

Camila Luisa Bernhardt Demeda

**BIOLOGIA REPRODUTIVA DE *ELEOCHARIS  
LAEVIGLUMIS* R. TREVIS. & BOLDRINI  
(CYPERACEAE) E  
FENOLOGIA DE *FUIRENA ROBUSTA* KUNTH  
(CYPERACEAE)**

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Orientador: Prof. Dr. Rafael Trevisan  
Coorientador: Dr. Guilherme Dubal  
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“Eu não vi o mar.  
Não sei se o mar é bonito,  
não sei se ele é bravo.  
O mar não me importa.

Eu vi a lagoa.  
A lagoa, sim.  
A lagoa é grande  
e calma também.

Na chuva de cores  
da tarde que explode  
a lagoa brilha  
a lagoa se pinta  
de todas as cores.  
Eu não vi o mar.  
Eu vi a lagoa...”

Carlos Drummond de Andrade, 1930



## RESUMO

*Eleocharis laeviglumis* e *Fuirena robusta* são macrófitas aquáticas emergentes bem representadas em áreas úmidas da costa sul brasileira. Ambas espécies reproduzem-se tanto vegetativamente quanto por sementes, mas a dinâmica reprodutiva das mesmas ainda não é conhecida. O estudo das duas espécies foi baseado em populações de uma lagoa costeira de água doce em Florianópolis, SC, Brasil. Marcamos e acompanhamos colmos de ambas espécies no período reprodutivo para determinar as etapas fenológicas da reprodução sexual, assim como estimamos a produção de flores e frutos. Testamos a germinabilidade e vigor de sementes de *E. laeviglumis* durante os quatro meses da estação reprodutiva. Realizamos observações fenológicas de *F. robusta* durante um ano, por meio de parcelas fixas divididas em dois transectos. Descrevemos os padrões fenológicos por índices de atividade e intensidade e os testamos quanto à sazonalidade por meio da estatística circular. Construímos modelos plausíveis, com variáveis ambientais, explicando as fenofases sazonais. Os modelos foram testados e selecionados por AIC. Ambas espécies são dicógamas e protóginas, com a seguinte produção de flores e frutos: *E. laeviglumis*: 57 flores e 36 frutos por espigueta; *F. robusta*: 207 espiguetas por colmo, 17,5 flores e 16 frutos por espigueta. Colmos reprodutivos de *E. laeviglumis* desenvolvem-se em média em 34 dias (pré-antese: 1,7d.; antese: 6,9d.; maturação de frutos: 22,3d.; dispersão de frutos: 3,2d.) enquanto que colmos reprodutivos de *F. robusta* desenvolvem-se em média em 63 dias (pré-antese: 9d.; antese: 20,3d.; maturação de frutos: 19,8d.; dispersão de frutos: 13,9d.). *E. laeviglumis* possui baixa germinabilidade (5,5%) e vigor de sementes (22,8%), sendo que a germinação e sua respectiva velocidade diminuiu com o passar da estação reprodutiva. Sugerimos que para possível uso da espécie para manejo de áreas úmidas, a propagação seja feita por sementes coletadas no início da estação reprodutiva em combinação com transplante de rizomas. Para *F. robusta*, somente as fenofases reprodutivas apresentaram-se como sazonais, sendo que dados de atividade e intensidade apresentaram resultados semelhantes. Encontramos diferença entre os dois transectos amostrados, a qual atribuímos a diferentes condições de vento. A floração foi explicada pelo fotoperíodo, pH e condutividade, o que sugere que *F. robusta* utiliza nutrientes da água para seu desenvolvimento. Possivelmente por ser uma espécie anemófila, a antese foi explicada pelo vento e por temperaturas máximas, que auxilia

no desenvolvimento das plantas. Para maturação e dispersão de frutos não encontramos modelos significativos. Indicamos *F. robusta* como uma boa candidata para manejo de áreas úmidas da costa sul brasileira.

**Palavras-chave:** Macrófitas aquáticas. Lagoas costeiras. Fenologia.

## ABSTRACT

*Eleocharis laeviglumis* and *Fuirena robusta* are emergent aquatic macrophytes well represented in Brazilian southern coast wetlands. Both species reproduce vegetatively and through seeds, but reproductive dynamics are still unknown. This study was based on populations of a freshwater coastal lake in Florianópolis, SC, Brazil. We marked and observed culms of both species during reproduction to determine phenological stages of sexual reproduction, as much as we estimated flower and fruit production. We tested *E. laeviglumis* seeds for germinability and vigor during the four months of the reproductive season. We performed *F. robusta* phenological observations during a year, by means of permanent quadrats divided into two transects. We described phenological patterns through activity and intensity indexes and tested them as to seasonality using circular statistics. We constructed plausible models, with environmental variables, explaining the seasonal phenophases. Models were tested and selected through AIC. Both species are dichogamous and protogynous, with the following flower and fruit production: *E. laeviglumis*: 57 flowers and 36 fruits per spikelet; *F. robusta*: 207 spikelets per culm, 17.5 flowers and 16 fruits per spikelet. *E. laeviglumis*' reproductive culms develop on average in 34 days (pre-anthesis: 1.7d.; anthesis: 6.9 d.; fruit maturation: 22.3 d.; fruit dispersion: 3.2 d.), while *F. robusta*'s reproductive culms develop on average in 63 days (pre-anthesis: 9d.; anthesis: 20.3 d.; fruit maturation: 19.8 d.; fruit dispersion: 13.9 d.). *E. laeviglumis* has low germinability (5.5%) and vigor of seeds (22.8%), being that germination and respective speed reduced with the passing of the reproductive season. We suggest that for possible use in wetlands management, the species should be propagated by combining sowing seeds collected in the beginning of the reproductive season, with rhizome transplantation. To *F. robusta*, only the reproductive phenophases were seasonal, being that activity and intensity data showed similar results. We found difference between the two transects which we attributed to different wind conditions. Flowering was explained by daylength, pH and conductivity, what suggests *F. robusta* uses water nutrients to develop. For being an anemophilous species, anthesis was explained by wind and high temperatures, what benefits plant development. For fruit maturation and dispersion we did not find any significant model. We indicate *F. robusta* as a good candidate for wetlands management in the southern Brazilian coast.

**Keywords:** Aquatic macrophytes. Coastal lakes. Phenology.

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## 1 INTRODUÇÃO GERAL

Macrófitas aquáticas compreendem um grupo artificial de plantas que toleram os mais diversos ambientes, desde úmidos até verdadeiramente aquáticos, tanto lênticos quanto lóticos, salinos, salobros ou de água doce (Thomaz & Esteves 2011). Em lagoas de água doce representam a porção mais produtiva e diversificada (Chambers et al. 2008), o que garante a estruturação e funcionamento do ecossistema (Thomaz & Estevez 2011). Possuem a capacidade de absorver nutrientes e outras substâncias da água, com potencial para utilização no tratamento de águas residuais (Dhote & Dixit 2009), e em alguns casos, podem se apresentar como invasoras (Chambers et al. 2008).

Apresentam alta diversidade em ambientes de água doce (Cook et al. 1974), sendo muito representativas em lagoas costeiras (Ferreira et al. 2017), que constituem habitats frágeis e biodiversos (Esteves et al. 2008). Alterações na composição dessas comunidades podem alterar a relação biótica entre espécies e em circunstâncias extremas, causar a extinção das mesmas (Thomaz & Estevez 2011).

No Brasil, a preservação desses corpos hídricos é teoricamente garantida pela Constituição Federal de 1988 (artigo 225, § 4º), que considera toda Zona Costeira, incluindo a Ilha de Santa Catarina, como patrimônio nacional (Brasil 1988), porém lagoas costeiras neotropicais estão entre os ambientes mais impactados do mundo (Esteves et al. 2008). Por exemplo, a Lagoa Pequena em Florianópolis, tombada como Patrimônio Natural e Paisagístico do Município (Florianópolis 1988), possui 77 espécies distribuídas em 31 famílias botânicas (Ferreira et al. 2017), porém sofre com diferentes impactos antrópicos (Pippi 2004, Geri 2007). Ecossistemas aquáticos impactados frequentemente necessitam de alguma forma de manejo, sendo as macrófitas utilizadas para reestabelecer comunidades de plantas nativas (Brown & Bedford 1997, Nienhuis et al. 2002, Hözel & Otte 2003, Nishihiro & Washitani 2007).

Dentre a diversidade macrofítica em habitats de água doce, Cyperaceae apresenta-se como a família mais diversa (Chambers et al. 2008), formando densas comunidades em lagoas costeiras do Sul do Brasil (Irgang & Gastal 1996, Ferreira et al. 2017). Cyperaceae é também considerada a terceira maior família de monocotiledôneas do mundo, compreendendo cerca de 5500 espécies e 109 gêneros (Govaerts

et al. 2007). De ampla distribuição e maior diversidade concentrada na região tropical, compreende espécies herbáceas, de aspecto graminóide e tamanhos variados. Em geral possuem folhas com bainha fechada, flores pequenas e discretas reunidas em espiguetas, e frutos do tipo aquênio (Goetghebeur 1998).

Diversos gêneros e espécies da família, em sua maioria de plantas emersas, são associados a habitats úmidos ou verdadeiramente aquáticos (23 gêneros citados por Cook et al. 1974), sendo no Brasil, os gêneros *Eleocharis* R.Br. e *Fuirena* Rottb. os mais diversos e abundantes nesses ambientes, respectivamente (Alves et al. 2009). Ambos possuem diásporos adaptados à dispersão pela água (Lye 2000), consistindo em estruturas acessórias, de origem tepalóide, aderidas ao aquênio, o que permite o acúmulo de bolhas de ar e assim, a flutuabilidade (Goetghebeur 1998).

A pesquisa com macrófitas aquáticas é, em grande parte, focada na influência que as mesmas exercem no meio abiótico, principalmente em reservatórios e com espécies submersas e flutuantes (Padial et al. 2008). Estudos que busquem compreender as fases do desenvolvimento dessas plantas, principalmente das emersas, são raros (e.g. Snyder & Richards 2005, Bertazzoni & Damasceno-Júnior 2011). O ramo da ciência que busca o conhecimento do ciclo de vida dos organismos é a fenologia, podendo ser definida como a arte de observar os fenômenos biológicos do ciclo de vida, buscando estabelecer relações entre fatores bióticos e abióticos e a ocorrência e duração desses eventos (Lieth 1974). Tais eventos biológicos são geralmente sazonais e são também chamados de fenofases e, no caso das plantas, correspondem às respostas morfológicas das mesmas (Rathcke & Lacey 1985, Fenner 1998). Estudos fenológicos podem abranger desde uma única espécie até todo um ecossistema e compõem uma importante ferramenta para o entendimento das interações presentes em comunidades (Lieth 1974, Fenner 1998).

Nas Américas do Sul e Central, a grande maioria dos estudos fenológicos são focados em espécies arbóreas e ambientes florestais (Morellato et al. 2013), sendo poucos os realizados com espécies herbáceas e incomuns os com macrófitas aquáticas. Representantes de Cyperaceae também não são o alvo de observações dessa natureza, sendo algumas poucas espécies incluídas em estudos de comunidades de dunas (Cordazzo & Selliger 1988, Castellani et al. 1999) e campos

(Tannus et al. 2006), enquanto as que recebem atenção individual, esta é direcionada à biologia floral e polinização (Snyder & Richards 2005, Costa & Machado 2012).

Ainda menos explorado é a fenologia de macrófitas, sendo os poucos estudos existentes focados somente no período reprodutivo (Snyder & Richards 2005, Michalski & Durka 2007), em comunidades excluindo espécies de Cyperaceae (Simão 2016) ou relacionados a espécies de importância agronômica (Bertazzoni & Damasceno-Júnior 2011). Porém, tais estudos também representam parte do conhecimento abrangido pela fenologia, pois buscam compreender os fenômenos observáveis no ciclo de vida das espécies estudadas (Lieth 1974).

No entanto, as relações entre respostas morfológicas das macrófitas e variáveis ambientais ainda não são muito claras. Para plantas terrestres sabe-se que a temperatura, o fotoperíodo e a pluviosidade desencadeiam respostas fenológicas (De Fina & Ravelo 1973, Fenner 1998, Bergamaschi 2007), podendo algumas dessas respostas serem reflexo de períodos pretéritos de altas taxas de acúmulo de reservas (Rathcke & Lacey 1985). Padrões fenológicos também podem ser complexos e irregulares, o que dificulta seu reconhecimento, assim como a falta de padronização de termos e métodos, como já apontado por Newstrom et al. (1994) .

Estudos fenológicos geralmente descrevem fenômenos desde o brotamento até a dispersão dos frutos (Rathcke & Lacey 1985, Fenner 1998), porém, a reprodução pode ser vegetativa e as sementes podem não germinar (Fenner & Thompson 2005, Baskin & Baskin 2014). O tamanho e o formato da semente, assim como a quantidade de endosperma e as condições do ambiente, podem afetar a germinação e a sobrevivência da plântula, influenciando o sucesso reprodutivo de um indivíduo e seu potencial *fitness* (Primack & Kang 1989, Trewawas 2009, Zukowski et al. 2010).

Nota-se assim, que explorar o destino das sementes após a dispersão também contribui ao conhecimento do ciclo de vida das espécies, pois representa a efetividade ou não dos fenômenos reprodutivos anteriores (Rathcke & Lacey 1985, Fenner & Thompson 2005). A ausência de germinação sugere inviabilidade ou algum tipo de dormência (Baskin & Baskin 2014), podendo o último caso ser indicativo de persistência em bancos de sementes (Fenner & Thompson 2005). Como em Cyperaceae a produção de diásporos é geralmente

numerosa e regular, muitas espécies são capazes de formar densos bancos de sementes (Leck & Schütz 2005).

As sementes são protegidas pelo pericarpo do aquênio e normalmente possuem um único saco embrionário e endosperma abundante (Goetghebeur 1998, Lye 2000). Para germinar, requerem luz e respondem a variações de temperatura (Baskin et al. 2004, Zukowski et al. 2010, Baskin & Baskin 2014). Porém, tais informações são baseadas, em sua maioria, em espécies de clima temperado, sendo raros os estudos nos trópicos e subtrópicos (Bell & Clarke 2004, Mendonça et al. 2015).

A forma como espécies de Cyperaceae se dispersam e colonizam ambientes aquáticos está começando a ser explorada (Ivey & Richards 2001). Compreender essa dinâmica pode ser de grande valia para o uso das espécies na restauração de áreas úmidas, no que diz respeito à sua forma de propagação (Brown & Bedford 1997). Sabe-se que *Eleocharis laeviglumis* R.Trevis. & Boldrini e *Fuirena robusta* Kunth são capazes de se reproduzir tanto por sementes, quanto vegetativamente (Walters 1950, Kral 1978, Muasya 1998, Trevisan & Boldrini 2006). O padrão de distribuição normalmente observado em lagoas são grandes agrupamentos monoespecíficos paralelos às margens. Espécies de maior porte, como *F. robusta*, agrupam-se nas margens internas, expostas a ação dos ventos (*fetch*), permitindo que espécies menores e mais sensíveis, como *E. laeviglumis*, possam se desenvolver no seu entorno, protegidas do *fetch* (Thomaz & Esteves 2011; Fig. 1).

O gênero *Fuirena* é composto por espécies em sua maioria perenes, eretas e rizomatosas, com colmos angulados e relativamente foliosos, podendo alcançar mais de um metro de altura. Possui cerca de 30 espécies concentradas em ambientes úmidos de baixas altitudes, principalmente em regiões tropicais e temperadas úmidas (Kral 1978, Goetghebeur 1998, Muasya 1998). Diásporos de uma espécie anual (*F. pumila* (Torr.) Spreng.; Wetzel et al. 2001) e uma perene (*F. squarrosa* Michaux; Collins & Wein 1995) já foram encontrados em bancos de sementes. Uma espécie do gênero, *F. umbellata* Rottb., já foi apontada como hiperacumuladora de cádmio e crômio (Mganga et al. 2011) e daninha em cultivos de arroz (Begum et al. 2005).

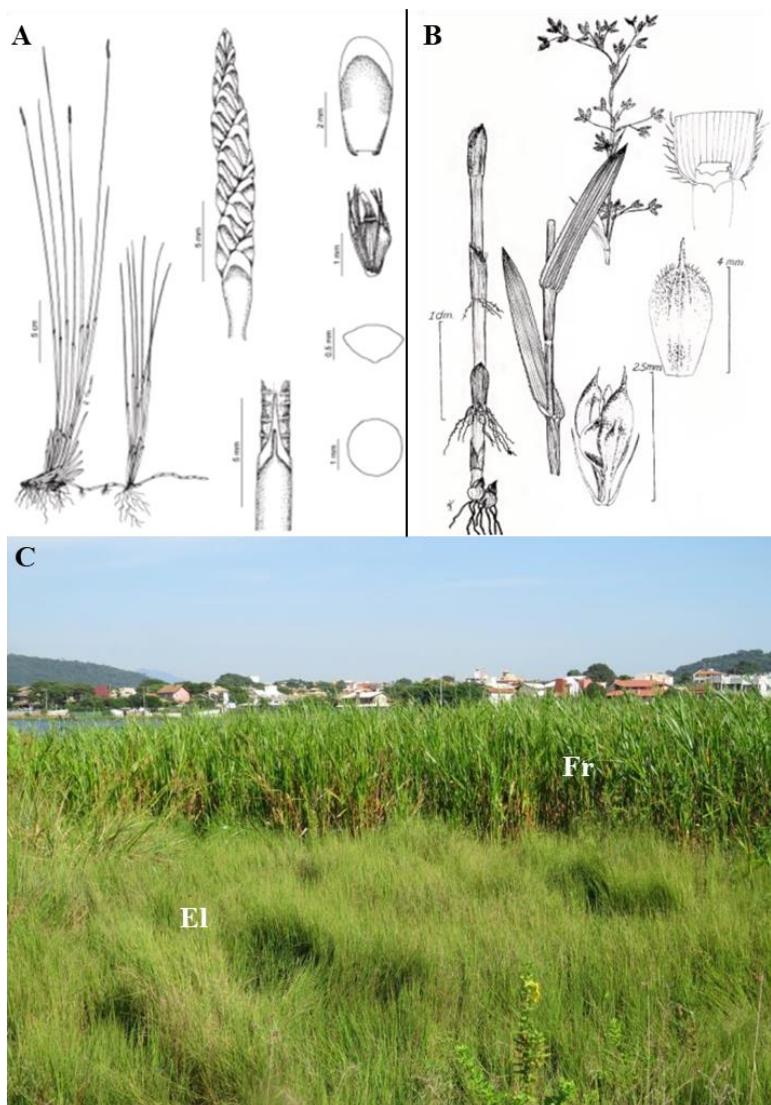


Figura 1. A: Prancha de *Eleocharis laeviglumis*, modificado de Trevisan & Boldrini 2006. B: Prancha de *Fuirena robusta*, modificado de Kral 1978. C: Distribuição de populações de *E. laeviglumis* (El) e *F. robusta* (Fr) às margens da Lagoa Pequena em Florianópolis, SC, Brasil.

A espécie *F. robusta* se caracteriza por possuir colmos pentangulados com altura alcançando mais de um metro. Possui como estruturas acessórias no diâsporo seis peças de origem tepalóide divididas em dois verticilos: três peças internas membranosas e três peças externas vestigiais. O aquênio é obovoide-trígonal, de superfície lisa e coloração castanha a castanha escura, apresentando estilopódio persistente e discreto (Barros 1960, Kral 1978, Muasya 1998, Vrijdaghs et al. 2004). Popularmente nomeada como Piri por índios Tupi-Guarani, deu origem ao nome da Lagoa do Peri, em Florianópolis, sendo utilizada pelos mesmos para manufatura de artesanatos (Carvalho Junior 2010).

Já *Eleocharis* distingue-se dos outros gêneros da família por apresentar colmos com uma única espiqueta terminal, folhas reduzidas à bainhas na base dos colmos e estilopódio engrossado e persistente no fruto. As espécies encontram-se total ou parcialmente submersas ou associadas à habitats temporariamente encharcados. São conhecidas cerca de 200 espécies, com distribuição cosmopolita e maior concentração na América tropical e subtropical (Goetghebeur 1998, Trevisan & Boldrini 2008). Diversas espécies do gênero já foram citadas como formadoras de bancos de semente (Leck & Schütz 2005).

*Eleocharis laeviglumis* foi recentemente descrita (Trevisan & Boldrini 2006) e possui colmos cilíndricos e não septados de até 65 cm de altura. Apresenta caule ereto e cespitoso-estolonífero com cáudice sublenhosso, formando aglomerados densos e homogêneos. O diâsporo é composto por um aquênio trígono, obovóide a obpiriforme, de superfície reticulada e coloração olivácea a palhete, além de estruturas acessórias como estilopódio persistente e cerdas hipóginas (Trevisan & Boldrini 2006, Trevisan & Boldrini 2008).

Apesar da importância ecológica das espécies aqui descritas, são raros os trabalhos com as mesmas. Enquanto *F. robusta*, uma das espécies mais abundantes em lagoas costeiras do Sul do Brasil (De Lourdes et al. 2007), não atraiu a atenção de pesquisadores, *E. laeviglumis* está inclusa em estudos citogenéticos (Da Silva et al. 2010) e já foi indicada como potencial fitorremediadora, acumulando metais em suas raízes e rizomas e tolerando resíduos de mineração (Da Silva 2015). Estratégias de propagação de ambas espécies para uso em reestabelecimento de comunidades de macrófitas ainda não são conhecidas. Dessa forma, descrevemos aqui a fenologia reprodutiva de ambas espécies, assim como sua respectiva produção de flores e frutos.

Para *F. robusta* também caracterizamos a fenologia populacional, enquanto que para *E. laeviglumis* descrevemos a germinação e o vigor das sementes durante uma estação reprodutiva.



## 2 ÁREA DE ESTUDO

O estudo fenológico, e parte do reprodutivo, foi conduzido às margens da Lagoa Pequena (LP), entre as coordenadas 27°39'10" e 27°39'36" S e 48°28'37" e 48°28'50" W, localizada na porção insular do município de Florianópolis, ou Ilha de Santa Catarina, no bairro Rio Tavares (Fig. 2). O município pertence ao setor central da unidade geomorfológica Planície Costeira do estado de SC e possui complexa formação geomorfológica. A ilha apresenta forma alongada no sentido norte-sul com 54 km de comprimento e largura máxima de 18 km no sentido leste-oeste (Florianópolis 2009).

O clima da Ilha de SC possui influência marítima, apresentando umidade relativa anual em média de 83% (Pandolfo et al. 2002). É condicionado por diferentes massas de ar, uma quente e úmida, Massa Tropical Atlântica, responsável pelos ventos norte e nordeste, e duas que dão um caráter mesotérmico à região, Massa de Ar Intertropical e Massa Polar Atlântica. Essa última é responsável pelos ventos sul e sudeste e pelo ritmo de chuvas da ilha (Florianópolis 2009). Desse modo, o clima na Ilha de SC apresenta-se como subtropical mesotérmico úmido (Cfa) na classificação de Köppen, com chuvas relativamente bem distribuídas ao longo do ano (entre 1500-1700 mm) e médias de temperatura máxima anual de 25°C, e mínima de 14°C (Pandolfo et al. 2002). Devido à urbanização, Florianópolis apresenta diferentes microclimas (Florianópolis 2009), sendo que a região da Lagoa Pequena apresenta verão quente e chuvoso, média de 23°C e 180 mm, e inverno ameno e menos chuvoso, média de 16°C e 90 mm (Pandolfo et al. 2002).

A LP possui superfície de 186.372 m<sup>2</sup> e é um afloramento do lençol freático da Planície do Campeche (Millon 2004). O aquífero, de origem pluvial, possui águas ácidas e é considerado altamente suscetível à incorporação de substâncias potencialmente poluidoras. Em função do excesso de bombeamento de poços tubulares, encontra-se em processo de salinização, colocando em risco a qualidade limnológica da lagoa (Borges 1996, Barbosa et al. 1999 apud Millon 2004). A LP localiza-se a cerca de 600m do oceano e é parcialmente cercada por áreas de restinga arbustiva, dunas e banhados (Falkenberg 1999). Possui grandes adensamentos de macrófitas aquáticas em suas margens, com presença de diversas espécies de Cyperaceae (Ferreira et al. 2017) e densos

agrupamentos de *E. laeviglumis*, *F. robusta*, *Typha domingensis* Pers e *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga.

Essa última, popularmente conhecida como braquiária-do-brejo, é uma espécie de Poaceae invasora, de origem africana, que domina extensas áreas das margens da lagoa, ameaçando a diversidade de macrófitas aquáticas nativas, principalmente de espécies submersas fixas e emergentes (Michelan et al. 2010, Fernandes et al. 2013). Já a população nativa de taboa, *T. domingensis*, na margem norte-noroeste, está avançando sob populações de *F. robusta*. O impacto humano já foi citado como causa desse mesmo processo de expansão de taboas sob populações de outra Cyperaceae, *Cladium jamaicense* Crantz, na Flórida (Lorenzen et al. 2000). Isso pode ser considerado um indício de influência antrópica sob a LP. A expansão da comunidade macrofítica como um todo pode ser observada em imagens históricas do Google Earth, provavelmente em função do fechamento de uma rua em 2011, que separava a margem norte em duas porções, assim como o despejo de esgoto doméstico na Lagoa em meados da década de 2000 (comunicação pessoal de uma moradora do Rio Tavares, 2016).

A LP e seu entorno (27,5 ha), também chamada pelos moradores e turistas de Lagoinha Pequena, é amparada por diversas leis ambientais, tanto em âmbito municipal quanto estadual e nacional, porém não são devidamente respeitadas (Geri 2007). É tombada como Patrimônio Natural e Paisagístico de Florianópolis (Decreto municipal no 135/88) e está incluída no Plano Municipal de Gerenciamento Costeiro (Brasil 2012). É considerada Área de Preservação Permanente pelo Código Florestal (Lei no 12.651/2012) e classificada pelo município como Área Verde de Lazer (Lei Comp. no 482/2014). Porém, impactos como ocupações ilegais do entorno, livre trânsito de pessoas e animais domésticos, invasão de espécies vegetais exóticas, além da falta de demarcação dos limites da área, ameaçam o ecossistema como um todo. Processo semelhante já foi observado em outra lagoa costeira da região, a Lagoa da Chica, que recentemente passou por processo de revitalização (Pippi 2004, Costa 2017).

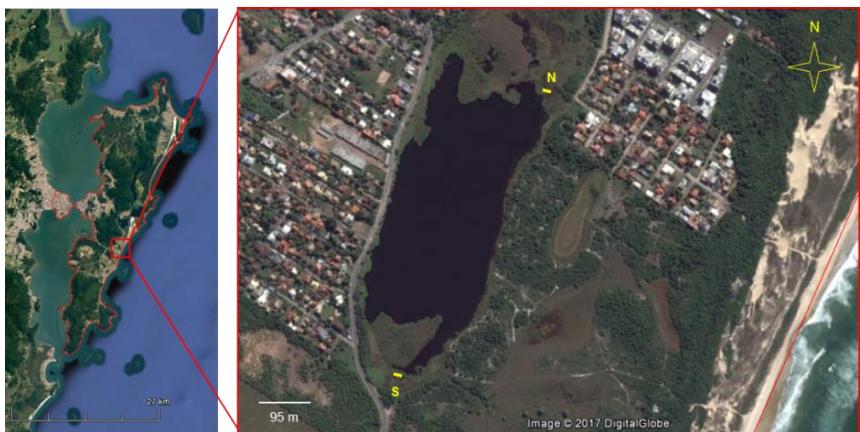


Figura 2. Localização geográfica da Lagoa Pequena no bairro Rio Tavares, Florianópolis - SC. Traços amarelos indicam populações amostrais de *F. robusta* nas margens norte e sul, bem como as de *E. laeviglumis* no entorno do transecto norte.



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## 4 CAPÍTULO 1

### Original article<sup>1</sup>

#### **Reproductive phenology and germination of *Eleocharis laeviglumis* R. Trevis. & Boldrini (Cyperaceae)**

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## Abstract

*E. laeviglumis* is an abundant emergent macrophyte in southern Brazil coastal wetlands. Details of sexual reproduction are not known for the species. To describe spikelet phenophases, we observed reproductive culms in a natural population. We collected and counted number of flowers and potentially viable fruits per inflorescence. We also collected seeds during four months of 2016/2017 reproductive season and tested seeds for germinability and vigor. Differences in germinability and vigor among replicates and temporal samples were determined separately by a Kruskal-Wallis test, with 95% reliability. A Dunnett post-hoc test was used to determine which samples differed from each other. We found each *E. laeviglumis* spikelet lasts, on average, 34 days (pre-anthesis, 1.7 d; anthesis, 6.9 d; fruit maturation, 22.3 d; fruit dispersion, 3.2 d). Spikelets are dichogamous and protogynous. More than half of the flowers (62.2%) developed into fruits and only 5.5% of the seeds germinated. Germinability and vigor decreased with the passing of the reproductive season. Probably part of *E. laeviglumis* culms are originated from asexual reproduction or sexual reproduction of clones. We suggest that for restoration purposes, *E. laeviglumis* propagation should be done by sowing seeds collected at the beginning of the reproductive season along with transplanting rhizomes.

**Keywords:** Aquatic macrophyte, Cyperaceae, Eleocharis, sexual reproduction, spikelet, germination, reproductive phenology, seed vigor

## Introduction

*Eleocharis laeviglumis* R. Trevis. & Boldrini is an emergent aquatic macrophyte frequently found grouped in monospecific clusters as a result of vegetative and sexual reproduction. It belongs to Cyperaceae which is the third largest monocotyledonous family (Govaerts *et al.* 2007) with wide dispersion around the globe and concentration in the tropics (Goetghebeur 1998). The family comprehends herbaceous species with graminoid aspect and varied sizes. In general, species possess leaves with closed sheaths, tiny and discrete wind-pollinated flowers settled on spikelets under different arrangements, and abundant and regular diaspore production (Goetghebeur 1998; Leck & Schütz 2005). Each diaspore is composed of an achene and reduced perianth parts, usually bristles (Goetghebeur 1998).

Several genera of the family are associated with humid or truly aquatic environments (Cook *et al.* 1974), comprehending the most diverse aquatic macrophyte family in freshwater ecosystems (Chambers *et al.* 2008). Most of Cyperaceae macrophyte species are emergent (Cook *et al.* 1974) and in Brazil *Eleocharis* R.Br. is one of the most diverse genera (Alves *et al.* 2009). *Eleocharis* distinguishes from other Cyperaceae genera for presenting culms with a single terminal spikelet, leaves reduced to tubular sheaths in the culm base and a thick stylopodium, persistent in the fruit (Goetghebeur 1998; Trevisan & Boldrini 2008). Along with other macrophytes (Dhote & Dixit 2009; Sakakibara *et al.* 2011), *E. laeviglumis* has the potential for use in phytoremediation of contaminated environments, mostly at mining sites, by accumulating heavy metals in its underground tissues (Da Silva 2015).

Freshwater ecosystems, mostly Neotropical coastal lakes, are one of the most vulnerable habitats in the world (Esteves *et al.* 2008) and frequently need to be restored. In that scenario, macrophyte species can be useful to recolonize disturbed habitats (Brown & Bedford 1997; Nishihiro & Washitani 2007). The species studied, *E. laeviglumis*, is endemic to southern Brazil and well represented in coastal wetlands (Trevisan & Boldrini 2006). As well as most perennial macrophytes, *E. laeviglumis* has a mixed reproductive strategy, both sexual and asexual reproduction, which can benefit its propagation (Eckert *et al.* 2016). Its flowers are hermaphrodite and the achenes hold bristles adapted to

water dispersion (Trevisan & Boldrini 2006). In addition to achene production, the species possesses a complex underground stem system which permits the formation of dense populations (Trevisan & Boldrini 2006).

However, *E. laeviglumis'* flower dynamics, diaspores production, and seed germinability are still not known, as well as its reproductive phenology. To understand the species reproductive success, knowing its reproductive phenology as well as seed germinability and vigor are of extreme importance. Therefore, our study aimed to describe part of *E. laeviglumis* reproductive cycle: spikelet phenology, fruit set, and seed germinability and vigor.

## Materials and methods

### Species and study area

*Eleocharis laeviglumis* is a perennial herb that produces culms up to 65 cm high. Culms are unbranched with leaves reduced to tubular sheaths. Clonal expansion occurs via rhizomes and can form big clonal clusters. Vegetative culms have an aborted inflorescence in its apex while fertile ones have one terminal spikelet. Flowers within a spikelet are hermaphrodite with three stamens, a pistil with three stigmatic branches and a single ovule. Diaspores, or dispersion units, are composed of a reticulated surface achene with a persistent stylopodium and 6-7 bristles adapted to flotation (Goetghebeur 1998; Trevisan & Boldrini 2006).

*E. laeviglumis* is endemic to southern Brazil coastal wetlands (Trevisan & Boldrini 2006) and is one of the dominant emergent macrophytes in Lagoa Pequena (LP), a freshwater coastal lake 600m far from the ocean in southern Florianópolis island, Santa Catarina, Brazil ( $27^{\circ}39'17.9''S$ ;  $48^{\circ}28'36.2''W$ ). The ecosystem supports a rich macrophytic flora, with Cyperaceae being the richest taxa (Ferreira *et al.* 2017). Although LP is located in an urban area and suffers with human impacts, it is partially surrounded by Restinga forests, dunes and wetlands (Falkenberg 1999).

## **Reproductive phenology**

A brief description of spikelet phenophases and its respective developmental time in days were accomplished by marking and following fertile culms daily in LP. A minimum of 20 and a maximum of 26 spikelets per phenophase were followed during Nov/2016 and Jan/2017, totaling 33 culms observed. Average and standard deviation were calculated for each phenophase length.

To estimate flower and seed set per spikelet, fertile culms were collected from LP during the beginning of 2016/2017 reproductive season (December and January). We collected 20 culms for each anthesis and fruit maturation phenophases, and counted the number of flowers and potentially viable fruits, respectively. As potentially viable fruits we considered the ones with a stuffed achene, which are clearly differentiated from the mummified ones, that is, the not developed ones. Average and standard deviation were calculated.

## **Germinability and seed vigor**

Diaspores, here also referred as seeds, were collected four times between December/2016 and March/2017. Seeds were processed in the laboratory by selection of the potentially viable ones, then randomly mixed (within each temporal sample separately) and separated into work samples for the germination test. For the test, seeds were immersed in alcohol 70% for 30 seconds followed by 40 seconds in a 2% sodium hypochlorite solution and then washed three times with distilled water (adapted from Baskin & Baskin 2014).

For each of the four temporal samples, seven replicates of 15 seeds each were placed in plastic Petri dishes with moistened filter papers and incubated under  $25 \pm 2^\circ\text{C}$  and 12 h photoperiod ( $142 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) in a germination chamber. Temperature and photoperiod simulated local averages during dispersion months (spring-summer) in the study area. Seeds were watered and counted daily for germination, and were considered germinated after coleoptile protrusion (Walters 1950, Bewley *et al.* 2013). The test lasted 39 days, finishing when no more seeds germinated for seven consecutive days.

To determine and compare seed vigor of each temporal sample using germination speed we calculated the Germination Speed Index (GSI) proposed by Maguire (1962). The index follows the formula:  $\text{GSI} = \sum(\text{NGS}/\text{DAS})$ , where NGS corresponds to the non-accumulated

number of germinated seeds and DAS to the number of days after the test started. For tetrazolium test we submitted part of the non-germinated seeds to a 2,3,5-triphenyl tetrazolium chloride solution (1%) for 24 hours at 35°C in the dark (Baskin & Baskin 2014). One third of seeds of each temporal sample were tested (35/105). Seeds were considered reacting positively to tetrazolium when embryo tissues stained pink.

### **Data analysis**

Since our data did not present a normal distribution and homoscedasticity, we used nonparametric statistics. Germination percentages, as much as GSI's, among replicates and samples were analyzed separately through a Kruskal-Wallis test. When significant differences were found, a Dunnett post-hoc test was performed. For both tests, Kruskal-Wallis and Dunnett, differences were considered significant at 95% confidence interval. We performed all statistical analysis using the R Statistical Environment v. 3.3.2 (R Core Team 2016).

## **Results**

### **Reproductive phenology**

*E. laeviglumis'* population sampled is relatively small and forms a dense and reasonably isolated monospecific cluster in LP's north margin. The species reproduces during spring and summer (November to March) with a flowering peak in November (personal observation). Each *E. laeviglumis* spikelet took, on average, 34.1 days to complete its developmental cycle (Tab. 1), with a relatively synchronous flowering. We observed the following reproductive phenophases: pre-anthesis, female anthesis ( $\text{♀}$ ), concomitant female and male anthesis ( $\text{♀}/\text{♂}$ ), male anthesis ( $\text{♂}$ ), fruit maturation, and fruit dispersion (Tab. 1 and Fig. 1). As fruit dispersion we considered diaspore detachment from the spikelet.

Spikelets were completely developed underwater, taking 1.7 days from emersion until anthesis. Flowers within a spikelet were hermaphrodite and dichogamous, with androecium and gynoecium anthesis segregated over time. Gynoecium anthesis preceded

androecium anthesis, comprehending a protogynous inflorescence. Gynoecium anthesis occurred in the first 3.6 days, and it was followed by a concomitant stigma and stamens exposition for 0.5 days in 53.8% of the spikelets observed. Both stigma and stamens were protruded from the inflorescence. Stamens exposition lasted 2.8 days, totaling 6.9 days for a spikelet to fully complete anthesis.

Every spikelet in anthesis produced  $57.2 \pm 6.1$  flowers (min. of 46 and max. of 67) (Fig. 1). The next and longest phenophase observed was fruit maturation, with duration of 22.3 days. In that stage, each spikelet produced  $35.6 \pm 11.5$  fruits (min. of 13 and max. of 50), which represented 62.2% of the flowers developed into potentially viable fruits. Fruit dispersion took 3.2 days with every fruit being dispersed with its respective glum. Diaspores on spikelet bottom were rarely dispersed, remaining attached to the inflorescence rachilla.

### **Germinability and seed vigor**

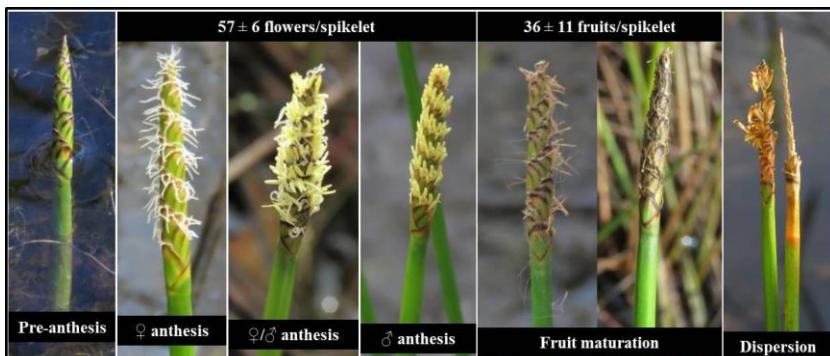
*E. laeviglumis* seeds started to germinate after 14 days in the test, and grouping the four temporal samples, only 5.5% germinated (23/420). Within the temporal samples, 15 seeds germinated (14.3%) in the first sample, six (5.7%) in the second, and only one seed (0.9%) in the third and fourth samples (Fig. 2A). Significant differences in germination among replicates averages were not observed ( $\chi^2=3.19$ ;  $P=0.78$ ) but among samples ( $\chi^2=13.05$ ;  $P=0.004$ ). The first sample, on the beginning of 2016/2017 reproductive season, differed from the last two (both with  $P=0.001$ ), which corresponded to the end of the season. Although seeds per sample were not quantified, the availability of seeds for collection from the last two samples was scarcer.

Significant differences in seed vigor, by means of GSI, were not found among replicates averages ( $\chi^2=3.78$ ;  $P=0.7$ ) but among samples ( $\chi^2=12.1$ ;  $P=0.007$ ). The calculated GSI reduced within the four temporal samples (first=0.08; second=0.03; third=0.01; fourth=0) (Fig. 2B). Likewise germination results, the GSI of the first temporal sample differed from the last two (both with  $P=0.001$ ). Of all seeds tested with tetrazolium, only 22.5% (32/140) presented a positive reaction. Seed vigor, by tetrazolium reaction, also reduced with the passing of the reproductive season. Of the first sample, 48% of seeds reacted positively

to tetrazolium, of the second 23%, of the third 11% and of the fourth 8% (Fig. 2C).

**Table 1.** Description of *Eleocharis laeviglumis'* reproductive phenophases observed in a population at the north margin of Lagoa Pequena, Florianópolis, SC, Brazil. Developmental time ( $\pm$  SD) and the maximum and minimum length in days for each phenophase are presented.

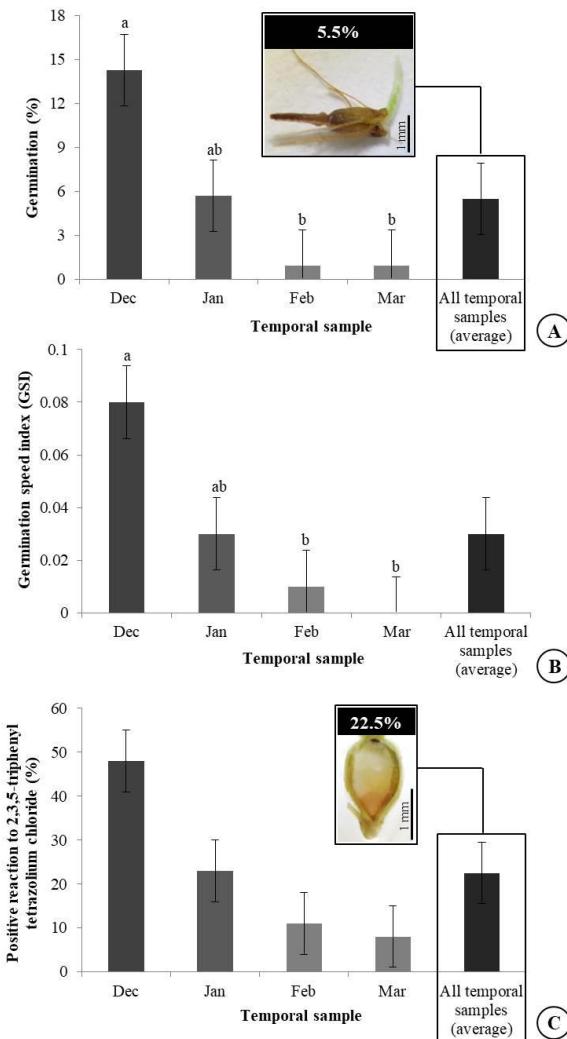
Phenophase	Description	Length in days	Min. length	Max. length
Pre-anthesis	Closed spikelet (from submerged to emerging) and glums with dark margins	1.7 ( $\pm$ 0.6)	1	3
♀ anthesis	Exposition of whitish trifid stigma	3.6 ( $\pm$ 1.1)	2	6
♀/♂ anthesis	Concomitant exposition of stigma and stamens	0.5 ( $\pm$ 0.5)	0	1
♂ anthesis	Exposition of bright yellow stamens	2.8 ( $\pm$ 1.2)	1	5
Fruit maturation	Dry and/or fall of anthers, light spikelet tumescence with glums turning yellowish and separated	22.3 ( $\pm$ 4.1)	17	31
Fruit dispersion	Fall of diaspore attached to glums	3.2 ( $\pm$ 1.1)	1	6
<b>Reproductive culm longevity</b>				34.1 days



**Figure 1.** Reproductive phenophases of *Eleocharis laeviglumis* and respective flower and fruit production per spikelet, presented as mean  $\pm$  SD.

## Discussion

*Eleocharis laeviglumis'* spikelet is dichogamous and protogynous, taking around 34 days to develop and disperse seeds, which have low germinability and vigor. Temporal segregation of androecium and gynoecium anthesis, dichogamy, is a strategy to promote outcrossing (Lloyd & Webb 1986) and it is common in wind-pollinated species (Friedman & Barrett 2009). Protogyny was previously attributed for Cyperaceae (Goetghebeur 1998), as much as concomitant exposition of stigma and stamens (Snyder & Richards 2005; Costa & Machado 2012). This concomitant exposition of female and male whorls comprehends an incomplete dichogamy and it can open a temporal gate for self-pollination (Lloyd & Webb 1986). Although little is known about breeding systems in Cyperaceae, both auto-compatibility (Snyder & Richards 2005) and auto-incompatibility (Charpentier *et al.* 2000; Costa & Machado 2012) were already described for the family. To *E. laeviglumis*, we cannot confirm any compatibility relations since it was not the scope of this study.



**Figure 2.** Germination (A), Germination Speed Index (B), and positive reaction to tetrazolium (C) of *Eleocharis laeviglumis*' seeds from the four collections of 2016/2017 reproductive season in the population studied at the north margin of Lagoa Pequena, Florianópolis, SC, Brazil. Different letters in A and B indicates statistical differences by Dunnet post-hoc test ( $P<0.05$ ).

We found each spikelet produced on average 57.2 flowers, what differed from the described by Trevisan & Boldrini (2006), which was 20-50 flowers per spikelet. Therefore it is known that number of flowers can be determined by environment and resource availability via selection of particular genotypes (Wiens 1984). Thus, according to the same author, number of flowers can vary in different sites and time scales. Seed set of 62.2% for *E. laeviglumis* can be considered reasonably high when compared to Wiens' estimative of seed-ovule ratio for herbaceous perennials of the North American flora, which is 57.2% (Wiens 1984).

Although seed set was reasonably high, seeds presented low germinability (5.5%). Low germinability rates were also described to other perennial *Eleocharis* species, from Australia, such as *E. acuta* R. Br. (0.9%), *E. dietrichiana* Boeckeler (3.4%) and *E. pusilla* R. Br. (2.6%). But even with low germinability, most seeds of the previously mentioned species kept vigor after a 33-month burial (*E. acuta* 91.4%, *E. dietrichiana* 83.1% and *E. pusilla* 90.4%), what indicates persistence in seed banks (Bell & Clarke 2004). That does not seem to be the case of *E. laeviglumis*, since seeds showed relatively low vigor (22.5%).

Seeds collected in December/2016 resulted from flowers fertilized during the flowering peak, in November/2016, what could explain the difference found between this sample and the last two, in both germinability and seed vigor. A higher density of fertile culms at the beginning of the reproductive season could affect the amount of pollen available for fertilization, increasing the probability of cross-fertilization. While at the end of the season, the relatively small height of the species, lower density, and bigger distances between culms could reduce pollen dispersion and the consequent fertilization (Friedman & Barrett 2009). In this way, the observed higher germinability and vigor of seeds collected at the beginning of the reproductive season could be result of cross-fertilization between flowers of the previous month.

Vegetative reproduction of *E. laeviglumis* can also be understood as a factor influencing sexual reproductive effectiveness. Perennial aquatic plants are known to use both strategies, sexual and asexual reproduction (Eckert *et al.* 2016), what can maximize fitness when combined (Fenner & Thompson 2005). However, *E. laeviglumis* can form extensive clonal clusters which can result in fertilization among clones, as was already observed in *Carex* L. species (Friedman &

Barrett 2009) and *Cladium jamaicense* C.B. Clarke (Ivey & Richards 2001), both wind-pollinated Cyperaceae with unisexual flowers. Geitonogamy, or fertilization among clones, can reduce fitness through inbreeding depression and stigmatic clogging in both self-compatible and self-incompatible plants, respectively (Eckert *et al.* 2016). We suggest pollination among clones can occur in the population sampled and can be causing the observed reduction in the seeds' vigor and germination.

Sexual reproductive dynamics of *E. laeviglumis* is consistent with what is observed for wind-pollinated species. We observed temporal spaces in flowering that can enable self-pollination within the same spikelet. Compatibility relations are not known for the species and we believe it is a subject worth to be explored. Nevertheless, our results suggest geitonogamy could be a plausible explanation for the low germinability and vigor of seeds in the studied population. However, this suggestion can only be confirmed by studying population's genetic composition.

Considering that *E. laeviglumis* fertile culms develop reasonably fast and produce a reasonable amount of fruits, we suggest the species could be a good candidate for wetlands restoration. We thus conclude that for restoration purposes the species mixed reproductive strategy should be taken into consideration, that is, propagation should be more effective by sowing seeds along with transplanting rhizomes. We also acknowledge that seeds should be collected at the beginning of the reproductive season. Such propagation strategy could also guarantee genetic variability for the population to be established.

## Acknowledgements

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## 5 CAPÍTULO 2

### Original research paper<sup>2</sup>

#### **Phenology of a dominant emergent macrophyte, *Fuirena robusta* Rottb. (Cyperaceae), in a costal lake in southern Brazil**

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#### **Highlights**

- Reproductive phenophases were highly seasonal.
- Activity and intensity indexes showed similar results to each seasonal phenophase.
- Temporal differences were found among all reproductive phenophases.
- Significant climatic models were found for pre-anthesis and both ♀ and ♂ anthesis.
- Flowering was related to daylength, pH, and electrical conductivity.

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<sup>2</sup> A ser submetido à revista Aquatic Botany

## Abstract

Aquatic macrophytes are an important component of freshwater communities, influencing production and ecosystem functioning. Within different macrophyte habits, emergent species, especially from Cyperaceae, constitute expressive communities in Brazilian coastal lakes, frequently dominating and surrounding internal lake margins. In spite of its importance, little is known about emergent macrophytes life cycle and its environmental drivers. This study aimed to evaluate the reproductive development and productivity, as well as the phenology of the emergent macrophyte species, *Fuirena robusta* (Cyperaceae), typical to freshwater habitats in the southern Brazilian coast. We evaluated vegetative and reproductive phenology of a population occurring at southern and northern margins of a coastal lake using activity and intensity indexes within a year. Flowering and fruiting culms were collected to estimate its production. The environmental drivers of species phenophases were evaluated by generalized least squares, controlling for temporal autocorrelation. The reproductive cycle is highly seasonal, occurring during the end of spring and throughout summer, while the vegetative cycle is non-seasonal. A slightly phenological difference was found between the north and south margins, which we attributed to different wind conditions. Flowering was mostly influenced by daylength, maximum temperature, pH, electrical conductivity, and wind, whereas fruiting was not influenced by any tested model. Every reproductive culm lasted around two months and more than 90% of flowers developed into fruits. According to these results, we point *F. robusta* as a possible good candidate for restoration projects at coastal lakes in southern Brazil.

**Keywords:** Aquatic macrophyte, Poales, freshwater lake, reproductive biology

## 1. Introduction

Aquatic macrophytes are the most diverse and productive portion of a freshwater ecosystem (Cook et al., 1974; Chambers et al., 2008; Thomaz and Esteves, 2011). Many macrophyte species are capable of absorbing nutrients and other substances from water (Dhote and Dixit, 2009; Mganga et al., 2011), besides ensuring ecosystem structure and functioning (Thomaz and Esteves, 2011). In freshwater habitats, Cyperaceae represents the most diverse family (Chambers et al., 2008), comprehending herbaceous species with graminoid aspect and varied sizes (Goetghebeur, 1998). Cyperaceae species constitute expressive communities in southern Brazil coastal lakes (Irgang and Gastal Jr., 1996; Ferreira et al., 2017), which are one of the most threatened ecosystems in the world (Esteves et al., 2008). In these ecosystems, emergent species frequently dominate and surround internal lake margins, forming large and dense clusters (De Lourdes et al., 2007).

Emergent macrophytes often use both sexual and asexual reproduction combined as a survival strategy, what suggests most of clusters are clonal (Eckert et al., 2016). Many Cyperaceae species show strong rhizome systems (Barros, 1960) but for most species, little is known about its reproductive dynamics. To understand life cycle dynamics, phenology stands out as the best tool (Lieth, 1974). Although macrophyte researches are a growing trend (Padial et al., 2008), phenology is still poorly explored (Snyder and Richards, 2005; Michalski and Durka, 2007; Bertazzoni and Damasceno-Júnior, 2011; Simão, 2016). Most of Central and South American phenological studies focused on terrestrial species, mainly forest trees (Morelatto et al., 2013). For terrestrial plants, phenophases seems to be influenced by environmental variables such as daylength, rainfall and temperature (De Fina and Ravelo, 1973; Rathcke and Lacey, 1985; Fenner, 1998; Bergamaschi, 2007). Yet for macrophytes, water characteristics can also be a determinant factor influencing life cycle. Water temperature can influence productivity and respiration (Carr et al., 1997) as much as pH can affect species composition (Catling, et al., 1986; Arts and Leuven, 1988).

Plant reproductive cycle is a fundamental research area for possible future use of species for phytoremediation (Dhote and Dixit,

2009) or for wetlands management (Brown and Bedford, 1997; Nishihiro and Washitani, 2007), because it can indicate the best way for species propagation. Most of what is known to influence macrophytes development is based on submerged or floating species (Titus and Hoover, 1993; Petrucio and Esteves, 2000). Therefore, for emergent macrophytes, water characteristics as much as climatic variables need to be tested to start understanding its relation with plant life cycle. In this study we analyzed phenology of the emergent macrophyte *Fuirena robusta* Rottb., a typical species of freshwater ecosystems in southern Brazilian coast (De Lourdes et al., 2007). We evaluated vegetative and reproductive phenophases and its relationships with environmental variables as well as *F. robusta* reproductive culms development and its respective flower and fruit production in a freshwater coastal lake in southern Brazil.

## 2. Materials and methods

### 2.1. Species and study area

*Fuirena robusta* is a perennial, erect and rhizomatous Cyperaceae herb. It has tall, pentangulate, and leafy culms, reaching more than one meter high (Barros, 1960; Kral, 1978; Goetghebeur, 1998). Each culm produces a mixed inflorescence with wind-pollinated and hermaphrodite flowers (Goetghebeur, 1998). Each flower develops into a brown achene with a smooth surface and a persistent and discrete stylopodium (Barros, 1960; Kral, 1978; Goetghebeur, 1998). Each achene also possesses six perianth pieces divided into two whorls: an internal with three bladed pieces and an external with three bristles (Vrijdaghs et al., 2004). Perianth pieces are adapted to water dispersion by flotation (Goetghebeur, 1998). *Fuirena robusta* usually forms big and dense populations surrounding freshwater lakes margins, what creates a belt that protects smaller species from *fetch* (De Lourdes et al., 2007; Thomaz and Esteves, 2011).

The population studied is located in Lagoa Pequena (LP), a freshwater coastal lake with 18.63ha in the Santa Catarina state, Florianópolis Island ( $27^{\circ}39'25''S$ ;  $48^{\circ}28'43''W$ ). Climate is classified as mesothermic subtropical humid (Cfa) in Köppen classification, with rainfall well distributed throughout the year (1500-1700mm) and annual mean temperatures being a maximum of  $25^{\circ}C$  and a minimum of  $14^{\circ}C$  (Pandolfo et al., 2002). Different air masses regulate the island climate,

the Atlantic Tropical Mass, hot and humid, is responsible for north and northeast winds; while the Intertropical Air Mass and the Atlantic Polar Mass characterize the climate as mesothermic, being that the last one is responsible for south and southeast winds (Florianópolis, 2009).

LP is located 600m far from the ocean and it is partially surrounded by shrubby restinga areas, wetlands and dunes (Falkenberg, 1999), and partially by an avenue and residential buildings. Although LP has been suffering from human occupation in its surroundings in the last decades (Geri, 2007), the lake has a rich macrophytic flora, with various species of Cyperaceae (Ferreira et al., 2017) and dense clusters of *Eleocharis laeviglumis* R. Trevis. & Boldrini, *F. robusta*, *Typha domingensis* Pers and *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga, being the latter an invasive alien species (Fernandes et al., 2013).

## 2.2. Population and inflorescence phenology

Phenological observations were conducted biweekly from November 2016 to November 2017, comprising 24 observations. Two transects, each one with 19 permanent  $1\text{m}^2$  quadrats, were placed at north and south margins of LP, 600m apart from each other. Each quadrat was 1m distant from each other and transects were partially parallel to the margins. In the northern transect, the population was co-occurring with large clusters of *T. domingensis* and *U. arrecta*, whereas in the southern transect *F. robusta* was the dominant species, without *U. arrecta* and only with a few individuals of *T. domingensis*. In both transects, emergent macrophytes such as *E. laeviglumis*, *E. interstincta* (Vahl) Roem. & Schult. and *Ludwigia* spp., besides floating species of *Salvinia* Ség. and the submerged *Utricularia gibba* L. were present among the populations.

The observed phenophases in each quadrat were: dead, senescent, vegetative, pre-anthesis, gynoecium anthesis, androecium anthesis, fruit maturation and fruit dispersion. As senescent we considered culms with shoot apical meristem dried, and as fruit dispersion we considered only the primary dispersion: diaspores detachment from the mother plant. To estimate the length in days of each fertile phenophase, culms were tape marked, numbered, and observed daily during the reproductive season. A minimum of 21 and a maximum of 31 culms per stage were observed during 52 consecutive

days. To estimate flower and fruit production per spikelet, we collected 16 inflorescences in anthesis and 16 inflorescences in fruit maturation and counted number of flowers and potentially viable fruits, respectively. As potentially viable fruits we considered the ones with a stuffed achene. We also estimated number of spikelets per culm.

### 2.3. Environmental data

To each phenological observation, water depth and temperature were collected *in situ*. Water temperature was measured using a portable chemical thermometer, while water depth measurements were taken with a permanent marked stake installed at the beginning of observations. Also at each phenological observation, water was collected to measure pH (pH Meter Orion Star A211, Waltham, USA) and electrical conductivity (Conductivity Meter NICVP, Piracicaba, Brazil).

Climatic data of air temperature, accumulated rainfall and maximum wind speeds were provided by Air Detachment of Florianópolis International Airport, Hercílio Luz, 6.5km far from LP. Daily temperature averages, maximum and minimum temperatures registered for the fortnight (Tmax and Tmin), and mean of maximum and minimum for the fortnight (mTmax and mTmin) were considered. Daylength was obtained from the website Online-Photoperiod Calculator (<http://www.sci.fi/~benefon/sol.html>). For each climatic variable we also tested the effects of time-lagged periods to up to three months before phenological observations started. For climatic graphics, see Appendix A.

### 2.4. Data analysis

To recognize and evaluate phenological patterns of *F. robusta*, both qualitative and semi-quantitative methods were used, as proposed by Bencke and Morellato (2002). To define the activity index of each phenophase, we considered the phenophase presence/absence in every quadrat. To evaluate phenophase intensity we used the Fournier's intensity index (Fournier, 1974), which classifies the phenophase coverage percentage into five classes with scores from 0 to 4, with a 25% interval between classes. For both indexes, each quadrat was considered as an individual.

We analyzed each phenophase by circular statistics, where the observation dates were converted into days of the year and rescaled from 0° to 360°, with one degree representing approximately one day of the year. To each phenophase, we calculated mean angle ( $a$ ), its respective circular standard deviation (CSD), and the length of mean vector ( $r$ ), representing the concentration of each phenophase, using both activity and intensity indexes (Morelatto et al., 2010; Zar, 2010). We performed a Rayleigh test to determine the absence of uniformity, i.e. the significance of mean angles. When the mean angles were significant, we used “ $r$ ” as a seasonality indicator, as proposed by Morelatto et al. (2000). To analyze if there were differences between phenophases, between north and south transects, and also between activity and intensity indexes, we performed a Watson-Williams test when the assumption of unimodal distribution was not violated for each phenophase (Morelatto et al., 2010; Zar, 2010).

To evaluate the association among environmental variables and phenological patterns, using the intensity index, we elaborated plausible models (Appendix B) explaining each phenophase, including one or more uncorrelated variables with time-lagged periods of up to three months (six phenological observations). Variables were log transformed and models were then tested both through generalized least squares (GLS), including an autocorrelation structure of order one with a continuous time covariate (corCAR1), and through ordinary least squares (OLS), which do not account for temporal autocorrelation. The best models were selected based on Akaike Information Criteria (AIC; Burnham and Anderson, 2002) and compared to a null model containing only the intercept. Within these models, we performed a model average procedure to identify the best predictor(s) presenting the highest weight values within models presenting a  $\Delta\text{AIC} \leq 2$ . All statistical analysis were performed in R Statistical Environment v. 3.3.2 (R Core Team, 2016). Circular statistics were performed using the packages *circular* v.0.4-93 and *CircStats* v.0.2-4.; GLS models in the package *nlme* v.3.1-131 and model selection procedures using package *MuMIn* v.1.40.4.

### **3. Results and Discussion**

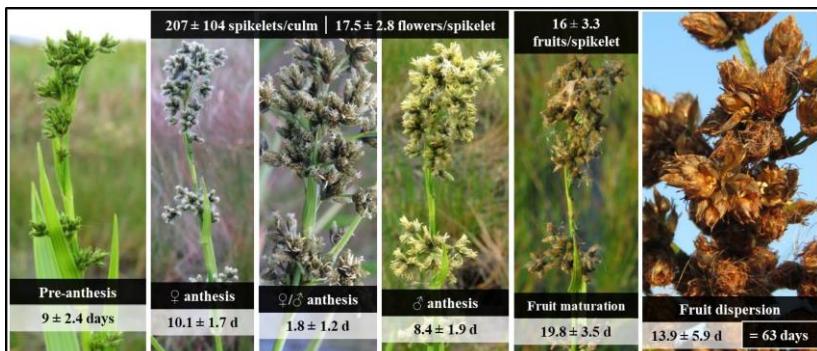
#### **3.1. Reproductive development and productivity**

Each reproductive culm produced, on average,  $207 \pm 104$  spikelets, took on average 63 days to complete the reproductive cycle

(Fig. 1) and died right after diaspores dispersion. Flowers took  $9 \pm 2.4$  days (minimum of 5 and maximum of 13 days) to bloom, comprehending pre-anthesis. Flowers within a spikelet were hermaphrodite and dichogamous. Temporal segregation of gynoecium and androecium anthesis, i.e. dichogamy, promotes outcrossing and it is a common strategy of wind-pollinated species (Lloyd and Webb, 1986; Friedman and Barrett, 2009).

Gynoecium anthesis preceded androecium anthesis, comprehending a protogynous inflorescence. Stigma exposition lasted  $10.1 \pm 1.7$  days (min. 6 and max. 12) and it was followed by a concomitant exposition of stigmas and stamens in the same culm for  $1.8 \pm 1.2$  days (min. 0 and max. 4), what characterizes an incomplete dichogamy (Lloyd and Webb, 1986). Protogyny was already attributed for Cyperaceae (Goetghebeur, 1998), as much as concomitant exposition of stigma and stamens (Snyder and Richards, 2005; Costa and Machado, 2012). Androecium anthesis lasted  $8.4 \pm 1.9$  days (min. 5 and max. 11) and it was followed by  $19.8 \pm 3.5$  days (min. 14 and max. 28) of fruit maturation. Fruit dispersion took  $13.9 \pm 5.9$  days (min. 6 and max. 31), being that not all diaspores were dispersed, remaining attached to the mother plant.

Each spikelet within a culm produced  $17.5 \pm 2.8$  flowers, being that  $16 \pm 3.3$  developed into fruits, what corresponded to 91.4% of flowers developed into fruits. Seed set of 91.4% can be considered high when compared to Wiens' estimative of seed-ovule ratio for herbaceous perennials of the North American flora, which is 57.2% (Wiens, 1984). Although the species spreads via rhizomes and forms big clusters, each reproductive culm produced an enormous amount of fruits. In average, each culm produced 3622.5 flowers and 3310.9 fruits respectively. For Cyperaceae, regular and numerous diaspores production is common, and can be an evidence of seed bank formation (Leck and Schütz, 2005).



**Figure 1.** Reproductive phenophases of *Fuirena robusta*. For each phenophase, its duration and respective standard deviation in days are presented, as much as spikelet production by culm, and flower and diaspores production per spikelet.

### 3.2. Phenology

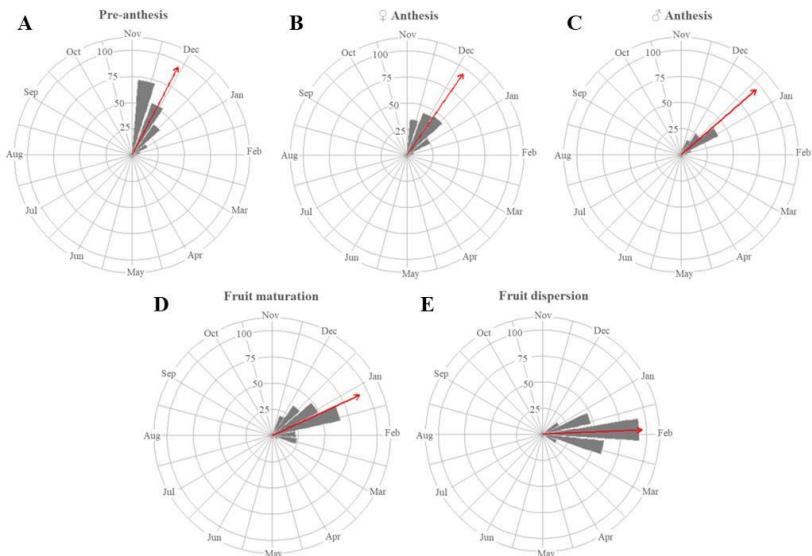
The reproductive phenophases are seasonal and started between the end of October and beginning of November 2016, with one flowering pulse. Dead, senescent and vegetative phenophases were uniformly distributed around the year, that is, were not seasonal, as indicated by Rayleigh test results and low “*r*” values (Tab. 1). Even though dead culms intensity and senescent culms activity presented significant mean angles by Rayleigh test, the very low “*r*” values (0.09 and 0.06 respectively) indicated no seasonality (Morelatto et al., 2000). Dead culms formed a permanent bed of organic matter covering the water mirror. We observed *F. robusta* seedlings germinated from seeds over the bed between June and July in the southern transect, as much as new culms from vegetative spread in both transects during the whole year. Vegetative spread occurred in two ways: by culms emitted from rhizomes and by thinner and longer culms that grew over the parcels and bend over other culms, emitting roots.

All fertile phenophases (pre-anthesis, ♀ anthesis, ♂ anthesis, fruit maturation, and fruit dispersion) presented significant mean angles and a high degree of seasonality, indicated by high “*r*” values (ranging from 0.92 to 0.96). Reproduction occurred during the end of spring and summer, when daylength was longer, temperature was higher and winds were slower. Plants from coastal dunes of southern Brazil also reproduce during the same period (Cordazzo and Seeliger, 1988).

The intensity of reproductive phenophases had consecutive mean angles, from the second fortnight of November (pre-anthesis) till the second fortnight of January (fruit dispersion). Activity data showed similar results, with the difference that pre-anthesis activity mean angle was later, in the first fortnight of December, close to ♀ anthesis' mean angle. Seasonal patterns, as much as intensity and activity mean angles, become evident in the circular histograms (Fig. 2 and 3).

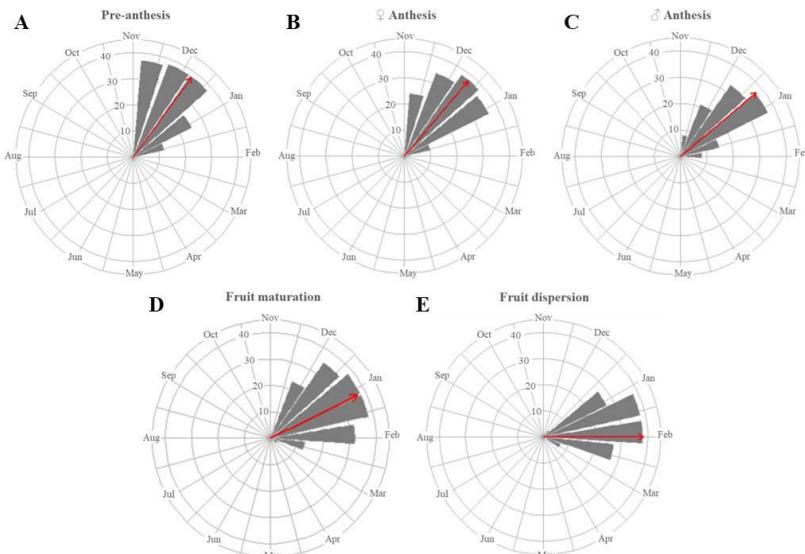
**Table 1.** Circular statistics analysis of intensity and activity phenological data from *F. robusta* population sampled in Lagoa Pequena, Florianópolis, SC, Brazil. Rayleigh test was performed with 95% reliability. CSD: circular standard deviation. NS: not significant.

Phenophase	Intensity				Activity			
	Mean angle ( $\alpha$ ) $\pm$ CSD	95% confidence interval (-+) for $\alpha$	Length of mean vector ( $r$ )	Rayleigh test (P)	Mean angle ( $\alpha$ ) $\pm$ CSD	95% confidence interval (-+) for $\alpha$	Length of mean vector ( $r$ )	Rayleigh test (P)
<b>Dead</b>	231.84° ( $\pm$ 126.48°)	199.12° 265.64°	0.09	0.004	76.82° ( $\pm$ 161.55°)	-60.96° 236.7°	0.02	0.72 NS
<b>Senescence</b>	215.04° ( $\pm$ 133.73°)	-204.16° -87.73°	0.06	0.09 NS	213.82° ( $\pm$ 136.1°)	161.58° 264.98°	0.06	0.05
<b>Vegetative</b>	30.39° ( $\pm$ 163.78°)	-125.77° 168.23°	0.01	0.58 NS	71.56° ( $\pm$ 160.28°)	-70.7° 201.72°	0.02	0.69 NS
<b>Pre-anthesis</b>	27.61° ( $\pm$ 17.09°)	25.09° 30.13°	0.95	<0.001	35.76° ( $\pm$ 19.86°)	32.79° 39.03°	0.94	<0.001
<b>♀ anthesis</b>	34.72° ( $\pm$ 17.34°)	32.07° 37.6°	0.95	<0.001	39.78° ( $\pm$ 19.70°)	36.69° 43.22°	0.94	<0.001
<b>♂ anthesis</b>	49.11° ( $\pm$ 17.37°)	45.78° 52.45°	0.95	<0.001	49.19° ( $\pm$ 20.43°)	45.87° 52.68°	0.93	<0.001
<b>Fruit maturation</b>	65.16° ( $\pm$ 22.52°)	62.41° 67.9°	0.92	<0.001	62.59° ( $\pm$ 23.25°)	58.93° 66.28°	0.92	<0.001
<b>Fruit dispersion</b>	87.65° ( $\pm$ 16.34°)	85.6° 89.69°	0.96	<0.001	80.75° ( $\pm$ 19.04°)	77.61° 83.85°	0.94	<0.001



**Figure 2.** Circular histograms of Fournier intensity index to each fertile stage of *F. robusta* population sampled during Nov/2016 and Nov/2017 in Lagoa Pequena, Florianólis, SC, Brazil. Red arrow length shows “ $r$ ” value and also represents the phenophase mean angle. A: pre -anthesis, B: ♀ anthesis, C: ♂ anthesis, D: fruit maturation, E: fruit dispersion.

Reproductive phenophases in both its intensity and activity presented significant mean angles through Rayleigh test ( $P<0.001$ ). Significant differences among phenophases, to each intensity and activity indexes separate, was found through Watson-Williams test (all possible comparisons, intensity with  $P<0.001$  and activity with  $P<0.05$ ). All reproductive phenophases also showed significant differences when pairwise compared between indexes ( $P<0.001$ ). The differences get evident by phenophases mean angles, that even when in the same fortnight, showed temporal separation of at least a few days. The Watson-Williams test results highlight the importance of measuring phenological patterns by different methods.



**Figure 3.** Circular histograms of activity index to each fertile stage of *F. robusta* population sampled during Nov/2016 and Nov/2017 in Lagoa Pequena, Florianópolis, SC, Brazil. Red arrow length shows “*r*” value and also represents the phenophase mean angle. A: pre-anthesis, B: ♀ anthesis, C: ♂ anthesis, D: fruit maturation, E: fruit dispersion.

When separated in northern and southern transects, reproductive phenophases also presented mean angles differences and seasonality (Tab. 2). Only the intensity of dead culms showed a significant mean angle ( $P<0.001$ ), but did not present a seasonal pattern ( $r = 0.17$ ), so it was not included in Watson-Williams comparisons. Within reproductive phenophases of northern and southern transects, we also found differences among phenophases (both intensity and activity with  $P<0.001$ ). Temporal difference between reproductive phenophases of each transect is small, as can be observed by mean angles (Tab.2). Southern transect population started the reproductive season earlier, probably because the population is more protected from south and southeast winds by the surrounding vegetation, what can create better conditions for reproduction. The northern population, on the other hand, is completely unprotected, with its south limits directly facing the water body.

**Table 2.** Circular statistics analysis of intensity and activity phenological data from *F. robusta* population (north and south transects) sampled in Lagoa Pequena, Florianópolis, SC, Brazil. Rayleigh test was performed with 95% reliability. CSD: circular standard deviation. NS: not significant.

Phenophase	Intensity			Activity		
	Mean angle ( $\alpha$ ) $\pm$ CSD	Length of mean vector ( $r$ )	Rayleigh test (P)	Mean angle ( $\alpha$ ) $\pm$ CSD	Length of mean vector ( $r$ )	Rayleigh test (P)
<b>North transect</b>						
<b>Dead</b>	214.8° ( $\pm 107.05^\circ$ )	0.17	<0.001	82.77° ( $\pm 162.69^\circ$ )	0.02	0.86 NS
<b>Senescent</b>	208.35° ( $\pm 136.43^\circ$ )	0.05	0.17 NS	206.91° ( $\pm 138.53^\circ$ )	0.05	0.29 NS
<b>Vegetative</b>	53.62° ( $\pm 160.74^\circ$ )	0.02	0.48 NS	71.56° ( $\pm 160.28^\circ$ )	0.02	0.83 NS
<b>Pre-anthesis</b>	29.15° ( $\pm 19.36^\circ$ )	0.94	<0.001	37.24° ( $\pm 24.59^\circ$ )	0.93	<0.001
<b>♀ anthesis</b>	34.9° ( $\pm 18.93^\circ$ )	0.94	<0.001	39.99° ( $\pm 21.13^\circ$ )	0.93	<0.001
<b>♂ anthesis</b>	49.33° ( $\pm 18.23^\circ$ )	0.95	<0.001	48.78° ( $\pm 20.38^\circ$ )	0.94	<0.001
<b>Fruit maturation</b>	66.72° ( $\pm 24.05^\circ$ )	0.91	<0.001	61.28° ( $\pm 24.36^\circ$ )	0.91	<0.001
<b>Fruit dispersion</b>	85.94° ( $\pm 17.91^\circ$ )	0.95	<0.001	78.91° ( $\pm 20.2^\circ$ )	0.94	<0.001
<b>South transect</b>						
<b>Dead</b>	208.68° ( $\pm 141.98^\circ$ )	0.04	0.23 NS	71.56° ( $\pm 160.28^\circ$ )	0.02	0.83 NS
<b>Senescent</b>	219.4° ( $\pm 132.86^\circ$ )	0.06	0.07 NS	219.51° ( $\pm 133.51^\circ$ )	0.06	0.16 NS
<b>Vegetative</b>	6.94° ( $\pm 162.52^\circ$ )	0.02	0.53 NS	71.56° ( $\pm 160.28^\circ$ )	0.02	0.83 NS
<b>Pre-anthesis</b>	27.01° ( $\pm 15.8^\circ$ )	0.96	<0.001	34.13° ( $\pm 17.61^\circ$ )	0.95	<0.001
<b>♀ anthesis</b>	35.43° ( $\pm 16.41^\circ$ )	0.95	<0.001	39.54° ( $\pm 17.98^\circ$ )	0.95	<0.001
<b>♂ anthesis</b>	50.4° ( $\pm 17.7^\circ$ )	0.95	<0.001	49.6° ( $\pm 20.47^\circ$ )	0.94	<0.001
<b>Fruit maturation</b>	64.66° ( $\pm 19.07^\circ$ )	0.94	<0.001	64.04° ( $\pm 21.86^\circ$ )	0.93	<0.001
<b>Fruit dispersion</b>	89.1° ( $\pm 15.17^\circ$ )	0.96	<0.001	82.59° ( $\pm 17.61^\circ$ )	0.95	<0.001

### 3.3. Environmental determinants of phenology

Since the only seasonal phenophases were the reproductive ones, we formulated and tested models for pre-anthesis, ♀ anthesis, ♂ anthesis, fruit maturation, and fruit dispersion. For all phenophases, GLS models, which account for temporal autocorrelation, were selected as the best ones. For pre-anthesis, the best model included electrical conductivity, pH, and daylength with a time-lagged period of six observations, or three months (Tab. 3). Daylength variation can be an important environmental trigger for flower initiation to many plants (De Fina and Ravelo, 1973; Fenner, 1998; Bergamaschi, 2007; Amasino, 2010). Therefore, daylength variation in the studied area could be the cause of the shared population response to changing from vegetative to reproductive culms. For floating macrophytes, daylength is also linked to nutrients absorption (Petrucio and Esteves, 2000). So time lagged period of three months can be an evidence that *F. robusta* needs continuous stimulus for flowering, possibly to accumulate enough nutrients for plants to reach a critical size for reproduction (Fenner, 1998).

Electrical conductivity is also closely linked with nutrients availability, as much as pH is associated with plant capacity to absorb nutrients (Thomaz and Esteves, 2011). Photosynthesis and consequently plant development are affected by pH, and in submerged species it is shown to be related to reproduction (Titus and Hoover, 1993). However, there are still doubts about relations between water pH and macrophytes; at the same time that species distribution and development can be influenced by pH (Catling et al., 1986; Arts et al., 1988), vegetation bed structure can also be influencing on pH levels (Carter et al., 1991).

Both ♀ and ♂ anthesis were explained by maximum temperatures (mean and maximum temperature registered) and wind speed. Temperature directly influences growth and development of plants (Bergamaschi, 2007), also influencing flowering (Rathcke and Lacey, 1985) and its respective synchrony (Schauber et al., 2002). One observation lag, for gynoecium anthesis, can indicate the need for a minimum temperature accumulation (heat sum) before anthesis can be completed (Rathcke and Lacey, 1985). Since *F. robusta* is an anemophilous species, wind is required for pollination. The smoother winds that occurred during anthesis could benefit pollen dispersal inside

each transect, being that pollen would hardly cross the water body without the proper wind speed (Niklas, 1985).

We could not find significant models for both fruit maturation and fruit dispersion (Tab. 3) and other plausible model remain to be investigated. Nevertheless, for fruit maturation the best model was marginally significant and similar to the pre-anthesis model, it contained variables related to nutrient availability and absorption (Fenner, 1998; Petrucio and Esteves, 2000; Esteves et al., 2011), what indicates that *F. robusta* could be using water nutrients to develop.

**Table 3.** Generalized least squares results of the best model for each reproductive phenophase. Variables with a succeeding lag number represent the respective fortnight lag. day: daylength; cond: electrical conductivity; Tmax: maximum temperature; mTmax: mean of maximum temperatures; wind: mean of maximum wind speed; rain: accumulated rainfall; NS: not significant.

Phenophase model	pseudo-R <sup>2</sup>	P-value	Δ AIC
<b>Pre-anthesis</b>			
day <sub>lag0</sub> + pH + cond	0.74	0.04	0
<b>♀ anthesis</b>			
mTmax <sub>lag1</sub> + wind	0.71	0.05	1.55
<b>♂ anthesis</b>			
Tmax + wind	0.56	0.05	0.35
<b>Fruit maturation</b>			
day <sub>lag1</sub> + pH + cond	0.67	0.07 NS	0
<b>Fruit dispersion</b>			
day <sub>lag0</sub> + wind + rain <sub>lag1</sub>	0.58	0.34 NS	0

#### 4. Conclusions

*F. robusta* culms in development, senescent and dead are present during the whole year, being uniformly distributed. Dead culms form an organic matter bed that creates suitable conditions for development of new culms, through both sexual and asexual reproduction. Every reproductive culm lasts around two months and produces a considerable amount of flowers and fruits, dying right after

completing its cycle. Thus, we indicate *F. robusta* as a good candidate for wetland managements in the southern Brazilian coast.

The species reproductive cycle is highly seasonal, occurring during the end of spring and throughout summer. A slight difference was found between the two transects sampled, which we attributed to different wind conditions. Since *F. robusta* flowers are wind pollinated, anthesis was related to wind speed and also to maximum temperatures, that relates to plant growth and development. Flowering seems to be modeled by daylength, water electrical conductivity, and pH, which we attributed to nutrients absorption and availability for plant development. However, water variables relation to macrophytes phenology still needs to be better explored.

### Acknowledgements

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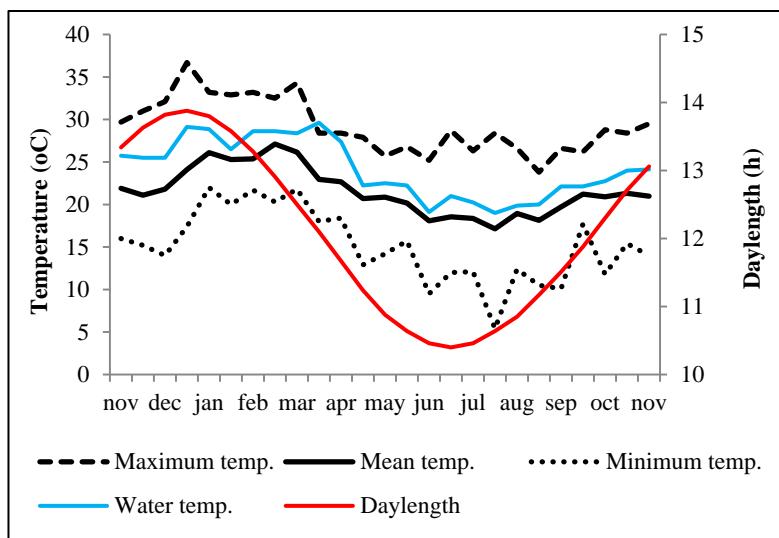
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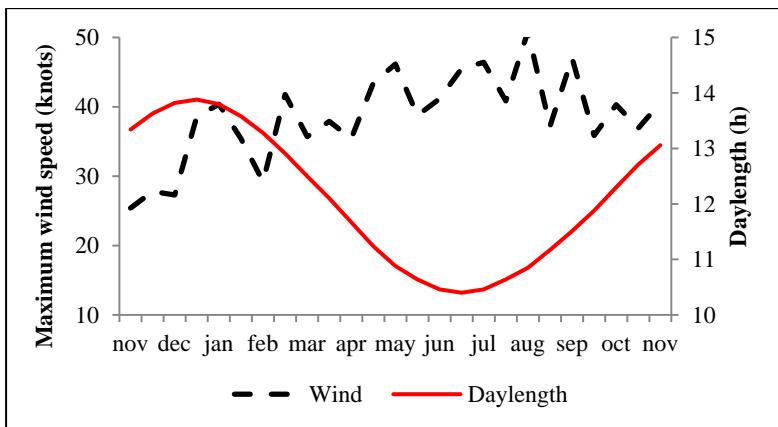
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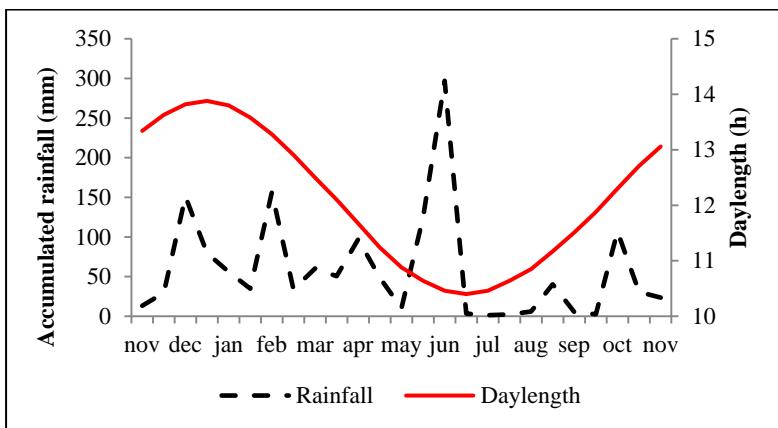
**APPENDIX A** - Graphics of environmental data collected for Lagoa Pequena, Florianópolis, SC, Brazil, during the period of *F. robusta* phenological observations (Nov. 2016 - Nov. 2017). 1: Mean, maximum and minimum temperature, water temperature, and daylength. 2: Maximum wind speed, and daylength. 3: Accumulated rainfall, and daylength. 4: Water pH, and daylength. 5: Water electrical conductivity, and daylength.



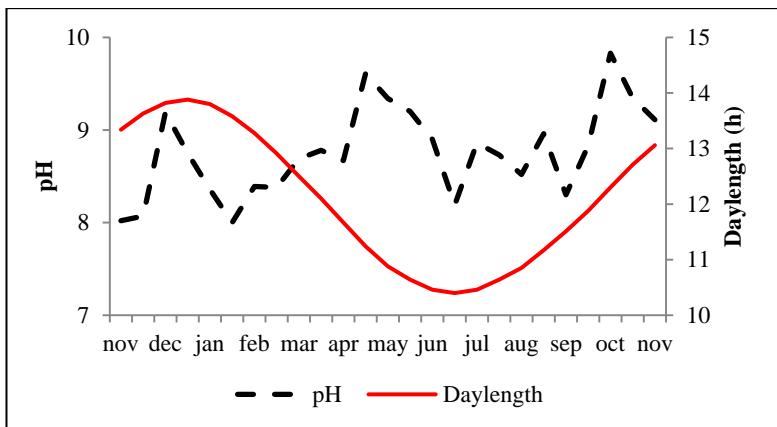
**Figure A.1.** Mean, maximum and minimum air temperature; water temperature; and daylength.



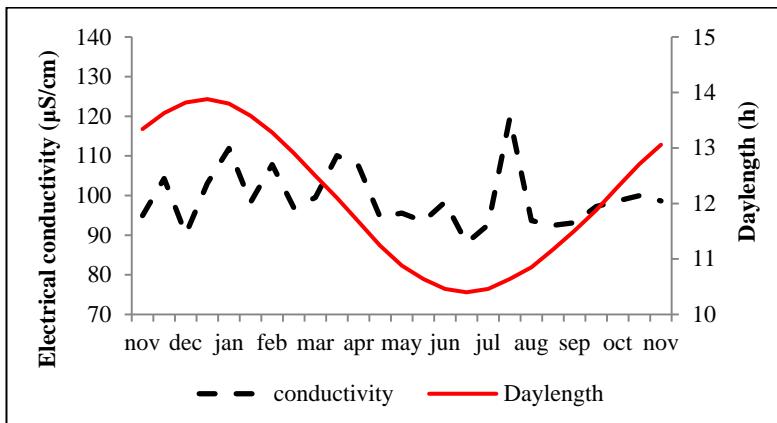
**Figure A.2.** Mean of maximum wind speed and daylength.



**Figure A.3.** Accumulated rainfall and daylength.



**Figure A.4.** Water pH and daylength.



**Figure A.5.** Water electrical conductivity and daylength.

**APPENDIX B** - Plausible models created for reproductive phenophases. Each model was tested through both ordinary least squares (OLS) and generalized least squares GLS). Variables with a succeeding lag number represent the respective fortnight lag. Day: daylength; cond: electrical conductivity; waterT: water temperature; Tmin: minimum temperature registered; mTmin: mean of minimum temperatures; Temp: mean temperature; Tmax: maximum temperature registered; mTmax: mean of maximum temperatures; rain: accumulated rainfall; wind: mean of maximum wind speed. 1. Pre-anthesis. 2. Gynoecium anthesis. 3. Androecium anthesis. 4. Fruit maturation. 5. Fruit dispersion.

### B.1. Pre-anthesis:

null	day <sub>lag2</sub> + cond	Tmax
day	day <sub>lag3</sub> + cond	Tmax <sub>lag1</sub>
day <sub>lag1</sub>	day <sub>lag4</sub> + cond	Tmax <sub>lag2</sub>
day <sub>lag2</sub>	day <sub>lag5</sub> + cond	mTmax
day <sub>lag3</sub>	day <sub>lag6</sub> + cond	mTmax <sub>lag1</sub>
day <sub>lag4</sub>	pH + cond	mTmax <sub>lag2</sub>
day <sub>lag5</sub>	day + pH + cond	waterT
day <sub>lag6</sub>	day <sub>lag1</sub> + pH + cond	Temp
pH	day <sub>lag2</sub> + pH + cond	Temp <sub>lag1</sub>
day + pH	day <sub>lag3</sub> + pH + cond	Temp <sub>lag2</sub>
day <sub>lag1</sub> + pH	day <sub>lag4</sub> + pH + cond	Temp <sub>lag3</sub>
day <sub>lag2</sub> + pH	day <sub>lag5</sub> + pH + cond	rain
day <sub>lag3</sub> + pH	day <sub>lag6</sub> + pH + cond	day + rain
day <sub>lag4</sub> + pH	Tmin	day <sub>lag1</sub> + rain
day <sub>lag5</sub> + pH	Tmin <sub>lag1</sub>	day <sub>lag2</sub> + rain
day <sub>lag6</sub> + pH	Tmin <sub>lag2</sub>	day <sub>lag3</sub> + rain
cond	mTmin	day <sub>lag4</sub> + rain
day + cond	mTmin <sub>lag1</sub>	day <sub>lag5</sub> + rain
day <sub>lag1</sub> + cond	mTmin <sub>lag2</sub>	day <sub>lag6</sub> + rain

### B.2. Gynoecium anthesis:

wind	day <sub>lag2</sub>	day + rain <sub>lag1</sub>
wind <sub>lag1</sub>	day <sub>lag3</sub>	day <sub>lag1</sub> + rain <sub>lag1</sub>
rain	day <sub>lag4</sub>	day <sub>lag2</sub> + rain <sub>lag1</sub>
rain <sub>lag1</sub>	day <sub>lag1</sub> + rain	day <sub>lag3</sub> + rain <sub>lag1</sub>
wind + rain	day <sub>lag2</sub> + rain	day <sub>lag4</sub> + rain <sub>lag1</sub>
wind + rain <sub>lag1</sub>	day <sub>lag3</sub> + rain	Temp + rain
day <sub>lag1</sub>	day <sub>lag4</sub> + rain	Temp <sub>lag1</sub> + rain

Temp <sub>lag2</sub> + rain	day <sub>lag1</sub> + wind	Temp + rain <sub>lag1</sub> +
Temp <sub>lag3</sub> + rain	day <sub>lag2</sub> + wind	wind
Temp <sub>lag4</sub> + rain	day <sub>lag3</sub> + wind	Temp <sub>lag1</sub> + rain <sub>lag1</sub> +
Temp + rain <sub>lag1</sub>	Tmax	wind
Temp <sub>lag1</sub> + rain <sub>lag1</sub>	Tmax <sub>lag1</sub>	Temp <sub>lag2</sub> + rain <sub>lag1</sub> +
Temp <sub>lag2</sub> + rain <sub>lag1</sub>	Tmax <sub>lag2</sub>	wind
Temp <sub>lag3</sub> + rain <sub>lag1</sub>	Tmax <sub>lag3</sub>	Temp <sub>lag3</sub> + rain <sub>lag1</sub> +
Temp <sub>lag4</sub> + rain <sub>lag1</sub>	mTmax	wind
Temp	mTmax <sub>lag1</sub>	mTmax + rain +
Temp <sub>lag1</sub>	mTmax <sub>lag2</sub>	wind
Temp <sub>lag2</sub>	mTmax <sub>lag3</sub>	mTmax <sub>lag1</sub> + rain +
Temp <sub>lag3</sub>	Tmax + wind	wind
Temp <sub>lag4</sub>	Tmax <sub>lag1</sub> + wind	mTmax <sub>lag2</sub> + rain +
day + rain + wind	Tmax <sub>lag2</sub> + wind	wind
day + rain <sub>lag1</sub> + wind	mTmax + wind	mTmax <sub>lag3</sub> + rain +
day <sub>lag1</sub> + rain + wind	mTmax <sub>lag1</sub> + wind	wind
day <sub>lag1</sub> + rain <sub>lag1</sub> + wind	mTmax <sub>lag2</sub> + wind	Tmax + rain + wind
rain <sub>lag1</sub> + wind	Temp + wind	Tmax <sub>lag1</sub> + rain +
day <sub>lag2</sub> + rain + wind	Temp <sub>lag1</sub> + wind	wind
day <sub>lag1</sub> + rain <sub>lag1</sub> + wind	Temp <sub>lag2</sub> + wind	Tmax <sub>lag2</sub> + rain +
day <sub>lag3</sub> + rain + wind	Temp <sub>lag3</sub> + wind	wind
day <sub>lag3</sub> + rain <sub>lag1</sub> + wind	Temp + rain + wind	Tmax <sub>lag3</sub> + rain +
day <sub>lag4</sub> + rain + wind	Temp <sub>lag1</sub> + rain + wind	wind
day <sub>lag4</sub> + rain <sub>lag1</sub> + wind	Temp <sub>lag2</sub> + rain + wind	pH
rain + rain <sub>lag1</sub>	Temp <sub>lag3</sub> + rain + wind	cond
day + wind	Temp <sub>lag4</sub> + rain + wind	pH + cond
		day <sub>lag1</sub> + pH
		day <sub>lag2</sub> + pH

### B.3. Androecium anthesis:

wind	day <sub>lag2</sub> + rain	Temp <sub>lag3</sub> + rain
wind <sub>lag1</sub>	day <sub>lag3</sub> + rain	Temp <sub>lag4</sub> + rain
rain	day <sub>lag4</sub> + rain	Temp + rain <sub>lag1</sub>
rain <sub>lag1</sub>	day + rain <sub>lag1</sub>	Temp <sub>lag1</sub> + rain <sub>lag1</sub>
wind + rain	day <sub>lag1</sub> + rain <sub>lag1</sub>	Temp <sub>lag2</sub> + rain <sub>lag1</sub>
wind + rain <sub>lag1</sub>	day <sub>lag2</sub> + rain <sub>lag1</sub>	Temp <sub>lag3</sub> + rain <sub>lag1</sub>
day <sub>lag1</sub>	day <sub>lag3</sub> + rain <sub>lag1</sub>	Temp <sub>lag4</sub> + rain <sub>lag1</sub>
day <sub>lag2</sub>	day <sub>lag4</sub> + rain <sub>lag1</sub>	Temp
day <sub>lag3</sub>	Temp + rain	Temp <sub>lag1</sub>
day <sub>lag4</sub>	Temp <sub>lag1</sub> + rain	Temp <sub>lag2</sub>
day <sub>lag1</sub> + rain	Temp <sub>lag2</sub> + rain	Temp <sub>lag3</sub>

$\text{Temp}_{\text{lag}4}$	$m\text{Tmax}_{\text{lag}1}$	$\text{Temp}_{\text{lag}2} + \text{rain}_{\text{lag}1} +$
day + rain + wind	$m\text{Tmax}_{\text{lag}2}$	wind
day + rain <sub>lag1</sub> + wind	$m\text{Tmax}_{\text{lag}3}$	$\text{Temp}_{\text{lag}3} + \text{rain}_{\text{lag}1} +$
day <sub>lag1</sub> + rain + wind	$\text{Tmax} + \text{wind}$	wind
day <sub>lag1</sub> + rain <sub>lag1</sub> + wind	$\text{Tmax}_{\text{lag}1} + \text{wind}$	$m\text{Tmax} + \text{rain} +$
day <sub>lag2</sub> + rain + wind	$\text{Tmax}_{\text{lag}2} + \text{wind}$	wind
day <sub>lag1</sub> + rain <sub>lag1</sub> + wind	$m\text{Tmax} + \text{wind}$	$m\text{Tmax}_{\text{lag}1} + \text{rain} +$
day <sub>lag3</sub> + rain + wind	$m\text{Tmax}_{\text{lag}1} + \text{wind}$	wind
day <sub>lag3</sub> + rain <sub>lag1</sub> + wind	$m\text{Tmax}_{\text{lag}2} + \text{wind}$	$m\text{Tmax}_{\text{lag}3} + \text{rain} +$
day <sub>lag4</sub> + rain + wind	$\text{Temp} + \text{wind}$	wind
day <sub>lag4</sub> + rain <sub>lag1</sub> + wind	$\text{Temp}_{\text{lag}1} + \text{wind}$	$\text{Tmax} + \text{rain} + \text{wind}$
rain + rain <sub>lag1</sub>	$\text{Temp}_{\text{lag}2} + \text{wind}$	$\text{Tmax}_{\text{lag}1} + \text{rain} +$
day + wind	$\text{Temp}_{\text{lag}3} + \text{wind}$	wind
day <sub>lag1</sub> + wind	$\text{Temp}_{\text{lag}1} + \text{rain} +$	$\text{Tmax}_{\text{lag}2} + \text{rain} +$
day <sub>lag2</sub> + wind	$\text{Temp}_{\text{lag}2} + \text{rain} +$	wind
day <sub>lag3</sub> + wind	$\text{Temp}_{\text{lag}3} + \text{rain} +$	$\text{Tmax}_{\text{lag}3} + \text{rain} +$
Tmax	$\text{Temp} + \text{rain}_{\text{lag}1} +$	pH
$\text{Tmax}_{\text{lag}1}$	$\text{wind}$	cond
$\text{Tmax}_{\text{lag}2}$	$\text{Temp}_{\text{lag}1} + \text{rain}_{\text{lag}1} +$	$\text{pH} + \text{cond}$
$\text{Tmax}_{\text{lag}3}$	$\text{wind}$	$\text{day}_{\text{lag}1} + \text{pH}$
$m\text{Tmax}$		$\text{day}_{\text{lag}2} + \text{pH}$

#### B.4. Fruit maturation:

wind	$\text{rain}_{\text{lag}6}$	$m\text{Tmax}_{\text{lag}3}$
$\text{wind}_{\text{lag}1}$	$\text{wind} + m\text{Tmax}$	$m\text{Tmax}_{\text{lag}4}$
$\text{wind}_{\text{lag}2}$	$\text{wind}_{\text{lag}1} + m\text{Tmax}$	day
$\text{wind}_{\text{lag}3}$	$\text{wind} + \text{Tmax}$	$\text{day}_{\text{lag}1}$
Temp	$\text{wind}_{\text{lag}1} + \text{Tmax}$	$\text{day}_{\text{lag}2}$
$\text{Temp}_{\text{lag}1}$	$\text{wind} + \text{Temp}$	$\text{day}_{\text{lag}3}$
$\text{Temp}_{\text{lag}2}$	$\text{wind}_{\text{lag}1} + \text{Temp}$	$\text{day}_{\text{lag}4}$
$\text{Temp}_{\text{lag}3}$	Tmax	Temp + rain
$\text{Temp}_{\text{lag}4}$	$\text{Tmax}_{\text{lag}1}$	Tmax + rain
rain	$\text{Tmax}_{\text{lag}2}$	$\text{Tmax} + \text{rain}_{\text{lag}1}$
$\text{rain}_{\text{lag}1}$	$\text{Tmax}_{\text{lag}3}$	$m\text{Tmax} + \text{rain}$
$\text{rain}_{\text{lag}2}$	$\text{Tmax}_{\text{lag}4}$	$m\text{Tmax} + \text{rain}_{\text{lag}1}$
$\text{rain}_{\text{lag}3}$	mTmax	$\text{Tmax}_{\text{lag}1} + \text{rain}$
$\text{rain}_{\text{lag}4}$	$m\text{Tmax}_{\text{lag}1}$	$m\text{Tmax}_{\text{lag}1} + \text{rain}$
$\text{rain}_{\text{lag}5}$	$m\text{Tmax}_{\text{lag}2}$	$\text{Tmax}_{\text{lag}2} + \text{rain}$

mTmax <sub>lag2</sub> + rain	day <sub>lag1</sub> + rain +	day <sub>lag4</sub> + rain +
day + rain	wind <sub>lag3</sub>	wind <sub>lag1</sub>
day + rain + wind	day <sub>lag1</sub> + rain <sub>lag1</sub> +	day <sub>lag4</sub> + rain +
day + rain +	wind	wind <sub>lag2</sub>
wind <sub>lag1</sub>	day <sub>lag1</sub> + rain <sub>lag1</sub> +	day <sub>lag4</sub> + rain +
day + rain +	wind <sub>lag1</sub>	wind <sub>lag3</sub>
wind <sub>lag2</sub>	day <sub>lag1</sub> + rain <sub>lag1</sub> +	day <sub>lag4</sub> + rain <sub>lag1</sub> +
day + rain +	wind <sub>lag2</sub>	wind
wind <sub>lag3</sub>	day <sub>lag1</sub> + rain <sub>lag1</sub> +	day <sub>lag4</sub> + rain <sub>lag1</sub> +
day + rain <sub>lag1</sub> + wind	wind <sub>lag3</sub>	wind <sub>lag1</sub>
day + rain <sub>lag1</sub> +	day <sub>lag2</sub> + rain + wind	day <sub>lag4</sub> + rain <sub>lag1</sub> +
wind <sub>lag1</sub>	day <sub>lag2</sub> + rain +	wind <sub>lag2</sub>
day + rain <sub>lag1</sub> +	wind <sub>lag1</sub>	day <sub>lag4</sub> + rain <sub>lag1</sub> +
wind <sub>lag2</sub>	day <sub>lag2</sub> + rain +	wind <sub>lag3</sub>
day + rain +	wind <sub>lag2</sub>	day <sub>lag5</sub> + rain + wind
wind <sub>lag3</sub>	day <sub>lag2</sub> + rain +	day <sub>lag5</sub> + rain +
day + rain <sub>lag2</sub> + wind	wind <sub>lag3</sub>	wind <sub>lag1</sub>
day + rain <sub>lag2</sub> +	day <sub>lag2</sub> + rain <sub>lag1</sub> +	day <sub>lag5</sub> + rain +
wind <sub>lag1</sub>	wind	wind <sub>lag2</sub>
day + rain <sub>lag2</sub> +	day <sub>lag2</sub> + rain <sub>lag1</sub> +	day <sub>lag5</sub> + rain +
wind <sub>lag2</sub>	wind <sub>lag1</sub>	wind <sub>lag3</sub>
day + rain <sub>lag2</sub> +	day <sub>lag2</sub> + rain <sub>lag1</sub> +	day <sub>lag5</sub> + rain <sub>lag1</sub> +
wind <sub>lag3</sub>	wind <sub>lag2</sub>	wind
Tmax + rain + wind	day <sub>lag2</sub> + rain <sub>lag1</sub> +	day <sub>lag5</sub> + rain <sub>lag1</sub> +
Tmax + rain +	wind <sub>lag3</sub>	wind <sub>lag1</sub>
wind <sub>lag1</sub>	day <sub>lag3</sub> + rain + wind	day <sub>lag5</sub> + rain <sub>lag1</sub> +
Tmax + rain +	day <sub>lag3</sub> + rain +	wind <sub>lag2</sub>
wind <sub>lag2</sub>	wind <sub>lag1</sub>	day <sub>lag5</sub> + rain <sub>lag1</sub> +
Tmax + rain +	day <sub>lag3</sub> + rain +	wind <sub>lag3</sub>
wind <sub>lag3</sub>	wind <sub>lag2</sub>	day <sub>lag6</sub> + rain + wind
pH	day <sub>lag3</sub> + rain +	day <sub>lag6</sub> + rain +
pH + cond	wind <sub>lag3</sub>	wind <sub>lag1</sub>
cond	day <sub>lag3</sub> + rain <sub>lag1</sub> +	day <sub>lag6</sub> + rain +
day <sub>lag1</sub> + rain	wind	wind <sub>lag2</sub>
day <sub>lag2</sub> + rain	day <sub>lag3</sub> + rain <sub>lag1</sub> +	day <sub>lag6</sub> + rain +
day <sub>lag1</sub> + rain +	wind <sub>lag1</sub>	wind <sub>lag3</sub>
wind	day <sub>lag3</sub> + rain <sub>lag1</sub> +	day <sub>lag6</sub> + rain <sub>lag1</sub> +
day <sub>lag1</sub> + rain +	wind <sub>lag2</sub>	wind
wind <sub>lag1</sub>	day <sub>lag3</sub> + rain <sub>lag1</sub> +	day <sub>lag6</sub> + rain <sub>lag1</sub> +
day <sub>lag1</sub> + rain +	wind <sub>lag3</sub>	wind <sub>lag1</sub>
wind <sub>lag2</sub>	day <sub>lag4</sub> + rain + wind	day <sub>lag6</sub> + rain <sub>lag1</sub> +

day <sub>lag6</sub> + rain <sub>lag1</sub> +	day <sub>lag1</sub> + pH + cond	day <sub>lag5</sub> + pH
wind <sub>lag3</sub>	day <sub>lag2</sub> + pH + cond	day <sub>lag6</sub> + pH
wind + rain	day <sub>lag3</sub> + pH + cond	day + cond
wind <sub>lag1</sub> + rain	day <sub>lag4</sub> + pH + cond	day <sub>lag1</sub> + cond
wind <sub>lag2</sub> + rain	day <sub>lag5</sub> + pH + cond	day <sub>lag2</sub> + cond
wind <sub>lag3</sub> + rain	day <sub>lag6</sub> + pH + cond	day <sub>lag3</sub> + cond
wind + rain <sub>lag1</sub>	day + pH	day <sub>lag4</sub> + cond
wind <sub>lag1</sub> + rain <sub>lag1</sub>	day <sub>lag1</sub> + pH	day <sub>lag5</sub> + cond
wind <sub>lag1</sub> + rain <sub>lag1</sub>	day <sub>lag2</sub> + pH	day <sub>lag6</sub> + cond
wind <sub>lag3</sub> + rain <sub>lag1</sub>	day <sub>lag3</sub> + pH	
day + pH + cond	day <sub>lag4</sub> + pH	

### B.5. Fruit dispersion:

wind	Tmax + wind + rain	day + wind + rain
rain	lag <sub>1</sub>	day + wind + rain
wind + rain	Tmax <sub>lag1</sub> + wind	lag <sub>1</sub>
Tmax	Tmax <sub>lag1</sub> + wind + rain	day <sub>lag1</sub>
Tmax <sub>lag1</sub>	Tmax <sub>lag1</sub> + wind + rain	day <sub>lag1</sub> + wind + rain
pH	Tmax <sub>lag1</sub> + wind + rain <sub>lag1</sub>	day <sub>lag1</sub> + wind + rain
cond	Tmax <sub>lag2</sub> + wind	day <sub>lag1</sub> + wind + rain <sub>lag1</sub>
pH + cond	Tmax <sub>lag2</sub> + wind	day <sub>lag2</sub>
wind + rain <sub>lag1</sub>	Tmax <sub>lag2</sub> + wind + rain	day <sub>lag2</sub> + wind + rain
mTmax	Tmax <sub>lag2</sub> + wind + rain <sub>lag1</sub>	day <sub>lag2</sub> + wind + rain
mTmax <sub>lag1</sub>	Tmax <sub>lag2</sub> + wind + rain <sub>lag1</sub>	day <sub>lag2</sub> + wind + rain
mTmax + wind	pH + wind	day <sub>lag3</sub>
mTmax + wind + rain <sub>lag1</sub>	pH + rain + wind	day <sub>lag3</sub> + wind + rain
mTmax + wind + rain	Temp + wind	day <sub>lag3</sub> + wind + rain
mTmax <sub>lag1</sub> + wind	Temp + wind + rain	day <sub>lag3</sub> + wind + rain
mTmax <sub>lag1</sub> + wind + rain <sub>lag1</sub>	Temp <sub>lag1</sub> + wind + rain	day <sub>lag4</sub>
mTmax <sub>lag2</sub> + wind	Temp <sub>lag1</sub> + wind + rain <sub>lag1</sub>	day <sub>lag4</sub> + wind + rain
mTmax <sub>lag2</sub> + wind + rain	Temp <sub>lag1</sub> + wind	day <sub>lag4</sub> + wind + rain <sub>lag1</sub>
mTmax <sub>lag2</sub> + wind + rain <sub>lag1</sub>	Temp <sub>lag2</sub> + wind	day <sub>lag5</sub>
Tmax + wind	Temp <sub>lag2</sub> + wind + rain <sub>lag1</sub>	day <sub>lag5</sub> + wind + rain
Tmax + wind + rain	Temp <sub>lag2</sub> + wind + rain <sub>lag1</sub>	day <sub>lag5</sub> + wind + rain <sub>lag1</sub>
	day	day <sub>lag6</sub>

day<sub>lag6</sub> + wind +  
rain

day<sub>lag6</sub> + wind +  
rain<sub>lag1</sub>

## 6 CONSIDERAÇÕES FINAIS

### 6.1 CONSIDERAÇÕES SOBRE AS ESPÉCIES ESTUDADAS

As duas espécies aqui estudadas, *E. laeviglumis* e *F. robusta*, de alguma forma apresentam potencial para uso em manejo de áreas úmidas e fitorremediação de águas residuais. Ambas se reproduzem tanto vegetativamente quanto por sementes e desenvolvem-se relativamente rápido. Pelo observado na área de estudo, a maior parte da propagação, para ambas espécies, ocorre por meios vegetativos, porém não mensuramos tal modo reprodutivo. Estudamos e descrevemos brevemente a fenologia reprodutiva das duas espécies e comprovamos que ambas são protóginas e produzem uma quantidade considerável de sementes.

Testamos a germinabilidade de *E. laeviglumis* e concluímos que a taxa de germinação é baixíssima, assim como o vigor das sementes. Compreendemos que estudos mais detalhados sobre a fisiologia das sementes são necessários para melhor entender a dinâmica reprodutiva da espécie, assim como um estudo genético da população. Por já ser de conhecimento da ciência que espécies de macrófitas emergentes podem se reproduzir clonalmente, sugerimos que *E. laeviglumis* pode estar se reproduzindo por geitonogamia, já que pouquíssimas sementes germinaram em nosso teste. Reprodução sexual entre clones pode gerar depressão endogâmica e pode estar ocasionando o baixo vigor das sementes produzidas. Entendemos que *E. laeviglumis* pode ser uma espécie interessante para estabelecer novas populações em áreas úmidas, e sugerimos que a propagação de sementes seja feita em conjunto com o transplante de rizomas.

Já para *F. robusta* pudemos descrever com mais detalhe sua dinâmica fenológica. A amostragem em parcelas mostrou-se eficiente, porém de difícil acesso devido às condições do ambiente, principalmente no transecto da margem sul. A população amostrada parece bem estabelecida, com colmos se desenvolvendo e senescendo durante todo o ano. A própria população parece se reciclar, colmos mortos formam uma cama de matéria orgânica sob os colmos em desenvolvimento, o que gera condições para que novos colmos possam se desenvolver. Cada colmo produziu uma enorme quantidade de

sementes, porém a maioria dos colmos em desenvolvimento observados parecem ser de origem vegetativa.

O papel de *F. robusta* como barreira contra o *fetch* é facilmente detectado pela presença de espécies menores em meio à população, inclusive de indivíduos de *E. laeviglumis*. Também observamos a espécie *U. arrecta* avançando sob a população de um dos transectos, porém os dados coletados não representaram bem essa situação.

Testamos duas metodologias de coleta de dados fenológicos, intensidade e atividade das fenofases, e observamos resultados semelhantes por ambos os métodos. A estação reprodutiva foi bem definida e constituiu a única parte do ciclo de vida da espécie apresentando sazonalidade. Testamos variáveis ambientais para explicar as fenofases sazonais e concluímos que características da água também influenciaram na expressão das fenofases. Isso indica que a fenologia de macrófitas deve ser melhor explorada para que possamos compreender o papel das condições limnológicas na expressão reprodutiva das plantas.

Decidimos não incluir na presente dissertação, mas também realizamos um teste de germinação com sementes de *F. robusta*, sob as mesmas condições do teste com sementes de *E. laeviglumis* (25° e 12h de luz) e nenhuma semente germinou. Quando testadas em solução de tetrazólio também não observamos nenhuma reação positiva, indicando a falta de vigor das sementes testadas.

## 6.2 CONSIDERAÇÕES SOBRE A ÁREA DE ESTUDO

A maioria dos corpos hídricos hoje em dia se encontra em situação crítica, sendo cada vez mais explorados e negligenciados. A legislação ambiental brasileira, em teoria, protege exemplarmente tais corpos d'água, porém tal fato não condiz com a realidade. Lagoas de água doce em áreas urbanas são vistas como de usufruto do homem, e não como ambientes dignos de preservação, mesmo que representem uma possível fonte de água para a população. A área de estudo, a Lagoa Pequena no bairro Rio Tavares, é um ótimo exemplo desse descaso para com os recursos naturais.

Por ser um afloramento de água subterrânea, a LP poderia representar uma importantíssima fonte de água potável. Porém, a displicênciça do desenvolvimento urbano do distrito do Campeche, e de toda ilha de Florianópolis, vem destruindo esse privilégio de desfrutar

de um recurso natural tão valioso. A construção indevida de fossas sépticas prejudica diretamente a qualidade da água da lagoa, assim como a construção imobiliária desenfreada em áreas do entorno do corpo d'água, que em teoria seriam consideradas como Área de Preservação Permanente. A própria Avenida Campeche, à margem oeste da LP, representa uma agressão ao funcionamento do ecossistema por destruir a vegetação circundante. A criação de animais domésticos na área da lagoa também é indevida, inclusive impediu que uma parte do nosso trabalho fosse realizada, a marcação de parcelas permanentes para o estudo da fenologia de *E. laeviglumis*.

Dentre os impactos causados pela atividade humana, a LP sofre com a invasão da espécie exótica e agressiva, braquiária-do-brejo (*U. arrecta*). A situação da invasão pode ser considerada crítica e de difícil manejo. Outros ambientes úmidos também tem sofrido com a invasão dessa espécie, até mesmo outras áreas no Campeche, e um manejo eficiente ainda não é realizado. Infelizmente o poder público responsável por essa área parece não se importar com a situação, talvez por falta de conhecimento, ou talvez por puro descaso. Para realização deste trabalho uma autorização para pesquisa científica em unidades de conservação foi concedida pela Fundação Municipal do Meio Ambiente de Florianópolis, FLORAM, mediante pagamento (nº processo: E 057319/2016).