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UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
Campus de Botucatu

BIOLOGIA REPRODUTIVA EM LENTIBULARIACEAE RICH.

FERNANDA GOMES RODRIGUES

Tese apresentada ao Instituto de Biociências, Câmpus de Botucatu, UNESP, para obtenção de título de Doutor no Programa de Pós-Graduação em Ciências Biológicas (Botânica), Área de concentração: Sistemática e Ecologia Vegetal.

BOTUCATU - SP
2022

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BIOLOGIA REPRODUTIVA EM LENTIBULARIACEAE RICH.

RESUMO – Lentibulariaceae é uma família de plantas carnívoras diversa por apresentar alto número de espécies com ampla distribuição e diferentes padrões morfólogicos. Além disso, são encontradas peculiaridades morfológicas (adaptação a diferentes ambientes) e genômicas (redução de genomas) de forma que algumas espécies têm sido propostas como organismos-modelos. No entanto, trabalhos em biologia reprodutiva e ecologia da polinização são escassos, os quais podem ser importantes para maior entendimento e subsídios para a preservação das espécies na família. Buscamos entender qual o estado da arte em biologia reprodutiva de Lentibulariaceae, por meio de uma revisão sistemática abrangente e análise crítica. Além de apontar características florais que possam interferir no sistema reprodutivo, mostramos como atributos florais e o sistema reprodutivo evoluíram na família por meio de uma filogenia existente para o grupo. Por fim, apontamos lacunas metodológicas e expomos direções futuras a trabalhos de biologia reprodutiva na família. Também avaliamos empiricamente, quais características florais são importantes para o sucesso reprodutivo de *Utricularia damazioi* e de que forma esta espécie anual se mantém em ambientes isolados (campos rupestres, Cerrado). Consideramos o espaço entre o lábio inferior da corola e os órgãos reprodutivos importantes ao encaixe planta-polinizador e consequente sucesso da polinização. Além desta característica, a reflectância floral parece ser promissora na predição de polinizadores. Devido ao seu tamanho e comportamento, abelhas de tamanho médio (~ 10 mm de comprimento) são polinizadores eficazes de *Utricularia damazioi*. Nesta espécie, quando a polinização cruzada não ocorre, a autopolinização espontânea tardia pode ocorrer. Assim, *U. damazioi* conta com a produção de sementes por autofecundação na ausência de vetores de polinização e a diversidade genética aumenta em sua presença, mantendo características florais atraentes. Essa flexibilidade representa uma maior possibilidade de manter populações isoladas. Devido à especificidade dos microambientes onde ocorrem espécies de Lentibulariaceae, perturbações antrópicas e ambientais, como aridez sazonal, são capazes de destruir populações, assim como diminuir a ocorrência de polinizadores adequados. Desta forma, as adaptações do sistema reprodutivo que promovem a autogamia, são derivadas na família e podem ter evoluído como respostas a perturbações ambientais e além de ser uma estratégia reprodutiva que mantêm a ocorrência de populações anuais nestes microambientes.

Palavras-chave: acoplamento flor-polinizador, autofecundação tardia, hercogamia, plantas carnívoras, polinizadores, reflectância floral, revisão sistemática.

REPRODUCTIVE BIOLOGY IN LENTIBULARIACEAE RICH.

ABSTRACT – Lentibulariaceae is a family of carnivorous plants that is diverse because it has a high number of species with a wide distribution and different morphological patterns. Furthermore, morphological (adaptation to different environments) and genomic (reduction of genomes) peculiarities are found, so some species have been proposed as model organisms. However, studies on reproductive biology and pollination ecology are scarce, which may be important for greater understanding and subsidies for the preservation of species in the family. Through a comprehensive systematic review and critical analysis, we seek to understand the state of the art in Lentibulariaceae reproductive biology. In addition to pointing out floral characteristics that may interfere with the reproductive system, we show how floral attributes and the reproductive system evolved in the family through an existing phylogeny for the group. Finally, we point out methodological gaps and expose future directions for work on reproductive biology in the family. We also empirically evaluated which floral characteristics are important for the reproductive success of *Utricularia damazioi* and how this annual species maintains itself in isolated environments (*campos rupestres*, Cerrado). We consider the space between the lower lip of the corolla and the reproductive organs to be important for the plant-pollinator fit and consequent pollination success. In addition to this feature, floral reflectance seems to be promising in predicting pollinators. Due to their size and behavior, medium-sized bees (~10mm length) are effective pollinators of *Utricularia damazioi*. When cross-pollination does not occur in this species, late spontaneous self-pollination can occur. Thus, *U. damazioi* relies on seed production by self-fertilization in the absence of pollination vectors, and genetic diversity increases in their presence, maintaining attractive floral characteristics. This flexibility represents a greater possibility of keeping isolated populations. Due to the specificity of the microenvironments where Lentibulariaceae species occur, anthropic and environmental disturbances, such as seasonal aridity, can destroy populations and reduce the occurrence of suitable pollinators. In this way, the adaptations of the reproductive system that promote autogamy, are derived in the family and may have evolved as responses to environmental disturbances in addition to being a reproductive strategy that maintains the occurrence of annual populations in these microenvironments.

Keywords: carnivorous plants, delayed selfing, floral reflectance, flower-pollinator coupling, herkogamy, pollinators, systematic review.

A partir das informações levantadas na revisão sistemática, observamos se existem características florais preditivas quanto aos polinizadores, buscando padrões nas corolas de espécies polinizadas pelos mesmos grupos taxonômicos. Adicionalmente, inferimos filogeneticamente como características do sistema reprodutivo, atrativos e recursos florais divergiram evolutivamente entre os três gêneros de modo a elucidar os estados primitivos ou derivados e propor a flor plesiomórfica de Lentibulariaceae.

Por fim, após uma análise crítica dos estudos levantados, apontamos lacunas metodológicas e no conhecimento e, consequentemente direções a futuros estudos em biologia da polinização em Lentibulariaceae.

No segundo capítulo, buscamos avaliar a importância da reprodução sexuada em *Utricularia damazioi* e se há dependência de polinizadores, de forma elucidar como a espécie se mantem em ambientes isolados. Adicionalmente, acompanhamos mudanças na corola e nos órgãos reprodutivos durante a antese com objetivo de avaliar a importância de tais mudanças no sucesso da reprodução sexuada.

Também testamos a hipótese de *U. damazioi* ser polinizada por abelhas por meio da avaliação de comportamento de visita e papel ecológico dos visitantes florais. Nesta análise, incluímos o ajuste planta-polinizador para verificar sua aplicabilidade como inferência de eficácia. Além disso, avaliamos de que forma características florais são percebidas por polinizadores eficazes e podem funcionar como atrativos.

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CAPÍTULO 1: Biologia reprodutiva em Lentibulariaceae Rich.: revisão sistemática e evolução

Capítulo formatado para publicação no periódico Plant Biology (normas em anexo)

REVISÃO

RESUMO

Lentibulariaceae é uma família de plantas carnívoras diversa por apresentar alto número de espécies com ampla distribuição e diferentes padrões morfológicos. Além disso, são encontradas peculiaridades morfológicas como a adaptação a diferentes ambientes e redução de genomas, de forma que algumas espécies têm sido propostas como organismos-modelos. Porém, trabalhos em biologia reprodutiva são escassos, os quais podem ser importantes para maior entendimento e subsídios para a preservação das espécies na família. Buscamos entender o estado da arte em biologia reprodutiva de Lentibulariaceae, por meio de uma revisão sistemática abrangente e análise crítica. Além de apontar características florais associadas à predição de polinizadores, e que possam interferir no sistema reprodutivo, mostramos como atributos florais e o sistema reprodutivo evoluíram na família por meio de uma filogenia existente para o grupo de forma a propor a flor plesiomórfica da família. Por fim, apontamos lacunas e expomos direções a trabalhos de biologia reprodutiva na família. Diversos táxons são visitantes em Lentibulariaceae, no entanto, o déficit de análises da performance do polinizador impossibilitou estabelecer relações significativas entre polinizadores e características florais. Consideramos o espaço entre o lábio inferior da corola e os órgãos reprodutivos importantes ao encaixe planta-polinizador e consequente sucesso da polinização. Além desta, a reflectância floral parece ser promissora na predição de polinizadores. Possivelmente o ancestral era

alógamo e autocompatível, com características associadas à melitofilia e polinização cruzada. Características recentes que promovem autofecundação, como a hercogamia temporária, corroboram uma possível mudança de alogamia para autogamia na família. Adicionalmente, características que promovem a fecundação cruzada são mantidas de forma a garantir o sucesso reprodutivo. Devido à especificidade dos microambientes onde ocorrem espécies de Lentibulariaceae, perturbações antrópicas são capazes de destruir populações, assim como reduzir populações de polinizadores adequados. Desta forma, adaptações do sistema reprodutivo que promovam a autogamia podem ter evoluído como respostas a perturbações ambientais.

Palavras-chave: flor plesiomórfica, hercogamia, plantas carnívoras, polinizadores, reflectância floral, tricomas florais, visitantes florais.

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CONSIDERAÇÕES FINAIS

Considerando as hipóteses propostas para o presente estudo, e levando-se em conta a carência de trabalhos em biologia reprodutiva na família Lentibulariaceae, nossos resultados forneceram pela primeira vez informações sobre o sistema reprodutivo do ponto de vista morfológico e evolutivo.

Consideramos o espaço entre o lábio inferior da corola e os órgãos reprodutivos importantes ao encaixe planta-polinizador e consequente sucesso da polinização. Quando aplicada empiricamente em *U. damazioi* a análise destas dimensões teve sucesso como forma de avaliação da eficiência dos polinizadores. Além desta característica, vimos a importância de acompanhamento de mudanças nas posições dos órgãos reprodutivos ao longo da antese, visto que a hercogamia temporária pode ocorrer, como garantia reprodutiva frente a condições ambientais desfavoráveis.

A avaliação da reflectância floral em conjunto com a observação do comportamento de polinizadores trouxe maior conhecimento da importância da manutenção de atrativos florais na corola, mesmo em espécies autoférteis.

Desta forma, ressaltamos que características levantadas da revisão sistemática que foram apontadas como promissoras à trabalhos de biologia reprodutiva na família, de fato quando aplicadas empiricamente trouxeram maior compreensão neste âmbito, com a espécie estudada *U. damazioi*. Assim, fornecemos subsídios teóricos que foram testados empíricamente aos próximos trabalhos de biologia reprodutiva em Lentibulariaceae.