	35	38
SAND (%)	15	23	14	28	24	73	40	57	31	16	16	14



Specific leaf Area (SLA) of *Guilandina bonduc* in the four areas Null, Initial, Intermediate and Advanced invasions

## Conclusão geral

De uma maneira geral ambientes insulares são mais suscetíveis a invasões, pois as espécies nativas de ilhas, em sua maioria, não desenvolveram mecanismos de defesa contra aquelas que não são nativas desses ambientes. Mesmo pequenos impactos podem levar a grandes desequilíbrios no ambiente natural. Historicamente em muitas ilhas a introdução de animais exóticos levou a profundas modificações da flora nativa, com extinções de espécies vegetais e animais. Devido a essa vulnerabilidade, muitas ilhas no mundo são áreas protegidas, na forma de unidades de conservação. Seguindo essa tendência, o governo brasileiro publicou, em 20 de março de 2018, o decreto número 9.312 que criou a Área de Proteção Ambiental do Arquipélago de Trindade e Martim Vaz e o Monumento Natural das Ilhas de Trindade, Martim Vaz e do Monte Columbia, a fim de preservar a biota remanescente do ecossistema insular, os recursos naturais e a biodiversidade marinha.

A Ilha da Trindade é um exemplo de profunda degradação do ambiente natural ocasionado pela introdução de animais exóticos. Desequilíbrios entre espécies são percebidos ainda hoje, mesmo 15 anos após a retirada desses animais. É razoável considerar que a atual expansão das populações de *Guilandina bonduc* pode ter sido em decorrência da dispersão de suas sementes pelas cabras, resultando no notável aumento na sua área de abrangência.

Como visto no presente trabalho, o aumento das populações de *G. bonduc* leva a diminuição das populações de *Cyperus atlanticus* e aumento de áreas de solo sem cobertura vegetal. *C. atlanticus*, por sua vez, é uma espécie endêmica de crucial importância no processo de revegetação da Ilha. Foi possível constatar diferenças na disponibilidade de água no solo em diferentes partes da Ilha e, conforme proposto, a interação das espécies responde a esse gradiente de hídrico. Apenas no Pico do Desejado, área com maior disponibilidade hídrica no solo e temperaturas mais amenas as duas espécies coexistem. Evidenciou-se, assim, a relação entre escassez de água no solo e a supressão de *C. atlanticus* por *G. bonduc*, o que adicionalmente seria ocasionado pela maior capacidade da *G. bonduc* em captar água, com consequente exclusão competitiva da endêmica.

Em suma, as distintas condições abióticas presentes na Ilha da Trindade, propiciaram o estudo de interações entre duas espécies ao longo de gradientes de

ambientais. Em outras palavras, conseguimos verificar a existência de gradientes de disponibilidade de água no solo, e que esses regem a interação entre as espécies estudadas. Em ambiente com restrição hídrica, a estabilidade das populações de *C. atlanticus* depende da ausência de *G. bonduc*, reafirmando o papel da água como um dos principais fatores determinantes na estruturação das comunidades. Ainda, conseguimos constatar que mesmo em um ambiente com chuvas quase diárias, sem uma estação de seca, as espécies podem estar sujeitas a competição hídrica, onde espécies com menor habilidade competitiva acabam tendo suas populações significativamente suprimidas.

As áreas onde anteriormente estavam as populações de *Cyperus* acabam ficando descobertas, o que aumenta os processos de erosão que já são bastante pronunciados na Ilha. Em eventos de chuvas fortes o processo erosivo fica especialmente evidente quando o solo, das áreas sem cobertura vegetal, é carreado para o mar pelas chuvas, o que prejudica também os corais e a vida marinha.

Ainda que haja supressão das populações da *C. atlanticus* não se pode afirmar que exista perigo de extinção da espécie pela ação da *G. bonduc*. Primeiramente porque nas áreas com maior disponibilidade hídrica as espécies coexistem. Ainda, a Cyperaceae é a espécie com maior cobertura vegetal da Ilha e em vários locais ela ocorre sem estar em contato com a leguminosa. E finalmente, a espécie tem apresentado bom potencial de revegetação, comprovado pelos experimentos de retirada de *G. bonduc*. por meio dos quais, verificou-se que mesmo na área de maior restrição hídrica houve retorno das populações de *Cyperus*.

Por fim, o manejo de *G. bonduc* deve ser considerado com cautela, pois a essa espécie é nativa e mesmo que sua dispersão possa ter sido aumentada pelas cabras o processo de interferência de uma espécie na outra pode ser um processo de sucessão natural. Entretanto, nas áreas que estão sendo ocupadas por *G. bonduc*, o que pode ser constatado é um estrato praticamente monoespecífico dominado pela espécie. Mesmo sendo verificada a melhora microclimática nas áreas cobertas por *Guilandina*, a presença dessa não parece estar favorecendo o estabelecimento de outras espécies, até o momento, visualmente não há uma maior diversidade nos locais. Isso posto, antes de qualquer ação, considera-se adequada a realização de experimentos de manejo com monitoramento de longo prazo.

Esse estudo reforça a importância de avaliações de interações entre espécies, especialmente no que tange a disponibilidade hídrica. E assim, permite aumentar a

compreensão acerca da resiliência de ambientes a distúrbios, servindo de base para ações de conservação e manejo de espécies.