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Endogenous and exogenous factors that influence the success of stem fragments of aquatic macrophytes

Fatores endógenos e exógenos que influenciam o sucesso de fragmentos caulinares de macrófitas aquáticas

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Sidinei Magela Thomaz[1]*

[1]Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura – Nupélia, PPG em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, Campus Universitário, CEP 87020-900, Maringá, PR, Brasil

*e-mail: smthomaz@nupelia.uem.br

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Abstract: Aim: Many macrophyte species rely on stem fragments as their primary or complementary means of asexual reproduction. This systematic review synthesizes the key endogenous and exogenous factors that influence the success of these fragments, evaluated by their potential for colonization, regeneration, and the establishment of new plants. **Methods:** Systematic review using the Web of Science and Scopus databases on 2 January 2025. This systematic review was complemented with additional sources identified through cross-referencing and manual searches. **Results:** Macrophyte growth from stem fragments has been documented in 157 investigations (110 studies investigated the determinants of fragment performance) and 76 macrophyte species. Endogenous factors most frequently explored include the presence of nodes, fragment size, and stem position on the parent plant. Among the exogenous factors, desiccation, nutrient availability, and light are the most commonly investigated abiotic influences, while competition, herbivory and facilitation are important biotic interactions affecting fragment performance. Climate change (alterations in temperature, CO_2 and precipitation) and eutrophication potentially drive shifts in macrophyte communities by impacting the success of asexual reproduction through stem fragments. Identified gaps include how the parent plant, grown in different conditions, influences fragment performance, a geographical bias toward economically important species in temperate regions, and insufficient integration of field and experimental research. **Conclusions:** This review highlights that environmental abiotic factors and biotic interactions, typically studied for their effects on adult macrophytes, also play a crucial role in macrophytes establishment during the early life stages by influencing their asexual reproduction success via stem fragments. Recognizing the factors governing stem fragment reproductive success is vital for understanding macrophyte species distributions, and this knowledge should be incorporated into macrophyte metacommunity models.

Keywords: aquatic plants; macrophyte asexual reproduction; invasive species; stem macrophyte colonization; stem macrophyte establishment.

Resumo: Objetivo: Muitas espécies de macrófitas dependem de fragmentos de caule como meio principal ou complementar de reprodução assexuada. Esta revisão sistemática sintetiza os principais fatores endógenos e exógenos que influenciam o sucesso desses fragmentos, avaliado por seu potencial de colonização, regeneração e estabelecimento de novas plantas. **Métodos:** Revisão bibliográfica usando as plataformas Web of Science e Scopus em 2 de janeiro de 2025. Esta revisão sistemática foi complementada com fontes adicionais identificadas através de revisões cruzadas e buscas manuais.

Resultados: O crescimento de macrófitas a partir de fragmentos de caule foi documentado em 157 investigações (110 estudos investigaram os determinantes do desempenho dos fragmentos) e 76 espécies de macrófitas. Entre os fatores endógenos mais frequentemente explorados estão a presença de nós, o tamanho do fragmento e a posição do caule na planta-mãe. Entre os fatores exógenos, a dessecação, a disponibilidade de nutrientes e a luz são as influências abióticas mais investigadas, enquanto a competição, herbivoria e facilitação constituem interações bióticas importantes que afetam o desempenho dos fragmentos. As mudanças climáticas (alterações na temperatura, CO_2 e precipitação) e a eutrofização podem impulsionar mudanças nas comunidades de macrófitas ao impactar o sucesso da reprodução assexuada por fragmentos caulinares. As lacunas identificadas incluem como a planta-mãe, cultivada em diferentes condições, influencia o desempenho dos fragmentos; um viés geográfico voltado para espécies economicamente importantes estudadas em regiões temperadas; e a insuficiente integração entre pesquisas de campo e experimentais. **Conclusões:** Esta revisão destaca que fatores ambientais abióticos e interações bióticas, tipicamente estudados por seus efeitos sobre macrófitas adultas, também desempenham um papel crucial no estabelecimento de macrófitas nos estágios iniciais de vida, ao influenciarem o sucesso da reprodução assexuada via fragmentos caulinares. Reconhecer os fatores que determinam o sucesso reprodutivo desses fragmentos é fundamental para compreender a distribuição das espécies de macrófitas e esse conhecimento deveria ser considerado em modelos de metacomunidades de macrófitas.

Palavras-chave: plantas aquáticas; reprodução asexual de macrófitas; espécies invasoras; colonização de macrófitas por caules; estabelecimento de macrófitas por caules.

1. Introduction

The ecological dynamics of macrophyte populations are influenced by the production and dispersal of plant propagules, and by the subsequent establishment of plants from those propagules at new sites. These three steps are related to core ecological principles. The two first steps, namely the propagule production and dispersal, underpin mass effects, which describe the net movement of individuals or propagules between patches due to differences in population size or density (Shmida & Wilson, 1985; Leibold et al., 2004). These steps are also closely related to the concept of propagule pressure, which specifically addresses the role of propagule dispersal for the success of invasive species establishment (Colautti et al., 2006; Duncan, 2011). The third step, namely the establishment of new plants from propagules, is associated with the species sorting paradigm (Leibold et al., 2004), which highlights the critical influence of environmental conditions on propagule survival and growth upon reaching a new site. While environmental conditions are key drivers of metacommunity structure, massive dispersal can enhance the chances of establishment in otherwise sub-optimal environmental conditions (Leung et al., 2004; Duncan, 2011) or can counteract local competitive exclusion by rescuing species (Leibold et al., 2004). Therefore, a comprehensive investigation into propagule dispersal dynamics, encompassing both mass effects and propagule pressure, as well as the primary factors influencing propagule establishment success, encompassing species sorting, is essential for understanding the spatial and temporal patterns of aquatic macrophyte metacommunities. In particular, species sorting plays a central role in habitats where environmental conditions limit plant establishment from propagules or where dispersal constraints restrict propagule arrival.

Macrophytes reproduce both sexually (via seeds) and asexually (via vegetative structures such as turions, tubers, perennating rhizomes, and shoot or stem fragments), with a general tendency for the latter to replace the former (Sculthorpe, 1967; Cronk & Fennessy, 2001). These diverse strategies likely contribute to the stability of aquatic macrophyte communities in disturbed habitats, such as river-floodplain ecosystems (Combroux et al., 2001; Combroux & Bornette, 2004).

Among the asexual reproductive strategies of macrophytes, plant fragmentation is particularly significant and can be the primary dispersal mechanism for many species. Macrophyte fragmentation results from endogenous processes or from physical and biotic disturbances that break the main stem and lateral branches, producing propagules that are unspecialized asexual structures (hereafter referred to as “stem fragments”). These propagules facilitate the dispersal and establishment of new plants and populations (Sculthorpe, 1967; Barrat-Segretain & Bornette, 2000; Thomaz et al., 2009; Li, 2014). In numerous streams, for instance, these fragments play a vital role in submerged macrophyte reproduction and plant establishment (Riis & Sand-Jensen, 2006; Riis, 2008; Sand-Jensen et al., 1999; Heidbüchel et al., 2016).

While sexual reproduction in plants offers well recognized advantages, asexual structures, such as stem fragments, also provide significant reproductive benefits. For example, many macrophyte species produce large quantities of these fragments (Barrat-Segretain, 1996; Riis, 2008; Xie et al., 2018), which are readily dispersed through various mechanisms (Jones et al., 2020; Thomaz, 2025). Moreover, fragmentation induced by disturbances (e.g., water flow, waves, or herbivory) is less dependent on seasonal factors, enabling macrophytes to exhibit a nearly aseasonal reproductive cycle (Amoros & Bornette, 1999; Barrat-Segretain et al., 1998; Barrat-Segretain & Bornette, 2000).

Researchers have explored the mechanisms and agents of plant fragmentation, alongside the vectors of fragment dispersal, through both experimental (e.g., Xie & Yu, 2011; Koch et al., 2010; Braga et al., 2020) and field studies (e.g., Kimbel, 1982; Riis & Sand-Jensen, 2006; Cornacchia et al., 2019; Gagné & Lavoie, 2023). A recent review by Thomaz (2025) synthesized these findings. The capacity of macrophyte stem fragments to generate new plants has also been explored in both field (e.g., Barrat-Segretain et al., 1998, 1999) and experimental settings (e.g., Hussner & Lösch, 2007; Silveira et al., 2009), although to a lesser extent than macrophyte germination via seeds.

To enhance the understanding of asexual reproduction in aquatic macrophytes, I conducted a literature review on the key factors that influence the success of macrophyte stem fragments in producing new plants. The focus on stem fragments is due to their prevalence and effectiveness as an asexual reproductive strategy in freshwater macrophytes. Specifically, I summarize the main endogenous and exogenous (abiotic and biotic) factors that affect stem fragment success, assessed by their potential for colonization, regeneration, and the establishment of new plants. Additionally, I point some gaps in the field and discuss how key human impacts on aquatic ecosystems influence fragment performance.

2. Methods

This work builds upon survey by Thomaz (2025), which summarized the mechanisms and agents of plant fragmentation and dispersal vectors. I updated this survey on January 2, 2025, using the Web of Science and Scopus databases with the following keyword combinations: macrophyte* AND fragment* OR "aquatic plant*" AND fragment* OR autofragment* AND macrophyte* OR allofragment* AND macrophyte* OR autofragment* AND "aquatic plant*" OR allofragment* AND "aquatic plant*". Marine species were excluded from the review.

The updated survey yielded 821 papers, which were partially or fully screened. These were supplemented with additional sources identified through cross-referencing and manual searches. A total of 157 papers were retained for the analysis (113 from the systematic review + 44 from other sources) (Figure 1).

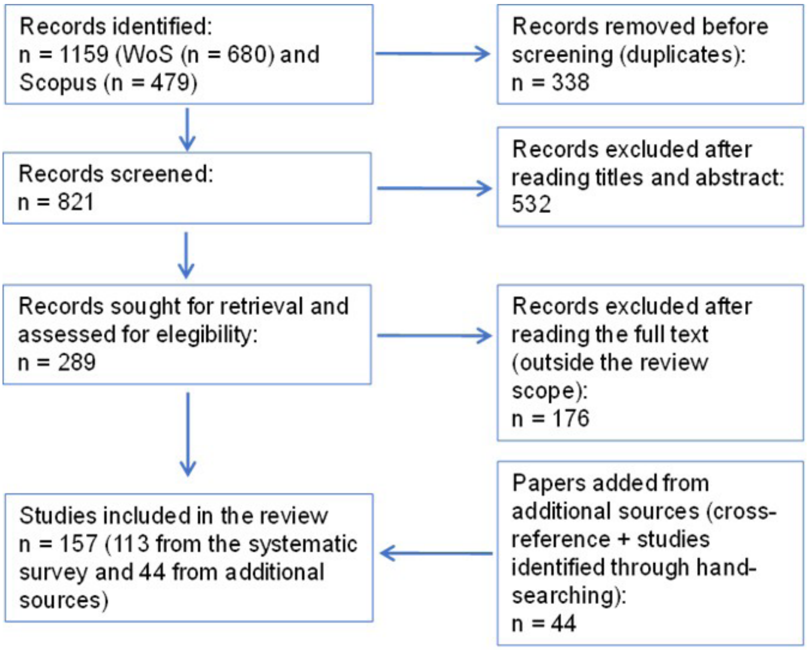

Figure 1. PRISMA flow-chat showing the main results from the systematic survey.

This review focused on fragments of varying sizes derived from apical and intermediate stem portions, or plant branches (lateral stems). A small number of studies (<5% of the papers) utilized severed stolons (e.g., Glover et al., 2015), shoots formed on pseudostolons (e.g., Nielsen et al., 2006), or macroalgae thalli (Glisson et al., 2020).

For the majority of papers, the type of macrophyte reproductive structure was verified in the Methods section. When a study examined multiple reproductive structures, findings unrelated to macrophyte stem fragments were excluded. Papers lacking clear descriptions of the fragment type and review papers, unless they presented primary data, were excluded. Fragment responses to herbicides, which fall outside the scope of this review, were also not considered.

Some studies that manipulated abiotic and biotic factors did not primarily aimed to investigate the role of environmental factors on stem fragment performance, nor did they focus on asexual reproduction via these structures. However, although not explicitly designed to examine asexual reproduction or plant recovery from stem fragments, these experiments effectively did so by using stem fragments to initiate plant growth (e.g., Lombardo & Cooke, 2003; Teixeira et al., 2017) and thus, they were retained in the review.

In a few studies, new plants were grown from stem fragments, and the authors investigated the effects of exogenous factors on plant growth parameters nearing maturity (Cao et al., 2012; McFarland & Barko, 1999; Owino et al., 2021). Despite not focusing on early growth, these studies were included in the survey because the influence of these factors likely extends beyond the initial growth stages and can impact macrophyte growth to maturity (Mangan & Baars, 2016).

Finally, for studies that tested multiple factors, resulting in complex interactions difficult to summarize, I focused on synthesizing the findings most relevant to the aims of this review.

3. Quantitative Evidence of Macrophyte Asexual Reproduction Via Stem Fragments

The studies included in this review used a variety of metrics to assess the success of macrophyte asexual reproduction via stem fragments, including fragment viability (survival ability), fragment growth, the growth of new shoots, branches, roots, and fragment sprouting (new plant establishment). The most frequently used growth measurements were final biomass, shoot length, and relative growth rates (RGR). Plant growth is a key trait associated with invasive macrophyte success (Bora & Padial, 2023a), and these measurements are likely suitable for estimating the establishment ability of macrophyte fragments in general.

The term “stem fragment performance” is used here to describe the response of stem fragments to abiotic and biotic factors, as quantified by any of the aforementioned metrics. This definition aligns with Puijalon et al. (2005) concept of performance, which builds on Koehl (1996), defining it as “the relative efficiency of an organism confronted with a given environmental pressure.” Enhanced fragment performance, manifested as higher biomass, RGR, and sprouting capacity, reflects increased viability and growth potential relative to lower-performing fragments.

The success of macrophyte reproduction through stem fragments was documented in 157 studies (Figure 2). Of these, 47 studies reported successful asexual reproduction via stem fragments but did not investigate the primary factors influencing this process (see list of papers at https://doi.org/10.48331/SCIELODATA.CFH1ZD). In contrast, 110 studies forming the basis of this review investigated the determinants of fragment performance. In total, 76 submerged and emergent macrophyte species were shown to successfully reproduce asexually using stem fragments (Table 1).

The consistent ability of numerous species to recover and establish from stem fragments, as evidenced by this review, supports a significant generalization that this type of propagule plays an important role in macrophyte asexual reproduction. This survey demonstrates that this overarching pattern extends across a diverse range of species and ecosystem types.

Focusing solely on studies that addressed the determinants of stem fragment performance, 49 species were investigated using endogenous, exogenous, or combined approaches (Table 1). Studies were concentrated on a few invasive species with economic or ecological impacts mainly in temperate regions, including *Myriophyllum spicatum* (31 studies), *Hydrilla verticillata* (27), *Elodea canadensis* (20), *Ceratophyllum demersum* (12), and *Elodea nuttallii* (12). In contrast, the majority of species (34) were examined in only one or two studies. This concentration of research on a few invasive species of human interest in temperate regions also applies to plant fragmentation and propagule dispersal vectors, which are the initial phases of asexual reproduction via stem fragments (Thomaz, 2025). Collectively, these findings indicate that asexual reproduction via stem fragments remains largely unexplored for most macrophyte species, particularly in tropical regions.

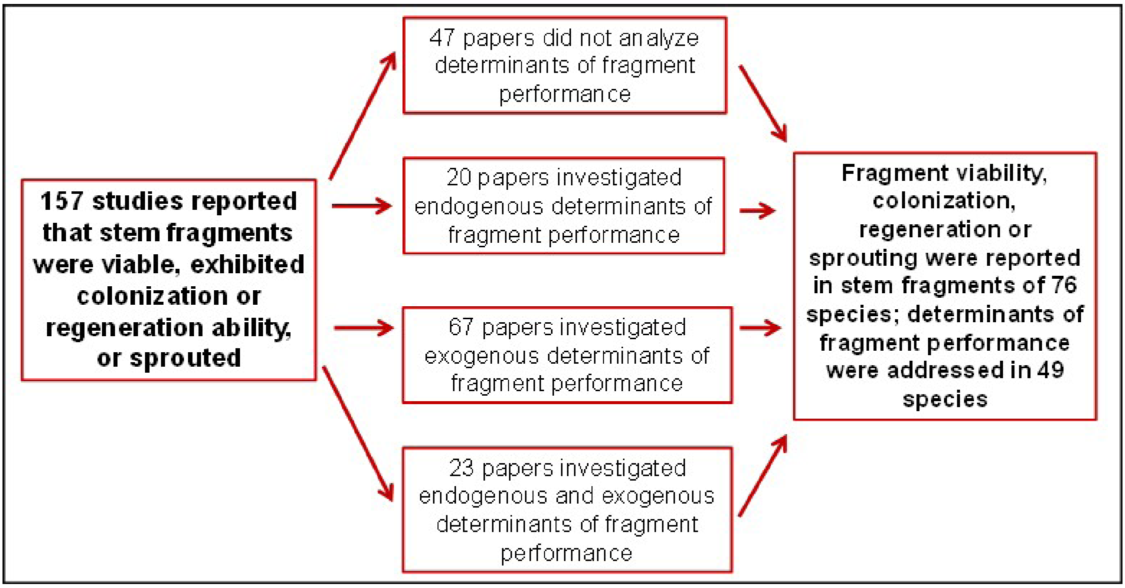

Figure 2. Summary of the main findings of the systematic review.

Table 1. Species of macrophytes that establish from stem fragments.

Alternanthera philoxeroides (Mart.) Griseb. *
*Berula erecta (*Huds.) Coville *
Cabomba caroliniana A.Gray *
Callitriche platycarpa Kütz.
Callitriche spp. *
Carex subspathacea Wormsk. ex Hornem.
Ceratophyllum demersum L. *
Chara aspera Willd.
Chara fragilis Desv.
Chara globularis Thuill. *
Chara rudis Ruprecht
Chara tomentosa L.
Chara vulgaris L.
Crassula helmsii (Kirk) Cockayne *
Didymodon insulanus (De Not.) M.O.Hill
Egeria densa (Planch.) Casp. *
Egeria najas (Planch.) Casp.*
Elodea canadensis Michx. *
Elodea nuttallii (Planch.) H.St.John *
Euryale ferox Salisb.
Groenlandia densa (L.) Fourr.
Heteranthera dubia (Jacq.) MacMill.
Hippuris vulgaris L.*
Hydrilla verticillata (L.f.) Royle *
Hydrocharis morsus-ranae L.
Hydrocotyle ranunculoides L.f. *
Hymenachne pernambucensis (Spreng.) Zuloaga *
Ipomea aquatica Forssk. *
Justicia americana (L.) Vahl *
Lagarosiphon ilicifolius Oberm.
Lagarosiphon major (Ridl.) Moss *
Ludwigia grandiflora (Michx.) Greuter & Burdet *
Ludwigia hexapétala (Hook. & Arn.) Zardini, H.Y.Gu & P.H.Raven *
Ludwigia peploides (Kunth) P.H.Raven *
Luronium natans (L.) Raf. *
Marsilea mutica Mett. *
Mayaca fluviatilis Aubl.*
Mentha aquatica L.
Menyanthes trifoliata L.
Myriophyllum aquaticum (Vell.) Verdc. *
Myriophyllum heterophyllum Michx. *
Myriophyllum oguraense Miki*
Myriophyllum propinquum A.Cunn. *
Myriophyllum spicatum L.*
Myriophyllum ussuriense (Regel) Maxim.*
Najas guadalupensis (Spreng.) Magnus *
Najas marina L.*
Najas minor All.
Nasturtium officinale W.T.Aiton *
Neptunia natans (L.f.) Druce
Nitellopsis obtusa (Desvaux) J.Groves *
Phalaris arundinacea L. *
Polygonum acuminatum Kunth
Polygonum ferrugineum Wedd.
Potamogeton coloratus Hornem.
Potamogeton crispus L.*
Potamogeton lucens L.
Potamogeton maackianus A.Benn.
Potamogeton ochreatus Raoul *
Potamogeton oxyphyllus Miq.
Potamogeton pectinatus L. (Syn. *Stucenia pectinata (*L.) Börner) *
Potamogeton perfoliatus L.*
Potamogeton pusillus L. *
Potamogeton richardsonii (A.Benn.) Rydb. *
Puccinellia phryganodes (Trin.) Scribn. & Merr.
Ranunculus baudotii Godr. *
Ranunculus trichophyllus Chaix *
Ranunculus *
Sparganium emersum Rehmann *
Urochloa arrecta (Hack. ex T.Durand & Schinz) Morrone & Zuloaga *
Utricularia inflata Walter *
Utricularia purpurea Walter
Utricularia vulgaris L.*
Vallisneria americana Michx. *
Vallisneria spiralis L.
Zannichellia palustres L.

*Species for which determinants of stem fragment performance were investigated.

4. Main Determinants of Stem Fragment Performance

Once stem fragments arrive at a site, become trapped, or sink, they can sprout if the habitat provides favorable abiotic and biotic conditions. The importance of habitat suitability for macrophyte establishment via stem fragments is demonstrated by numerous examples highlighting a trade-off between propagule dispersal and habitat suitability. For instance, some studies on submerged species in streams and experimental settings indicate that propagule pressure is less limiting than poor establishment success (Riis, 2008; Bickel, 2017). Another illustrative example is the invasion history of *Hydrilla verticillata* in Brazil, where 25 years after its first record, this plant still does not colonize floodplain lakes, likely in response to several abiotic and biotic factors that limit fragment performance and plant growth (Silveira, 2015; Silveira & Thomaz, 2015; Ribas et al., 2017; Silveira & Thomaz, 2023).

These examples demonstrate that successful establishment of new plants from stem fragments depends on endogenous features of the fragment or of the habitat suitability. A high influx of propagules to a site does not guarantee macrophyte establishment success. However, in suitable habitats, stem fragments of many macrophyte species can thrive and develop into new plants, sometimes initiating new populations (see pictures at https://doi.org/10.48331/SCIELODATA.CFH1ZD).

The performance of macrophyte stem fragments is determined by endogenous characteristics of the fragment or the parent plant, and exogenous factors (abiotic characteristics and biotic interactions). The next sections will follow this categorization to address the main determinants of fragment performance.

4.1. Endogenous characteristics

The most frequently studied endogenous factors were those related to inter-specific differences, node presence, fragment size (length, weight, or node count), and stem position on the parent plant (apex presence/absence or distance from the apex). Others, less frequently studied, endogenous factors included fragment origin (autofragments vs. allofragments), cytotypes, plant sexual arrangement, and fragment ecotype (see table at https://doi.org/10.48331/SCIELODATA.CFH1ZD).

4.1.1. Interspecific differences

Species-specific differences influence fragments performance (e.g., Kadono, 1984; Heidbüchel et al., 2019a; Umetsu et al., 2012b). For instance, differences of survival rates between *Elodea* species may arise from different resistance to desiccation, in growth rates and shade tolerance (Barrat-Segretain & Cellot, 2007).

Furthermore, evidence suggests that some species differ in relation to regeneration and colonization abilities (Barrat-Segretain et al., 1998, 1999; Barrat-Segretain & Bornette, 2000; Barrat-Segretain & Cellot, 2007). This implies that fragments allocate energy either toward root development and sediment establishment, or toward producing new propagules that disperse without establishing (Barrat-Segretain et al., 1998).

In macroalgae, interspecific differences in growth strategies from thalli may be linked to habitat preference. For example, species of macroalgae that prefer to colonize wind-disturbed habitats, grows from multi-axis thalli that anchor on the substrate while those that colonize less wind-disturbed waters grow from less complex thalli (Bociag & Rekowska, 2012).

These examples illustrate that intrinsic macrophyte characteristics, such as desiccation tolerance, light requirements, and thallus morphology, can determine interspecific differences in fragment performance. It's likely that any ecological, morphological, or physiological distinction between species will lead to variations in fragment performance.

4.1.2. Node presence

Plant regeneration can occur through *de novo* organogenesis, in which plant cuttings form ectopic apical meristems that develop into shoots and roots (Ikeuchi et al., 2016). In some species, shoots can develop from shoot tips or from stem nodes containing buds, while in others, both roots and shoots can be generated even from leaf cuttings (Ikeuchi et al., 2016).

Studies have shown that the presence of nodes is necessary for stem fragment regeneration, colonization, and sprouting in various macrophyte species if tips are not present (Barrat-Segretain et al., 1998; Hussner & Lösch, 2007; Bok et al., 2025). The importance of nodes for fragment performance is further highlighted by findings showing that fragment performance increases with the number of nodes per fragment (Langeland & Sutton, 1980; Bickel, 2017). The regenerative potential of nodes is directly related to the presence of meristematic tissues within these structures (Barrat-Segretain et al., 1998; Riis et al., 2009; Ikeuchi et al., 2016).

4.1.3. Fragment size

The size of a stem fragment, measured by dry weight, length, and number of nodes, directly affects its performance. Generally, larger fragments boast higher survival rates and superior regeneration and colonization abilities compared to smaller ones (e.g., Langeland & Sutton, 1980; Johnstone et al., 1985; Yakandawala & Dissanayake, 2010; Lin et al., 2012; Hoffmann et al., 2015; Li et al., 2015a; Pennington & Sytsma, 2016; Redekop et al., 2016; Heidbüchel et al., 2019a; Dai et al., 2024; Zou et al., 2024). This improved performance in larger fragments stems from their greater accumulation of reserves (like nonstructural carbohydrates, an indicator of propagule vigor), more photosynthetic tissue, and a higher number of potential nodes (Riis et al., 2009; Umetsu et al., 2012a; Baniszewski et al., 2016; Bickel, 2017). Therefore, it is important that experimental studies using sprout growth or elongation to measure plant performance should utilize RGR, which account for initial plant size, instead of final biomass or plant length (Gibson et al., 1999; Bando et al., 2016).

It is important to note that even single-node fragments (Langeland & Sutton, 1980; Hussner, 2009) or very small fragments (around 1-2 cm) can produce new plants (Yakandawala & Dissanayake, 2010; Titus & Urban, 2013). In an extreme example, nodal fragments of *Crassula helmsii* as tiny as 0.5cm regenerated (Bok et al., 2025). Furthermore, some macrophyte species can regenerate new shoots from single leaves (Hussner, 2009; Chou et al., 1992). These findings underscore that some macrophyte species possess a remarkable ability to spread and colonize new sites even after extensive fragmentation.

However, some studies show similar performances in both smaller and larger stem fragments because the former exhibited higher elongation, allowing them to more effectively acquire light and build biomass (Li et al., 2016a). An experiment with *Elodea canadensis* revealed that cut plants produced a greater number of lateral shoots and thus, greater dispersal ability, than whole plants (Mielecki & Pieczyńska, 2005). Fragments of varying sizes of *Elodea nuttallii* demonstrated nearly 100% establishment success and smaller fragments exhibited a higher RGR, with only extremely small stem fragments in highly shaded conditions not establishing successfully (Zefferman, 2014).

Fragment size may interact with presence of apical tips to determine fragment performance (Umetsu et al., 2012a). For example, Zou et al. (2024) observed that fragment length did not influence survival when tips were present, but lenght influenced survival when tips were absent. These findings may be explained by the presence of meristematic tissues in apical tips and potentially higher carbohydrate contents in middle sections (Umetsu et al., 2012a).

In summary, while larger fragments generally provide higher fragment performance, even very small fragments can generate new plants. The relationship between fragment size and performance is a complex one, often mediated by other critical factors such as the presence of apical tips.

4.1.4. Stem position in the parental plant and presence of tip

The presence of apical tips and the stem fragment's original position on the parent plant (apical, middle, or lower portions) influence its performance. Generally, apical fragments exhibit superior performance (RGR and biomass accumulation) compared to fragments from other plant sections (Riis et al., 2009; Yakandawala & Dissanayake, 2010; Michelan et al., 2010; Umetsu et al., 2012b; Bickel, 2017; Heidbüchel & Hussner, 2019; Coughlan et al., 2022; Zou et al., 2024; Bok et al., 2025).

Likewise, plantlets derived from the apical stems display greater shoot length and root development than those from middle-stem fragments (Zhenbin et al., 2007). Beyond biomass growth, apical fragments of various submerged species also exhibit higher elongation than other fragment types (Mielecki & Pieczyńska, 2005; Cao & Wang, 2012; Vári, 2013; Bickel, 2017; Zhenbin et al., 2007; Zou et al., 2024). These findings collectively suggest that apical stem fragments generally outperform those without tips, a phenomenon likely attributed to the presence of meristematic tissue in the apical portions of the plant (Mielecki & Pieczyńska, 2005; Vári, 2013; Ikeuchi et al., 2016; Bok et al., 2025).

While shoot tips are undeniably important for plant growth, stem fragments can regenerate new plants even without apical meristematic tissue (e.g., Zhenbin et al., 2007; Cao & Wang, 2012; Umetsu et al., 2012b). For instance, nodes located in the upper sections of the plant can exhibit more efficient regrowth after the removal of the apex compared to middle or basal nodes (Jiang et al., 2009). Similarly, in some macrophytes the younger stolon portions located closer to the apex produce more ramets than older sections (Dong et al., 2012). There are even instances where apical fragments show reduced performance (Jiang et al., 2009) or apex removal does not affect plant growth (Dong et al., 2012). On one hand, apical stem fragments, with their meristem and apical dominance, tend to invest more in plant elongation and overall growth. However, this characteristic can reduce their ability to produce lateral shoots when compared to middle or basal-stem fragments (Mielecki & Pieczyńska, 2005;

Cao & Wang, 2012; Jiang et al., 2009; Vári, 2013; Umetsu et al., 2012b; Zou et al., 2024) (Figure 3). The increased production of branches in middle and basal fragments after abscission occurs because meristems in axillary buds remain dormant in the presence of apical meristems, while the apex removal disrupts this apical dominance, allowing axillary buds to grow (Cline, 1991; Ikeuchi et al., 2016).

In summary, apical stem fragments generally exhibit superior performance than fragments from other plant sections. This strategy offers a significant advantage: the upper sections with a greater atility to regrow are more susceptible to disturbances and detach more easily, thereby enhancing the species' ability to spread and colonize new sites (Jiang et al., 2009; Dong et al., 2012). However, middle and basal fragments retain the ability to regenerate, colonize, and produce new plants; moreover, they can produce a significant number of lateral shoots (branches). These branches act as propagules, thereby enhancing the overall dispersal ability of the plant.

4.1.5. Other endogenous determinants of fragment performance

Several other endogenous factors influence fragment performance. For instance, autofragments generally perform better than allofragments, which can be attributed to differing amounts of total nonstructural carbohydrates in each fragment type (Kimbel, 1982; Madsen, 1997). Additionally, fragments of different cytotypes (e.g., diploid vs. polyploid) from some species may also exhibit varying performances (Grewell et al., 2016).

Another endogenous feature influencing fragment performance is a plant's sexual arrangement; *Hydrilla verticillata* individuals grown from a monoecious biotype differ in performance from those originating from dioecious ones (McFarland & Barko, 1999). Fragment ecotype can also affect performance, with emergent fragments of some macrophytes achieving a higher RGR than amphibious ones (Xie et al., 2018). Moreover, the size of the parent plant may influence fragment performance. Sprout biomass of an aquatic grass was significantly correlated with fragment size in fragments produced by small plants, whereas no such correlation was observed in those produced by large plants (Bando et al., 2016).

Finally, fragment performance varies according to the metric used. For instance, the apical stems of three submerged species exhibited higher growth rates (measured as total biomass) than the mid-stems; however, their colonization ability (assessed by root number and dry weight) did not differ (Umetsu et al., 2012b). These differences were attributed to apical dominance in stems where apices were not removed.

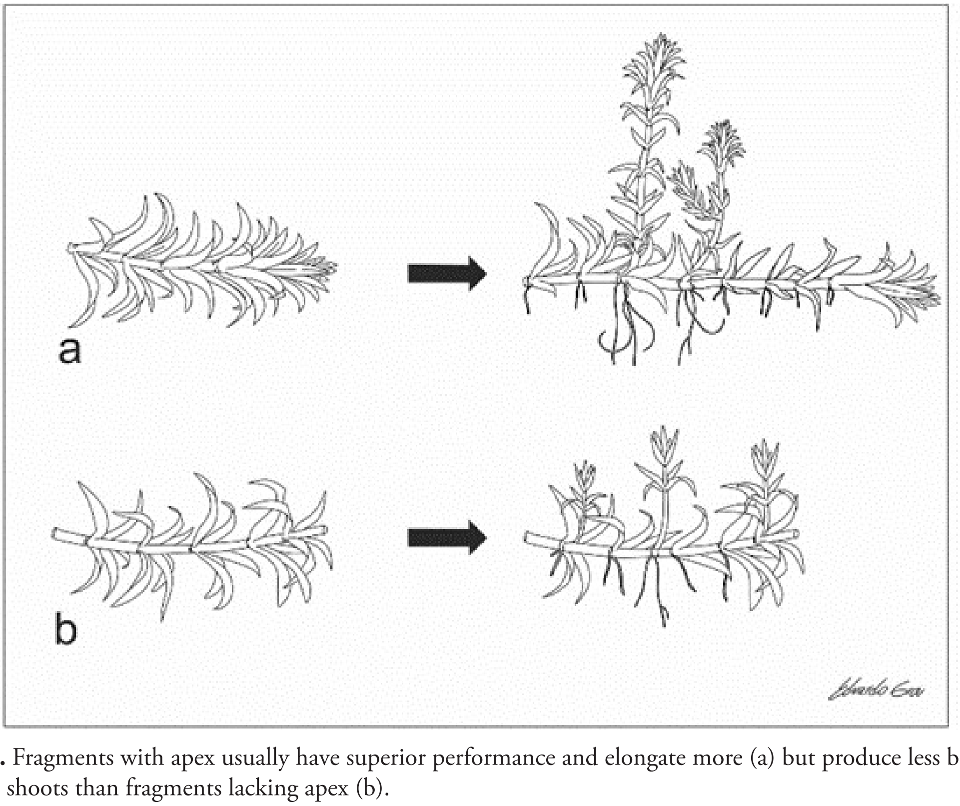

Figure 3. Fragments with apex usually have superior performance and elongate more (a) but produce less branches or lateral shoots than fragments lacking apex (b).

Thus, inferences should be made carefully, as responses are metric-dependent.

4.2. Exogenous abiotic factors

Among the exogenous factors affecting fragment performance, desiccation, nutrients, and light are the most thoroughly investigated. Other, less studied factors that influence fragment performance include seasons, flow, temperature, CO_2, alkalinity, salinity, water and sediment depth (burial), water level fluctuations, wind exposure, acetic acid, and microplastics (see table at https://doi.org/10.48331/SCIELODATA.CFH1ZD).

4.2.1. Desiccation

Desiccation is a primary determinant that negatively affects fragment performance, playing a relevant role in the success of overland dispersal for aquatic macrophytes (Barnes et al., 2013; Pickman & Barnes, 2017). The large number of studies focusing on desiccation highlights its importance, making it one of the most investigated environmental conditions explaining invasive macrophyte success (Bora & Padial, 2023a). This is expected, as macrophytes (particularly submerged ones) desiccate very rapidly when exposed to air due to their leaves having a thin cuticle (Sculthorpe, 1967).

Fragment desiccation occurs when fragments are exposed to wind, sunlight or high temperatures. Experiments with both submerged and emergent macrophytes have demonstrated that desiccation can significantly reduce fragment performance (e.g., Silveira et al., 2009; Michelan et al., 2010; Evans et al., 2011; Dugdale et al., 2012; Jerde et al., 2012; Bickel, 2017; Coughlan et al., 2018; Heidbüchel et al., 2019b). However, even completely desiccated fragments (Evans et al., 2011), those with all leaves dead (Johnstone et al., 1985), or seemingly unviable fragments (Bora & Padial, 2023b) can eventually generate new sprouts. These fragments retain the ability to regrow and produce new plants from lateral buds (Johnstone et al., 1985).

Invasive macrophytes, in particular, tend to be highly resistant to desiccation (Bora & Padial, 2023a). For instance, some have produced sprouts after 6-17 days of desiccation (Michelan et al., 2010; Bora & Padial, 2023b), and fragment survival has been observed to tolerate up to 90% desiccation (Bickel, 2017). In extreme cases, fragments have even retained a 10% survival probability after complete desiccation (Barnes et al., 2013).

Desiccation rates are influenced by various factors, increasing with wind and in higher temperatures (Coughlan et al., 2018) and decreasing with higher humidity (Bickel, 2017). Stem fragments that coil (e.g., in boat propellers; Jerde et al., 2012; Bruckerhoff et al., 2015), remain buried in sediment (Pickman & Barnes, 2017), are sheltered within plant mounds after lake drawdown (Barrat-Segretain & Cellot, 2007; Dugdale et al., 2012), or clump together (Bickel, 2017; Glisson et al., 2020) generally exhibit extended viability or improved performance following desiccation. Similarly, fragments embedded in mud (Schooler et al., 2009) or dried in clay rather than sand (Silveira et al., 2009) also demonstrate enhanced performance.

The findings generally indicate that desiccated stem fragments can remain viable for a few days to weeks. This allows them to be transported long distances outside of water and still thrive in new locations. The desiccation resistance of many species, coupled with the fact that fragments retain viability when coiled or clumped, complicates efforts to control the spread of invasive macrophytes. These macrophytes can be introduced into various aquatic ecosystems by boat trailing (McCracken et al., 2013) and birds (Coughlan et al., 2015; Silva et al., 2018). Additional concerns arise because fragments retain viability when protected in plant mounds. This makes controlling macrophytes through lake drawdown challenging (Barrat-Segretain & Cellot, 2007; Dugdale et al., 2012). These findings have important implications for strategies aimed at controlling the spread and establishment of these species, demonstrating that many macrophytes can still spread and succeed even if their fragments undergo significant water loss and experience drought for several hours or even days.

4.2.2. Nutrients

Nutrients, primarily nitrogen and phosphorus, emerged as one of the most significant factors enhancing stem fragment performance in the survey. This was true for both submerged (Cao et al., 2012; Xie et al., 2010; Hoffmann et al., 2015) and emergent macrophytes (Yen & Myerscough, 1989; Hussner & Lösch, 2007; Fasoli et al., 2015; Teixeira et al., 2017; Grewell et al., 2016; Dai et al., 2024; Machado et al., 2025). Beyond experiments on nutrient addition, fragment performance also improves when fragments grow in clay or mud rather than sand, because these finer substrates typically have higher nutrient concentrations (Silveira et al., 2009; Li et al., 2015a, 2016b). The improved performance observed with nutrient additions in sediment occurs because fragments root rapidly during the colonization phase.

Furthermore, nutrients already accumulated within the fragments themselves can contribute to short-term plant growth, typically over days to weeks (Xie et al., 2018).

While less studied than sediment, water nutrients similarly enhance fragment performance (Ozimek et al., 1993; Kuntz et al., 2014; Xie et al., 2018; Dainez-Filho et al., 2019). It is probable that the positive effects of water nutrients on fragment performance stem from the capacity of stem fragments and newly formed tissues to absorb nutrients directly from the surrounding water (Ozimek et al., 1993; Madsen & Cedergreen, 2002; Wersal & Madsen, 2011; Takayanagi et al., 2015; Skovsholt et al., 2023). These nutrients are then stored in plant tissues and can be utilized for growth, aligning with the 'luxury consumption hypothesis' (Lombardo & Cooke, 2003; Thiébaut et al., 2016).

However, some contrasting results exist regarding the effects of nutrients on fragment performance. Specifically, N toxicity at high concentrations has been shown to decrease fragment performance (Ozimek et al., 1993; Lombardo & Cooke, 2003; Cao et al., 2011; Zhu et al., 2014). These findings suggest that NH_4^+ toxicity, which is commonly known to reduce adult plant growth, may also impact fragment regeneration and, consequently, early plant establishment. Moreover, nutrient addition may not be sufficient to overcome the negative effects of other limiting factors, such as shading (Machado et al., 2025).

Finally, how fragments respond to nutrients also depends on the trait tested. For example, while the survival rates of *Myriophyllum aquaticum* fragments did not increase with high phosphorus concentration, both branch number and length were enhanced in this treatment (Xie et al., 2018).

The findings indicate that eutrophication aids the early establishment of macrophytes from stem fragments (Figure 4). However, in some situations, the negative effects of algal blooms may override the positive impacts of nutrients. The beneficial effects of eutrophication on fragment performance are further amplified by its ability to stimulate plant branching (an indicator of propagule pressure) and plant fragmentation (Thomaz, 2025). Thus, the proliferation of macrophyte populations, particularly those of invasive species, in eutrophic ecosystems may be linked to this sequence of events: beginning with an increase in propagule pressure (associated with plant branching) and culminating in the successful establishment of new plants from stem fragments (Figure 4).

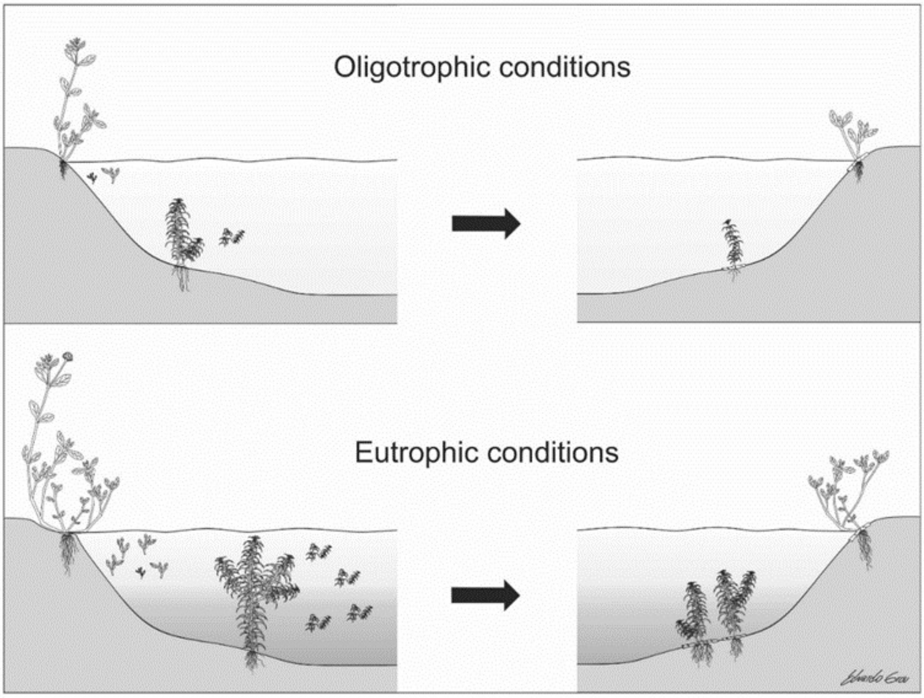

Figure 4. Eutrophication enhances asexual reproduction and plant establishment via stem fragments in many macrophyte species. Relative to oligotrophic conditions (upper panel), eutrophic conditions generally increase propagule pressure by promoting plant branching and fragmentation (bottom left panel) and enhance fragment performance (bottom right panel). However, eutrophication may partially reduce fragment performance due to decreased underwater light availability (bottom panels).

4.2.3. Light

The impact of light on fragment performance has primarily been studied in relation to water level fluctuations, as greater depths lead to shading, and other determinants, as the presence of riparian vegetation. Numerous studies have shown that light positively influences the performance of fragments from various macrophyte species (Going et al., 2008; Zefferman, 2014; Glover et al., 2015; Li et al., 2015b; Evangelista et al., 2017; Heidbüchel & Hussner, 2019; Cao et al., 2023; Skovsholt et al., 2023; Silveira & Harthman, 2024; Machado et al., 2025). These findings suggest that beyond just depth, eutrophication and its resulting reduction in underwater light could sometimes limit fragment growth, especially after they sink.

Despite reduced performance in low light, fragments can still survive, root, establish, or produce new plants even under significant shading (90–94%) (Mielecki & Pieczyńska, 2005; Zefferman, 2014; Evangelista et al., 2017; Zhang et al., 2024). However, excessive light can, conversely, hinder macrophyte fragment performance. For example, full light negatively affected the growth of *Elodea nuttallii*, a finding consistent with the photoinhibition observed in many macrophyte species (Zefferman, 2014).

It is worth noting that these findings on how light influences fragment performance have practical implications, particularly for invasive macrophyte reduction strategies. For instance, while restoring riparian vegetation might not prevent macrophyte establishment by reducing light in the aquatic environment, it can reduce their growth and create favorable conditions for native species to outcompete them (Zefferman, 2014; Evangelista et al., 2017). These results, combined with the earlier points, suggest that reducing light in aquatic ecosystems by maintaining or restoring riparian vegetation could discourage plant establishment from stem fragments, aiding in the control of early invasion stages of undesirable macrophytes.

4.2.4. Other exogenous abiotic determinants of fragment performance

Seasonal conditions significantly affect fragment performance, particularly in temperate regions. For instance, fragments may perform better in spring than in autumn (Barrat-Segretain et al., 2002). Similarly, macrophyte fragments planted earlier in the summer often exhibit higher performance than those planted later, likely because they have sufficient time to develop roots before winter dormancy (Collingsworth et al., 2009).

Flow is a critical determinant of propagule success. It can be a major bottleneck for recolonization, as it often leads to low fragment retention and unsuccessful colonization of any shoots that do remain (Riis, 2008).

Temperature is another key factor influencing fragment performance, often enhancing it for some species (McFarland & Barko, 1987; Calvo et al., 2019). However, responses depended on metric used: increases in temperature in colder waters may favor apical growth, whereas increases in warmer waters may stimulate the regeneration and colonisation abilities (Thiébaut et al., 2016). Despite this, the biomass produced by fragments of some species decreases significantly at extreme temperatures of 35-40°C (Yen & Myerscough, 1989; McFarland & Barko, 1999). High temperatures also accelerate the decomposition of stem fragments (Carvalho et al., 2005, Passerini et al., 2016), which may contribute to their poor performance.

Studies on the influence of CO_2 on both submerged (Mormul et al., 2020; Titus & Urban, 2013) and emergent macrophytes (Owino et al., 2021) indicate that the biomass of sprouts originating from stem fragments increases under elevated CO_2 levels. These findings, combined with the positive effects of temperature, suggest that invasive macrophytes might establish more successfully from stem fragments in future global change scenarios.

Bicarbonate, an ion directly linked to alkalinity, can also serve as a carbon source for submerged macrophytes, alongside CO_2. Accordingly, experiments have demonstrated that fragment growth is positively influenced by HCO_3^- and alkalinity (Freitas & Thomaz, 2011; Tattersdill et al., 2017; Fasoli et al., 2018). Consequently, in some locations, the early sprout growth from stem fragments of submerged species adapted to bicarbonate uptake might be limited by carbon availability rather than by nitrogen and phosphorus.

Regarding salinity, one experiment with submerged macrophyte stem fragments found that their growth decreased with increasing salinity (Haller et al., 1974). The authors concluded that salinity might be an important factor influencing stem fragment performance in coastal habitats.

Water and sediment depths also influence fragment performance. Generally, greater water depth negatively affects stem fragment performance. In addition to reducing light availability, greater depths can restrict a fragment's ability to sink and establish contact with the sediment, thereby hindering root development (Nielsen et al., 2006; Lin et al., 2012).

For some emergent macrophytes, waterlogging stress inhibits stem fragment regeneration, leading to a negative impact of depth on fragment performance (Zhang et al., 2024). Water level fluctuations also affect fragment performance; stem fragment propagation is reduced under high fluctuations, likely a result of suboptimal conditions associated with respiration and anoxia during these stressful periods (Cao et al., 2012).

The influence of sediment burial on fragment performance is not straightforward; its effects can be either positive or negative, depending on the species (Cao & Wang, 2012). While some studies show increased performance when fragments are planted in deeper sediment layers (Bonilla-Warford & Zedler, 2002; Laitala et al., 2012), other experiments using detached shoots have found the opposite (Chen et al., 2014).

Another sediment-related factor influencing fragment performance is acetic acid, a substance released during decomposition (Jin-Cheng et al., 2012). The authors demonstrated that a three-day exposure to 4 mmol/L acetic acid was lethal to *Elodea nuttallii* fragments.

Microplastics, extensively studied in aquatic ecosystems, have been the focus of few investigations concerning stem fragment performance. While experiments using environmentally relevant concentrations of microplastics showed non-significant impacts on plant growth (Polechońska et al., 2023), fragments of some macrophytes exhibited reduced growth under high microplastic concentrations, evidencing ecotoxicological effects of these particles (Yu et al., 2020; 2022). These negative impacts coincided with decreases in plant chlorophyll and detrimental effects on plant physiology (Yu et al., 2022).

Finally, the general conditions of a macrophyte's original habitat also determine stem fragment performance. For example, stem fragments from a population previously grown in nutrient-limited or high-flow environments showed better survival rates than those from more benign conditions (Puijalon et al., 2008). The authors suggest these delayed responses are due to the nature of stored substances, such as high starch accumulation in nutrient-poor conditions. In another example, the vegetative offspring of a macroalgae originating from wave-exposed sites performed worse than those from protected sites (Bociag et al., 2013). However, another experiment did not find significant effects of previous conditions on fragment performance (Smith et al., 2002). Despite this last example, there are indications that under certain conditions the features of the parent plants may influence fragment performance.

4.3. Exogenous biotic factors

Studies on biotic factors influencing fragment performance encompass both negative and positive interspecific interactions. Negative interactions are medited by competition and herbivory, while positive interactions refer to facilitation (see table at https://doi.org/10.48331/SCIELODATA.CFH1ZD). Though less frequently reported, neutral interactions have also been observed.

4.3.1. The role of negative interactions

Experiments conducted in both field settings and mesocosms show that competition and herbivory (biotic resistance in Invasion Biology field) are key factors determining the performance of stem fragments across various macrophyte species. Field data from submerged macrophyte colonization studies revealed that stem fragments achieved higher colonization rates in outer plot sections than in inner ones (Vári & Tóth, 2017). This highlights the importance of surrounding vegetation in this process and suggests that competition within inner sections plays a significant role in resisting stem fragment performance. Further experiments demonstrate that higher stem fragment mortality (Xie et al., 2013), lower colonization (Chadwell & Engelhardt, 2008), and higher mortality combined with lower sprout growth (Evangelista et al., 2017; Teixeira et al., 2017; Leal et al., 2022) all occur when competitors are present. Additionally, fragment sprout biomass decreases with increasing richness and biomass of native macrophytes (Michelan et al., 2013) (Figure 5).

These experiments indicate that fragment performance can decline due to a combination of resident density and richness, in response to complementarity and sampling effects, all of which may occur simultaneously in freshwater ecosystems. These findings also highlight that the mechanisms behind reduced fragment performance involve competition with resident macrophytes for space, nutrients (pre-emption hypothesis; Chadwell & Engelhardt, 2008), and light (e.g., Michelan et al., 2013). Beyond these mechanisms, resident macrophytes can also create a physical barrier that limits a fragment's rooting ability (Thiébaut & Martinez, 2015).

In addition to interspecific interactions, intraspecific competition also influences fragment performance. For example, *Myriophyllum spicatum* fragments show lower performance across several attributes when subjected to high plant density (Li et al., 2015a).

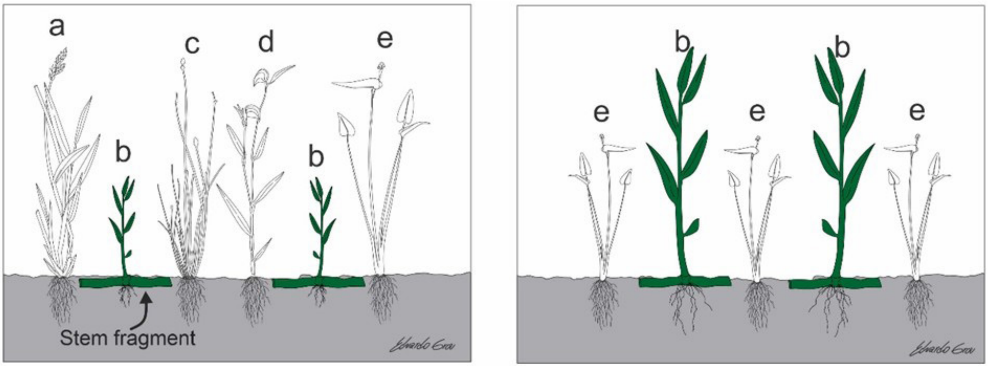

Figure 5. Sprout growth, a measure of fragment performance, decreases in mesocosms with higher species richness and greater plant biomass (left panel) compared with mesocosms with lower species richness and plant biomass (right panel). Higher species richness and resident plant biomass are associated with stronger interspecific competition, reflecting increased biotic resistance. Plants a, c, d, and e depict different native macrophyte species, while plants b represents *Urochloa arrecta* (a higlhy invasive aquatic grass), all growing in mesocosms. Based on Michelan et al. (2013).

Herbivory also negatively affects fragment performance. For instance, herbivory by snails (Calvo et al., 2019) and by the weevil *Euhrychiopsis lecontei* (Dietz, 1896) (Creed Junior & Sheldon, 1995) reduced the performance of submerged macrophyte fragments. In this last case, invertebrates suppress root formation by destroying lacunae and stem vascular tissue, and they significantly reduce tissue production by damaging meristems. Leaf-mining by some invertebrates also diminishes fragment growth and their ability to settle into the sediment and produce roots (Owens et al., 2008).

The effects of animals on fragment performance are amplified when organism with different feeding styles are involved. A combination of herbivorous gastropods, along with herbivorous and shredder fish, significantly decreased the performance of *Hydrilla verticillata* fragments. This helps explain the absence of this macrophyte in the floodplain lakes of the Paraná River in Brazil (Ribas et al., 2017).

Invertebrate larval damage to fragments can have long-term effects on subsequent macrophyte growth. For example, damage caused by *Hydrellia lagarosiphon* Deeming, 2012 larvae on *Lagarosiphon major* fragments reduced establishment success 134 days after the plants began to grow, compared to the undamaged control (Mangan & Baars, 2016). This demonstrates that stem fragment performance exhibits a delayed response to larval damage.

These examples show that competition and herbivory do not just affect mature plants; they can also have an impact much earlier, starting during the macrophyte establishment phase from stem fragments. It is also worth noting that herbivory can play a dual role in macrophyte asexual reproduction via stem fragments. While herbivores may reduce stem fragment viability, they can also increase plant fragmentation, thereby facilitating plant spread (Thouvenot et al., 2017). This occurs because even if fragment performance is reduced, a percentage of fragments remain viable, and in certain cases, damaged plant fragments can still exhibit high survival and growth rates (Pieczyńska, 2003). Therefore, invertebrates have a negative impact during the propagule establishment phase but a positive role for the macrophyte during the fragmentation and spread phases.

4.3.2. The role of positive interactions

In contrast to competition, interactions between macrophyte species can be positive, actually enhancing fragment performance (Figure 6). Facilitation might occur when fragments are trapped by riparian vegetation and other macrophytes, potentially allowing for colonization and plant establishment (Riis & Sand-Jensen, 2006; Cornacchia et al., 2019) (Figure 6a). However, this trapping effect can sometimes be counteracted by competition (Chadwell & Engelhardt, 2008). While fragment retention is not the same as plant establishment, it's a necessary step for plants to root in stream sediment (Cornacchia et al., 2019). Thus, it can be considered a proxy for facilitation during the dispersal and colonization phases (Cornacchia et al., 2019).

Facilitation can begin with fragment retention and be further bolstered by additional facilitative mechanisms. Thiébaut & Martinez (2015) demonstrated a chain of such mechanisms: *Elodea canadensis* enhanced the anchorage of *Ludwigia grandiflora*, which, in turn, increased the RGR of *Myriophyllum aquaticum*, possibly due to improved sediment oxygenation.

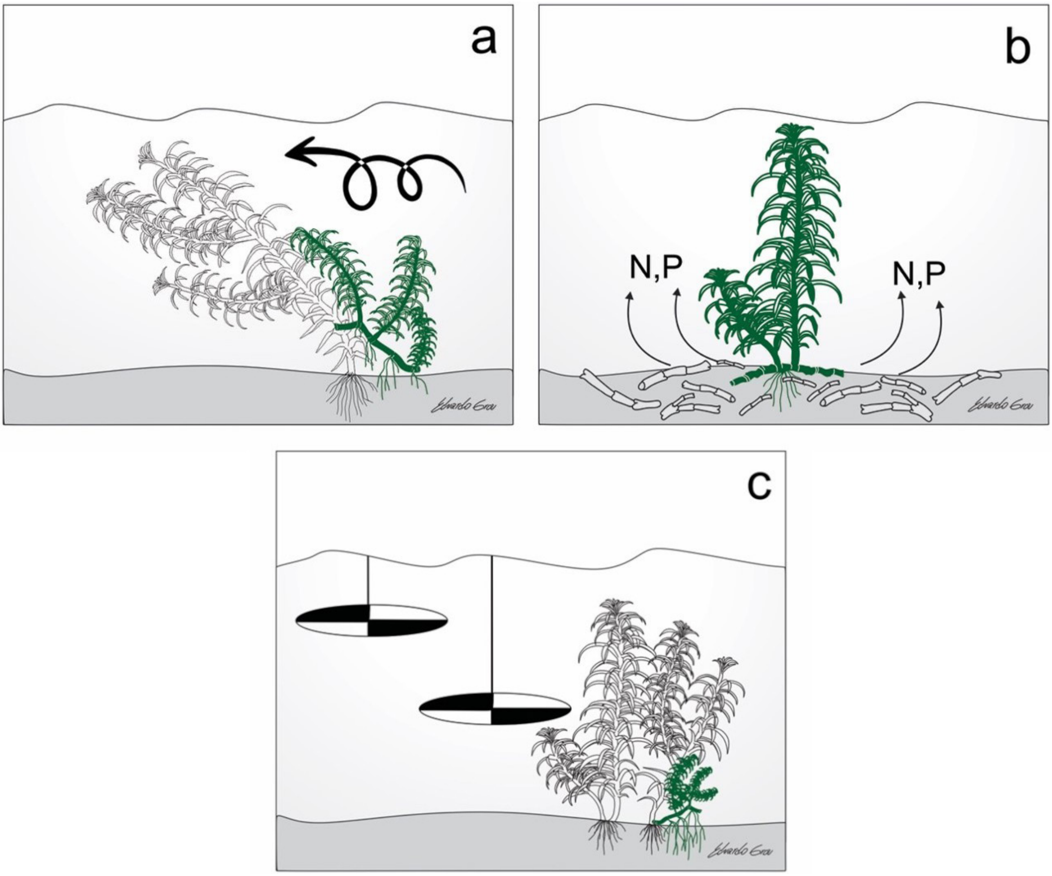

Figure 6. Facilitation mechanisms that enhance fragment performance. Facilitation may occur when fragments are trapped by riparian vegetation or other macrophytes, a necessary step for rooting in flowing waters (a). Detritus accumulation in the sediment also promotes fragment trapping and sprouting by releasing nutrients (b). Increased underwater light and reduced disturbance caused by submerged macrophytes in lentic ecosystems create favorable conditions that further enhance fragment performance (c).

In lentic ecosystems, facilitation can also occur indirectly when macrophyte detritus accumulates in sediment, enhancing fragment trapping and sprouting in response to nutrient release (Xie et al., 2013; Dainez-Filho et al., 2019) (Figure 6b). Other indirect facilitative mechanisms include an increase in underwater light (Rybicki & Landwehr, 2007; Le Bagousse-Pinguet et al., 2012) and decreased wave disturbances (Silveira & Thomaz, 2019) (Figure 6c). These latter factors can even lead to intraspecific facilitation. For instance, the growth of shoots produced by *Elodea canadensis* fragments planted in a lake increased with rising plant coverage, suggesting intraspecific facilitation (Tattersdill et al., 2017).

These examples highlight that facilitation, a process often overshadowed by competition in ecological studies (Bruno et al., 2003), may actually be an important determinant of fragment performance and the early establishment of macrophytes via stem fragments. Therefore, experimental and observational investigations should consider this positive interaction to fully explain macrophyte establishment and stand recovery from stem fragment propagules.

4.3.3. Neutral interactions

There are instances where fragments overcome resistance from competition with other species, showing that native plants do not always affect fragment performance. Evidence for this comes from experiments with *Hydrilla verticillata*, where resident species coul not prevent its establishment. For example, a field experiment found that the same amount of *Hydrilla verticillata* biomass accumulated in trays both with and without another macrophyte present (Chadwell & Engelhardt, 2008). In another experiment, an isoetid-like macrophyte failed to prevent colonization by *Hydrilla verticillata* fragments (Louback-Franco et al., 2020). Isoetid or isoetid-like species typically grow slowly and produce little biomass, resulting in poor competitive ability. Furthermore, another experiment demonstrated that the growth of *Hydrilla verticillata* fragment sprouts was similar when grown in monoculture and when grown in association with a native macrophyte species (Dainez-Filho et al., 2019). In this instance, a neutral interaction likely occurred because both species exhibited similar morphologies and environmental requirements.

These examples indicate that fragment performance, as measured by various growth parameters of their sprouts, may not always respond to the presence of neighboring plants. In such cases, fragment performance is more closely related to factors other than biotic interactions, such as the abiotic conditions or endogenous characteristics discussed in previous sections.

4.4. Interaction between abiotic and biotic factors

The examples above explore individual determinants of fragment performance, but in nature, abiotic and biotic factors interact. While several such interactions have been described (see table at https://doi.org/10.48331/SCIELODATA.CFH1ZD), here I will briefly summarize a few particularly interesting types.

The influence of nutrients on fragment performance, widely demonstrated in this review, does not occur in isolation, but as an interactive process. For instance, algal blooms, typical of eutrophic ecosystems, reduced submerged macrophyte fragment performance due to low underwater light. However, inorganic carbon additions buffered this effect (Mormul et al., 2020). Another experiment showed that fragment performance decreased with increasing water phosphorus, which was attributed to competition with phytoplankton for nutrients and light (Wersal & Madsen, 2011). These experiments clearly demonstrate that eutrophic environments can lead to reduced fragment performance because of high phytoplankton biomass and diminished light.

Other examples of these interactions include those between plant density and nutrients (Li et al., 2015a), and between nutrient availability and biotic resistance (Teixeira et al., 2017). Interestingly, the type of interaction (competition *vs.* facilitation) can change with eutrophication. For example, in three species of submerged macrophytes growing from apical shoot fragments, biotic interactions shifted from competition to indirect facilitation (mediated by underwater light) as eutrophication increased (Le Bagousse-Pinguet et al., 2012).

Herbivory can interact with temperature to influence fragment performance. For instance, Calvo et al. (2019) found that snail herbivory mitigated plant growth under a warmer scenario. However, the snail's negative effect was not enough to prevent fragment colonization. Additionally, the interaction among temperature, neighbor identity, and plant density can modify the outcome of biotic interactions for stem fragment sprouts, shifting from competition to facilitation, as observed in submerged macrophyte species (Silveira et al., 2023). At low density and 23°C, *Lagarosiphon major* was more competitive than *Egeria densa*, but this interaction transformed into facilitation at high density and 16°C.

Fragment size can also interact with desiccation to determine fragment performance. For instance, larger fragments of various submerged macrophyte species show greater sprouting potential after desiccation than smaller ones (Johnstone et al., 1985; Barrat-Segretain & Cellot, 2007; Baniszewski et al., 2016). This is likely due to the higher carbohydrate content in larger fragments (Baniszewski et al., 2016).

These examples highlight that the performance of stem fragments and young sprouts growing from them depends on multiple interactive factors. These interactions are sometimes difficult to capture in single-factor experiments. Thus, while more challenging to conduct, experiments testing various factors simultaneously are necessary for simulating at least part of the multitude of factors acting in nature.

5. Fragment Performance in the Face of Anthropogenic Disturbances

Disturbances that impact macrophyte propagule production or establishment success can alter community structure. Climatic global changes, with their widespread planetary effects, are a prime example of this. Based on this review, we can anticipate some consequences. For instance, increases in temperature and CO_2, coupled with altered precipitation patterns leading to more frequent droughts and changes in water depth and flow, will affect macrophyte communities by influencing fragment performance.

This review highlights the critical role of desiccation in propagule performance. Consequently, we can predict that basins experiencing more frequent and severe droughts will show reduced plant regeneration via stem fragments. This negative impact might be worsened by drought-induced habitat fragmentation, which limits propagule dispersal (Thomaz, 2025). Ecosystems in basins with more frequent rains might face greater depths and water flows, which reduce stem fragment performance.

Therefore, these two contrasting transformations, linked to global changes, could negatively affect macrophyte community maintenance and post-disturbance recovery.

Moreover, anthropogenic increases in temperature and CO_2 have the potential to boost macrophyte establishment via stem fragments, as experiments show fragment performance improves with these factors. While this may benefit many macrophyte species, there is a risk that invasive species, being more tolerant of diverse environmental conditions, will attain higher success than rare or native species.

Eutrophication, another common human-caused disturbance, also impacts fragment performance, potentially changing macrophyte communities. Eutrophication's effect on stem fragment performance is complex and potentially dual. While nutrient enrichment often boosts fragment performance and macrophyte establishment from stem fragments, it can also favor invasive species better suited to eutrophic conditions than native ones, leading to ecological and economic impacts. Conversely, high nutrient levels can hinder sprout survival (especially with NH_4^+) and encourage algal blooms, which reduce light and negatively impact plant fragment performance. Thus, some eutrophic ecosystems might actually see a decline in macrophyte establishment from stem fragments. Despite strong evidence of eutrophication's positive effects on stem fragment performance and macrophyte recovery, it remains challenging to predict exactly where its positive or negative impacts will dominate.

6. Potential Research Gaps and Future Directions

Based on this review, some research gaps have been identified that could guide future studies. While most research focuses on the immediate effects of abiotic or biotic conditions on fragment performance, few studies have examined delayed effects. That is, how prior conditions experienced by parent plants influence the performance of their stem fragments (e.g., Smith et al., 2002; Puijalon et al., 2008; Bociag et al., 2013; Bando et al., 2016). Thus, a key research gap is studying the delayed responses of macrophytes to environmental conditions, particularly by testing fragments from parent plants grown under different conditions to observe their sprout response long-term.

A second research gap is the limited number of studies on most macrophyte species. As this review shows, research has primarily focused on a few invasive species in temperate regions. In contrast, native tropical species remain largely understudied, creating a significant geographical bias. It is crucial to highlight that Neotropical and other tropical regions are home to the majority of macrophyte species (Murphy et al., 2019). Most of these have yet to be investigated regarding the key factors that determine how successfully their stem fragments establish new plants.

Additionally, few studies have compared auto- and allofragment performances (e.g., Kimbel, 1982; Madsen, 1997). Since macrophytes use both strategies for asexual reproduction via stem fragments, it is essential to assess the factors influencing each fragment type's performance and how they differ in their ability to generate new plants.

Finally, while experimental and observational data offer complementary insights into ecological patterns and mechanisms, the scarcity of integrated field and laboratory studies represents a significant research gap. Bridging this gap is essential for a more complete understanding of macrophyte recovery dynamics from stem fragments.

7. Conclusions

This review demonstrates that a myriad of endogenous, exogenous abiotic, and biotic factors, along with their interactions, influence macrophyte regeneration and establishment from stem fragment propagules. Endogenous factors, particularly fragment size, type (its position on the parent plant), and node presence, are critical determinants of stem fragment performance. Among abiotic factors, desiccation, nutrients, and light exert the most substantial impacts, while competition and facilitation represent the key biotic interactions affecting stem fragment performance and early plant establishment.

Thus, environmental abiotic factors and biotic interactions, commonly studied for their effects on adult macrophytes, also significantly influence establishment during the early life stages of species that reproduce asexually via stem fragments. Furthermore, propagule pressure assessments should include stem fragments alongside seeds and other asexual propagules. Even if only a small proportion of fragments survive and sprout under limiting conditions, they still have the potential to start new populations in unfavorable environments. Recognizing the factors governing stem fragment success in generating new plants is crucial for understanding macrophyte species distribution. This knowledge should be integrated into macrophyte metacommunity models, given that many species rely largely on this type of asexual propagule for reproduction and dispersal.

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Data availability

All research data analyzed in the research is freely available in SciELO Data, at https://doi.org/10.48331/SCIELODATA.CFH1ZD

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