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REVIEW ARTICLE

The ecology of *Egeria densa* Planchon (Liliopsida: Alismatales): A wetland ecosystem engineer?

La ecología de *Egeria densa* Planchon (Liliopsida: Alismatales): ¿Una especie ingeniera de humedales?

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ABSTRACT

Egeria densa Planchon is considered an invasive species in continental aquatic systems in Chile. Its original geographical distribution was limited to the subtropical regions of Brazil, Argentina and Uruguay. Its fast growth and dense canopy-forming habit are associated with the clear water state of shallow water continental ecosystems. As a dominant species in many of the systems in which it occurs, *E. densa* behaves as an ecosystem engineer by preventing the re-suspension of sediments and controlling the growth of phytoplankton by removing nutrients from the water column. At the same time, this invasive species produces unwanted effects such as: (1) clogging waterways and hydroelectric turbines, (2) out-competing native vegetation, and (3) negatively affecting the sediment seed bank. Given its importance in the recent (2004) change of state of the Río Cruces wetland, Chile, we felt it appropriate to undertake a comprehensive literature review of this species. We conclude by discussing the role of *E. densa* as an ecosystem engineer while cautioning against the impression that *E. densa* is always a highly competitive invader.

Key words: *Egeria densa,* ecosystem engineer, invasive species.

RESUMEN

Egeria densa Planchon es considerada una especie invasora en los sistemas acuáticos de Chile. Su distribución geográfica original estaba limitada a regiones subtropicales de Brasil, Argentina y Uruguay. Su crecimiento rápido y su tendencia a formar densas coberturas suelen estar asociadas con el estado de aguas claras en ecosistemas acuáticos continentales de aguas someras. Su dominancia sugiere que *E. densa* puede comportarse como una especie ingeniera, previniendo la resuspensión de sedimentos y controlando el crecimiento del fitoplancton a través de la utilización de los nutrientes. Sin embargo, al mismo tiempo, como especie invasora produce efectos no deseados tales como: (1) no permitir el crecimiento de otras macrófitas nativas, (2) disminuir la diversidad en el banco de semillas, y (3) interferir con la navegación y generación de electricidad por turbina. Dada su importancia en el reciente (2004) cambio de estado del humedal del Río Cruces, nos ha parecido oportuno realizar una recopilación de artículos científicos disponibles en la literatura sobre esta macrófita. Concluimos con una discusión sobre el rol de *E. densa* como especie ingeniera; a la vez que indicamos que la especie tiene ciertas vulnerabilidades y que no cumple siempre con la idea que es una especie invasora muy competitiva.

Palabras clave: *Egeria densa,* especie ingeniera, especie invasora.

INTRODUCTION

Egeria densa Planchon is in some ways a poster child for aquatic invasive species. It is found on all continents (except Antarctica); it has a relatively high rate of growth under ideal conditions, forming mono-specific stands and can propagate vegetatively (Barko & Smart 1981, Cook & Urmi-König 1984). The physical structure of *E. densa* affects the light and nutrients available to other organisms meeting the definition of an autogenic ecosystem engineer (Jones et al. 1994). However, the number of cases where this species represents a real threat to local diversity and ecosystem function appear to be low in number (e.g. Roberts et al. 1999). In this paper, we review the literature that describes the biology and ecology of this species in both its native and introduced ranges. We identify characteristics that give this species the ability to invade freshwater aquatic ecosystems around the world and also describe vulnerabilities that could lead to the decline of local populations.

A comprehensive review of *E. densa* seemed appropriate given the continued debate over the changes that occurred in the Ramsar wetland "Carlos Andwanter Sanctuary" (Río Cruces, Valdivia) in Southern Chile in 2004. The Río Cruces wetland abruptly shifted from a clear water to a turbid water state in the fall (May-June) 2004 (Lopetegui et al. 2007). Associated with this change in state, an emblematic species of swan, the black-necked *Cygnus melancoryphus* (Molina 1782), declined sharply in the wetland. The proximity of a major pulp mill (CELCO), that began functioning only months before, sparked intense public interest in what had happened and who was to blame. *E. densa* was at the center of the discussion as the major food source for the black-necked swan, since it experienced a dramatic decline in distribution and density in the wetland prior to the emigration and mortality of swans. Various hypotheses have been proposed to explain the changes witnessed in the wetland (e.g. Ramírez et al. 2006, Lopetegui et al. 2007). Although our goal is not to evaluate these hypotheses in this article, we intend that the information and discussion of *E. densa* presented herein will enlighten the debate.

BIOLOGICAL CHARACTERISTICS

Biological description

Egeria densa is a submerged, freshwater perennial plant that is found in both lentic and lotic environments (Fig. 1). It is usually rooted between 1 to 2 m below the surface, but a 7 m rooting depth has been observed in a high altitude lake in Colombia (Carrillo et al. 2006). *E. densa* also persists as fragments drifting in the water column; and as long as a double-node exists, these fragments can root and continue to grow (Cook & Urmi-König 1984). It tends to form dense monospecific stands that can cover extensive areas (Ramirez et al. 2006).

The stems of *E. densa* are elongated: 1-3 mm in diameter and can grow to over 3 m long. The stems are irregularly branched, with buds and branches developing between 0-15 internodes (Cook & Urmi-König 1984). These internodes are between 2.5 and 24 mm long. Nodes can be either fertile (bearing leaves, buds, flowers and branches) or sterile (bearing just leaves). The leaves of *Egeria densa* are 1-3 cm long, up to 5 mm across, and occur in whorls of four at sterile nodes, and in whorls of up to 10 at fertile nodes (Cook & Urmi-König 1984). The stems grow until they reach the surface of the water, where leafy branches can create dense mats.

The flowers of *Egeria densa* grow up to 3 cm above the surface of the water. When the flowers are submerged by waves the petals close, trapping an air bubble so that the stamens and stigmas remain dry (Cook & Urmi-König 1984). The 18-25 mm white flowers have three petals and are dioecious. Only, females occur near Concepción and in Central Chile, while *E. densa* in Valdivia is made up only of male plants (Hauenstein 2004).

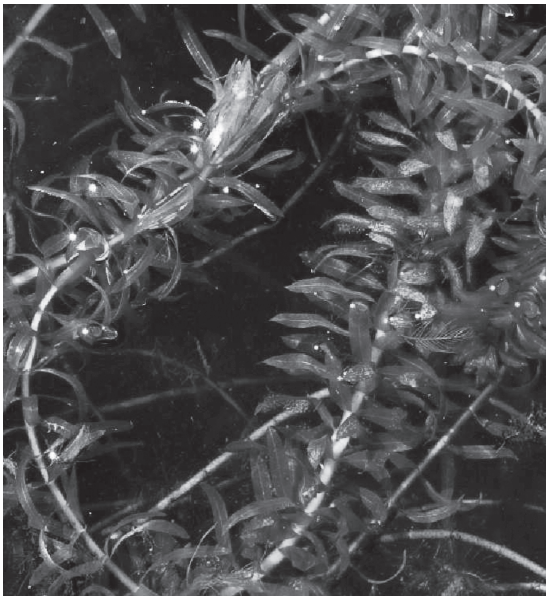

Fig. 1: Photograph of *Egeria densa* (Planchon).
Fotografía de *Egeria densa* (Planchon).

Metabolism of E. densa

To a large extent, *E. densa* has been successful as an introduced species because of physiological traits related to its metabolism. During the last decade, it was discovered that *E. densa* and other submerged macrophytes such as *Hydrilla verticillata* (L.f.) Royle, exhibit changes in their metabolism under conditions of low carbon dioxide (CO_2) (Casati et al. 2000, Bowes et al. 2002). CO_2 diffuses slowly in water (as compared to air) and often limits photosynthetic rates in submerged macrophytes. This stems from the fact that Rubisco, a principal enzyme in photosynthesis, has both carboxylating and oxygenating properties. Under conditions of a low CO_2:O_2 ratio, the oxygenation reaction will be favored, leading to a reduction in the amount of fixed carbon (Casati et al. 2000). C_4 photosynthesis is an adaptation that helps plants increase photosynthetic efficiency by surrounding Rubisco with high concentrations of CO_2. C_4 metabolism is really a collection of morphological and biochemical changes that has evolved, independently, approximately 45 times in higher plants (Sage 2004). Unlike other C_4 plants that show distinct morphological changes (Kranz anatomy), *E. densa* employs a C_4-like mechanism that takes place in a single cell and can be induced by environmental conditions. Casati et al. (2000) analyzed two enzymes involved in the C_4 pathway over 23 days in *E. densa*: phosphoenolpyruvate carboxylase (PEPC) and NADP-malic enzyme (NADP-ME). They found that under stressful conditions of high temperature and light (HTL) in which CO_2 availability is decreased, these two enzymes increase in activity. As in other C_4 plants, the PEPC was located in the cytosol, whereas the NADP-ME was located in the chloroplasts, showing that intracellular location is important for the carbon concentrating mechanism to take place. Additionally, the CO_2 compensation point decreased substantially, indicating that the oxygenating activity of Rubisco was prevented by the induced C_4 biochemical pathway. It should be noted that although an estimated 50 % of aquatic plants use hydrogen bicarbonate (HCO_3-) as carbon source in photosynthesis, its use does not indicate the presence of a C_4 pathway (Bowes et al. 2002). Nevertheless, it has been shown that in low CO_2 concentrations, one of the induced C_4 enzymes in *E. densa* has a very high affinity for HCO_3^- (Casati et al. 2000).

This C_4-like pathway operates intracellularly –CO_2 is collected from the cytoplasm and concentrated in the chloroplasts– with no apparent barrier to prevent CO_2 from leaking out of the chloroplasts (Sage 2004). The C_4 pathway requires energy to concentrate CO_2 near Rubisco. However, because the C_4-like pathway allows *E. densa* to continue to photosynthesize and grow at very low CO_2 levels which are common in lentic freshwater systems, it is considered adaptive (Bowes et al. 2002). Thus, it can be said that *E. densa* has a flexible carbon incorporation strategy - it can switch to a C_4-like pathway under conditions of low CO_2, high oxygen concentration and high temperature (which favors high rates of photorespiration).

Phylogenetic description

Egeria densa belongs to the Hydrocharitaceae (subclass Alismatidae), a family of marine and fresh water aquatic plants belonging to the monocotyledons. Nine of the seventeen genera occur in South America, mostly in tropical and subtropical climates (Koehler & Bove 2001). The Hydrocharitaceae is often divided into three sub-families, but a recent molecular phylogenetic analysis indicates that there are four major sub-families (Les et al. 2006). Divisions within the Hydrocharitaceae indicate that traits such as submerged lifeforms, hydrophilous pollination and marine habitation are derived relative to the basal genera in the family and a closely related outgroup (Les et al. 2006). Two lifeforms are common within the family: those having a creeping monopodial rhizome with leaves arranged in two vertical rows and a more erect lifeform with basal roots and whorled or spiral leaf arrangements. Most species have unisexual flowers (although a few are hermaphroditic) which are born solitarily or in inflorescences (Watson & Dallwitz 2008). There are four distinct pollination mechanisms in the Hydrocharitaceae, which in addition to other diverse traits has created confusion about the taxonomy of the family (Tanaka et al. 1997). *E. densa* is entomophilous - that is, flowers bloom above the water surface and are pollinated by insects. The other mechanisms involve water-based pollination (Tanaka et al. 1997).

There are three congeners in the genus *Egeria*. *E. najas* and *E. densa,* described by Planchon in 1849, are largely sympatric in their original range (Cook & Urmi-König 1984). A third species, *E. heterostemon* Koehler & Bove, was more recently described from Matto Grosso and Goiás in central Brazil (Koehler & Bove 2001). All members of the genus *Egeria* have unisexual flowers, 9 stamens, basal leaves (prophylls) paired at the base of lateral shoots, leaves with transparent idioblasts (specialized cell lacking chlorophyll) and leaf margins without fiber cells (Cook & Urmi-König 1984, Koehler & Bove 2001). The genetic diversity of different *E. densa* populations has not been extensively examined. However, Carter & Sytsma (2001) found that the population of *E. densa* in the Río Cruces near Valdivia, Chile and several populations in Western Oregon, USA have remarkably similar genotypes. These authors propose that either the genetic diversity of the species is relatively low or that some common bottleneck or selection pressure occurred in the introduction of both the Chilean and Oregonian populations.

Distribution

The original distribution of *Egeria densa* ranges from the central Minas Gerais region of Brazil to the coastal areas of Uruguay and Argentina. It is common in the Paraná basin of Argentina. In the first decades of the 1900s, *E. densa* was promoted as a good "oxygenator" of fresh water– a plant useful in raising fish for mosquito eradication programs (Cook & Urmi-König 1984). An attractive and robust plant, *E. densa* was also sold around the world as an aquarium plant. The earliest report of *E. densa* outside of its native range is from 1893, when a plant was collected on Long Island, New York. However, there were many reports of *E. densa* from Europe beginning in 1910 in Germany. Currently, this species is naturalized in at least 27 countries around the world in subtropical and temperate regions (Fig. 2). In Chile, *E. densa* has an ample, if discontinuous, distribution (Hauenstein 2004). It can be found in streams and reservoirs in Central Chile (~33° S) (Estero Limache and Quebrada Macul), (Cook & Urmi-König 1984, Hauenstein 2004). Near the city of Concepción (36° S), *E. densa* has been found in several lakes. In the basin of

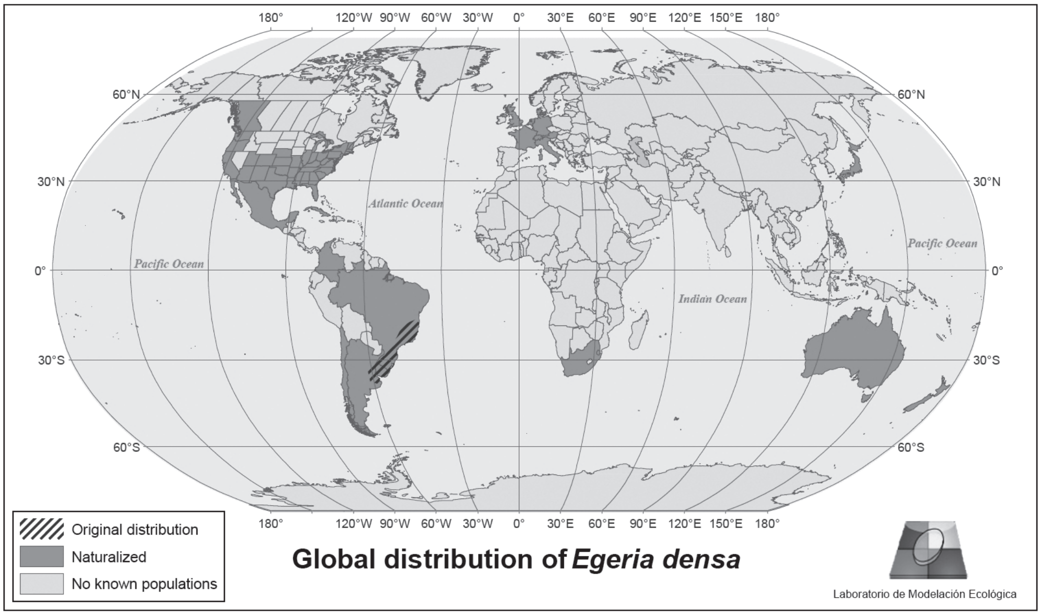

Fig. 2: Global distribution of *E. densa*. (Source: Cook & Urmi-Kbnig 1984; Haramoto & Ikusima 1998; Roberts et al. 1999; Hauenstein 2004; Carrillo 2006).

Distribución global de *E. densa* (Fuente: Cook & Urmi-Kbnig 1984, Haramoto & Ikusima 1998, Roberts et al. 1999, Hauenstein 2004; Carrillo 2006).

the Valdivia River (~40° S), it is common in the Río Cruces and Río Calle Calle (Ramirez et al. 1989, Hauenstein 2004). Cook & Urmi-König (1984) and Hauenstein (2004) both indicate that *E. densa* was naturalized in Chile by the 1960s. Although some vendors have ceased to sell *E. densa* as an aquarium plant due to its invasiveness, it can still be purchased over the Internet.

ECOLOGY: ENVIRONMENTAL FACTORS AFFECTING *EGERIA DENSA* OCCURRENCE, GROWTH AND PRODUCTION

Submerged aquatic macrophytes like *E. densa* face very different conditions compared to terrestrial plants. Besides CO_2 concentration, photosynthetic active radiation (PAR), temperature, water-level and the nutrient content of sediment and water affect the metabolism of individuals, the distribution of species and ultimately community structure and composition.

Light

Barko & Smart (1981) examined the photosynthetic capacity of *E. densa* and *Hydrilla verticillata* under different light and temperature conditions. They found that *E. densa* is able to increase its photosynthetic rate with increasing light in a nearly linear fashion. In addition, photosynthesis was not saturated at the highest light level of the experiment (1050 $\mu E\ m^{-2}\ s^{-1}$, as measured at middepth in tanks that had approximately a 69 cm deep water column). At low levels of light the growth patterns favor the elongation of shoots (instead of increased shoot number) and the development of upper (canopy) branches. Barko & Smart (1981) suggest that because *E. densa* can achieve net photosynthesis and form a canopy in low light, that it could have a competitive advantage over other macrophytes in eutrophic systems. Nonetheless, Tanner et al. (1993) found that with suspended solids concentrations above 30 mg m^{-3}, or a light attenuation coefficient (K_d) above two, the establishment of *E. densa* would be unlikely. Furthermore, it is also clear from several authors that *E. densa* is frequently dominant in clear waters with low light attenuation (e.g. Bini et al. 1999, Carrillo et al. 2006). Thus, although Barko & Smart (1981) show the species' ability to adapt to low light conditions in the laboratory, in natural systems it appears to compete best under conditions of low light attenuation.

Temperature

Temperature may be the most critical factor impacting *E. densa* metabolism (Barko & Smart 1981). The temperature of water and sediment affects the physiology, growth rates and dormancy onset of aquatic plants (Lacoul & Freedman 2006). For *E. densa*, it appears that growth is relatively constant in the range between 16 °C and 28 °C (Barko & Smart 1981). Although gross photosynthesis increases over this range, respiration also increases, notably above 16 °C, limiting biomass production. At 32 °C, this species showed morphological changes such as reduced shoot number and length and displayed a net photosynthetic rate significantly lower than that observed at 16 °C. This would indicate that the species reaches an upper temperature bound for optimal growth above 32 °C. However, Haramoto & Ikusima (1988) indicate that when this species demonstrates summer-type growth, it can thrive at 35 °C. Most species of macrophyte die or become dormant at temperatures below 3 °C (Lacoul & Freedman 2006). *E. densa* appears to have some degree of tolerance for cold waters: it can survive winter in a ditch under a cap of ice (Haramoto & Ikusima 1988). However, freezing is lethal (Leslie, 1992).

Seasonal patterns

Seasonal effects on metabolism and biomass production are in essence the combination of two factors: light (photoperiod) and temperature. Tropical systems usually present relatively uniform conditions for macrophytes, although seasonally lower PAR and higher water levels and/or flood pulses during rainy seasons can impact growth (Camargo et al. 2006). In fact, *E. densa* does appear to present little seasonal variation in growth rate compared to other macrophytes in tropical and subtropical systems (Camargo et al. 2006, Mony et al. 2007). However, in temperate systems, *E. densa* does show strong differences. In Japan, the P:R ratio (photosynthesis:respiration ratio) was compared during different seasons; the highest ratio was in spring (20 °C) while both low winter temperatures (5 °C) and high summer temperatures (40 °C) caused the P:R ratio to fall to 1.57 and 1.61, respectively (Haramoto & Ikusima 1988). Observing a bimodal biomass curve, these authors proposed that *E. densa* can present winter and summer-type growth. Winter growth is slow and seems to focus on storing starch that aids subsequent spring growth. Winter plants lack canopy branches, have short internodes and tend to have a prostate habit on the bottom. The summer growth type produces an extensive canopy at the water surface and is apparently able to maintain positive net primary productivity at higher temperatures than reported in Barko & Smart (1981). In Southern Chile, one recent study found that, paradoxically, decaying *E. densa* material was greater in the spring, while biomass production achieved its highest level in fall (Boettcher 2007). Ultimately, the literature shows that *E. densa* is highly adaptable, presenting continual or seasonal growth as the local conditions dictate (Haramoto & Ikusima 1988, Carrillo et al. 2006, Mony et al. 2007).

Nutrient uptake and content

Nitrogen and phosphorus are generally considered the most important limiting nutrients for macrophytes (Barko & Smart 1981, Hung et al. 2007). However, in many cases, nutrient concentration is not as important factor as temperature and PAR for rooted submerged macrophytes like *E. densa* (Barko & Smart 1981). This is primarily because these plants are able to extract nutrients from both the sediment and the water column. Several other studies indicate that nutrients are not a major limiting factor in most systems. Mony et al. (2007) in an experiment in Florida concluded that fertilizing the sand substrate of *E. densa* mono-crops did not enhance biomass production. This reinforces the idea that *E. densa* readily uptakes nutrients through passive diffusion from the water column. One result of the study by Bini et al. (1999) in a Brazilian reservoir was that the group typified by *E. densa* was correlated with the lowest total phosphorous (TP) levels in the sediment and low TP in the water column.

The question of whether macrophytes get their nutrients from the sediments or from the water column has been an open question for decades. Carignan & Kalff (1980) found that under a variety of conditions, sediment contributed an average of 72 % of the phosphorus taken up during growth. Feijoó et al. (2002) looked at P uptake of *E. densa* in nutrient rich streams in Argentina. They found that between 8-10 % of P incorporated in the plant biomass derived from the sediment. Indeed, *E. densa* biomass gain was closely related to soluble reactive phosphorus (SRP) concentration in the water column. It was also discovered that *E. densa* shows a clear preference for ammonium over nitrate and that most N was absorbed from the water column. These authors' results suggest that phosphorus may be more of a limiting factor for *E. densa* than nitrogen, given that P, not N, was tied to increased growth (Feijoó et al. 2002). Table 1 shows N and P concentrations in *E. densa* biomass.

TABLE 1

N and P content in *E. densa* dry biomass. Note that ranges include experimental treatments.

Contenido de N y P en biomasa seca de *E. densa*. Note que los rangos incluyen tratamientos experimentales.

Reference	Location	N content in biomass	P content in biomass
Barko & Smart 1981	Experiment, Mississippi, USA	1.6 - 3.3 %	0.33 - 0.49 %
Mazzeo et al. 2003	Shallow lake, Uruguay	3.5 %	0.2 %
Feijoó et al. 2002	Experiment, modeled on Pampean stream, Argentina	3.25 - 3.96 %	0.67 - 0.72 %
Pinochet et al. 2004	Valdivia, Chile	1.9 %	0.22 %

Metal toxicity

In general, iron and other metals are required in low concentrations by aquatic plants. In saturated sediments, iron and manganese are reduced and become readily available, often to the degree where, if adsorbed, they can become toxic to plant tissues (Mitsch & Gosselink 2000, Sinha et al. 2008). Submerged macrophytes often release oxygen through their roots in order to oxidize iron, creating iron crusts around roots. This has been shown to occur in *Elodea canadensis* Michx., a submerged macrophyte from the same family as *E. densa* (Hupfer & Dollan 2003). Heavy metals, such as iron, stress plants by inducing reactive oxygen species (i.e. free radicals) within plant cells and by decreasing antioxidants (Sinha et al. 2008). These free radicals can damage membranes, proteins, pigments and nucleic acids resulting in a reduction of plant growth and potentially death. A study by Sinha et al. (2008) showed a negative and significant correlation between iron uptake and protein and chlorophyll content in tissues of a creeping wetland herb. This is consistent with the slower growth, smaller leaves, leaf dieback and the formation of necrotic leaf spots observed by many authors in *E. densa* and other macrophytes (Pinochet et al. 2004, Lopetegui et al. 2007, van der Welle et al. 2008). On the other hand, many aquatic plants have been identified as hyper-accumulators of heavy metals. One study found that three wetland plants, grown for three weeks in experimental tanks, rapidly absorbed the iron present and to different degrees were able to tolerate concentrations between 3.2 % to 4.6 % of dry biomass (Kamal et al. 2003). The genus *Egeria* has not been mentioned as a hyper-accumulator of iron in the literature, but evidently its tolerance is high (Correa 2003). For example, the study by Saldivia (2005) in the Río Cruces wetland, show maximum iron concentrations of 3.56 x 10^3 mg kg^{-1} dry weight (3.56 % of iron) in the southern zone of the wetland (Punucapa).

Finally, an important issue related to the comparison of the concentration of microelements of one species in different ecosystems is related to their concentration in the environment. Yurukova & Kochev (1994) have shown that the incorporation of microelements in aquatic macrophytes is related to environmental concentrations, producing enrichment factors that may range between 10^2 and 10^5. Consequently, when comparing microelement concentrations in aquatic macrophytes, care should be taken to relate them to their concentrations in the environment.

THE ROLE OF *EGERIA DENSA* IN AQUATIC ECOSYSTEMS

In this section, we review work done on the effects of *E. densa* on the structure and function of aquatic ecosystems. It would be interesting to consider the differences between the role of *E. densa* in natural systems in its native range versus its role in human-created aquatic systems and/or systems where it represents an invasive species. However, there is surprisingly little information on the ecology of any of the three species of the genus *Egeria* in their native ecosystems (Tavechio & Thomaz 2003). In fact, many of the studies done in the native range of *Egeria* have examined cases where man-made reservoirs were being invaded and dominated by *E. densa* or *E. najas* (e.g. Oliveira et al. 2005). Thus, what is presented below attempts to characterize the major role that *E. densa* can play in aquatic ecosystems of different types.

Egeria *and sediment dynamics*

Streams and rivers often have spatial (channels vs. pools or submerged floodplain areas) and temporal (i.e. flooding/drought cycles) heterogeneity that affects and is affected by submerged macrophyte stands. Fast flowing water not only physically impedes macrophyte growth, but also causes sediment resuspension, increasing turbidity and light attenuation, which also limits macrophyte growth. Established submerged macrophyte stands can significantly lower water velocity, allowing sedimentation of suspended particles and contributing to water clarity and reduced light attenuation (Sand-Jensen & Pederson 1999). In this regard, it is interesting to cite here the work by Scheffer & Van Nes (2007) as related to the regime shift in shallow water continental ecosystems (from clear water to turbid waters).

The process is mostly related to a declined submerged vegetation due to increases in turbidity. For example, Hauenstein et al. (2002), describing the vegetation of the wetlands of the Toltén coast (IX Region, Chile), state that *Egeria densa* belongs to those species associated with open water, and that it may be lost when there is accumulation of sediments favoring the colonization of California bulrush (*Schoenoplectus californicus* (C.A.Mey.) Palla). Thus, there is interplay between macrophyte stands, sediment and water movement involving several feedback loops (Madsen et al. 2001). Due to their role in stabilizing sediment and reducing turbidity, submerged macrophytes can be considered "ecosystem engineers" (Fig. 3).

Growth and biomass production in different aquatic systems

Egeria densa is considered an aquatic "weed", able to produce biomass rapidly under ideal conditions (Pistori et al. 2004). Haramoto & Ikusima (1988) calculated a relative growth rate (RGR) of 0.049 day^{-1} at 20.7° C. At a high altitude reservoir in Colombia, Carrillo et al. (2006) reported an average in situ RGR of 0.017 day^{-1} (range 0.003-0.035) at an average temperature of 15-17 °C. Pistori et al. (2004) found that RGR ranged from 0.009-0.063 day^{-1} over a period of 44 days and that *E. densa* showed a logistic growth curve under laboratory conditions. During the period of maximum RGR, the doubling time was only 12

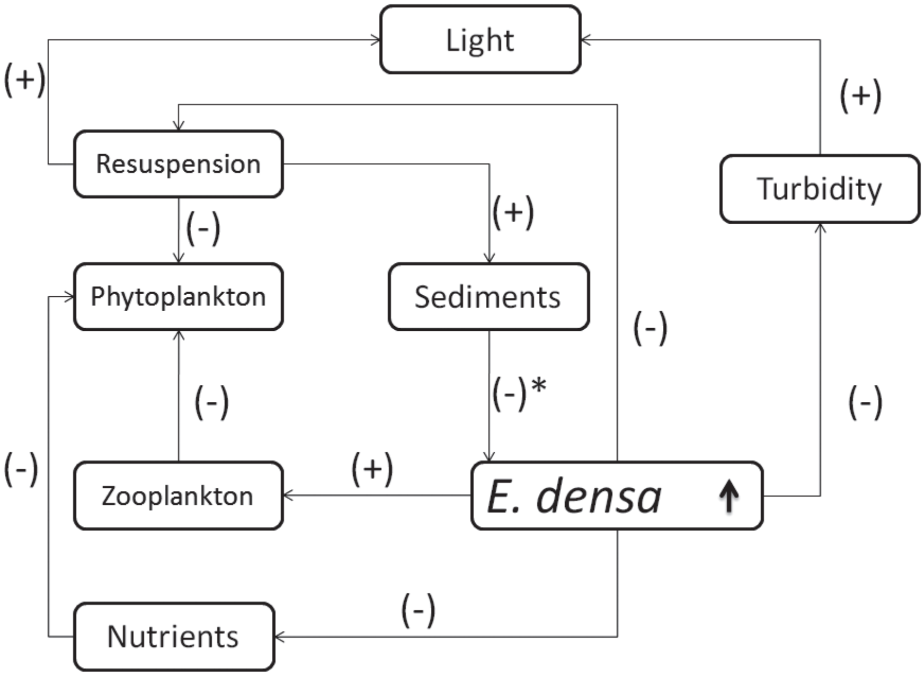

Fig. 3: Egeria densa as ecosystem engineer (sensu Jones et al. 1994). The presence of high coverage of *E. densa* decreases water turbulence, decreasing resuspension of sediments and increasing sedimentation. The decrease in resuspension increases the light available in the water column maintaining the clear water ecosystem state. It also decreases the standing stock of phytoplankton by sequestering nutrients into the sediments. It finally increases the concentration of zooplankton since it acts as a refuge decreasing its predation. However, in the long term these feedback mechanisms may self-generate adverse conditions through the increase in sediment height (-)*.

Egeria densa como especie ingeniera (sensu Jones et al. 1994). La presencia de una cobertura alta de *E. densa* reduce la turbulencia del agua, reduciendo así la resuspensión de sedimentos y el aumento de la sedimentación. La disminución en la resuspensión aumenta la luz disponible en la columna de agua manteniendo el estado ecosistémico de aguas claras. También disminuye la biomasa del fitoplancton a través de la secuestración de nutrientes en los sedimentos. Por último, aumenta la concentración de zooplancton, ya que actúa como un refugio disminuyendo su depredación. Sin embargo, en el largo plazo, estos mecanismos de retroalimentación podrían generar condiciones adversas mediante el aumento de la altura de los sedimentos (-)*.

days. This growth rate is comparable to other submerged macrophytes, although perhaps near the lower end of the scale. *Elodea canadensis*, which bears a strong physical resemblance to *E. densa,* was found to have a RGR of 0.04-0.09 day^{-1} under controlled conditions (Larson 2007). An earlier study provided an RGR range of 0.046 to 0.94 day^{-1} for several submerged macrophytes grown in high light conditions (Nielsen & Sand-Jensen, 1991). Mony et al. (2007) indicated that *E. densa* was out-competed by a faster growing *Hydrilla verticillata* in high nutrient conditions.

As a dense canopy forming plant, *E. densa* can achieve a large standing biomass. In a study of a rapidly expanding population of *E. densa* in an Australian river, Roberts et al. (1999) reported that the estimated fresh biomass of *E. densa* was 9047 g m^{-2}. Table 2 presents average and ranges of biomass for four study sites in dry weight. These studies indicate that *E. densa* is capable of tremendous primary productivity, but that standing biomass of more than 800-1000 g dry wt m^{-2} occurs only during periods of rapid growth.

Interactions with aquatic communities

As a dominant species in the systems where it occurs, *E. densa* plays an important role in trophic dynamics. This species frequently influences phytoplankton biomass, contributing to smaller crops through a variety of mechanisms (Mazzeo et al. 2003). Submerged macrophytes can provide shelter for zooplankton and planktivorous fish in the presence of piscivorous fish. Canopy forming macrophytes such as *E. densa* also shade out phytoplankton lower in the water column. Given its tendency to acquire nutrients from the water column, *E. densa*, can reduce nutrient availability for phytoplankton (Feijoó et al. 2002; Mazzeo et al. 2003). *E. densa* can rapidly absorb ammonium (more so than nitrate), resulting in the accumulation of nitrogen in tissues without necessarily leading to an increase in plant biomass (Feijoó et al. 2002). As an example of the magnitude of nutrient sequestration, Søndergaard & Moss (1998) cite an instance where *Elodea* (same family as *Egeria*) contained over 60 % of N and P in a shallow lake system (excluding sediment). This nutrient regulating capacity may have had an important effect on Laguna Chica de San Pedro near Concepción, Chile. Diatom data collected from lake sediments indicated that the lake spent decades in a eutrophic state (associated with turbid waters). When *E. densa* became established in the 1980s, conditions in the lake shifted to oligotrophic (associated with clear waters) despite a peak in sedimentation rates in the early 1990s and continued high nutrient loading (Urrutia et al. 2000). In larger and deeper reservoirs, submerged macrophytes may exert less influence on phytoplankton due to reduced relative coverage. Anecdotal evidence cited in Thomaz & Bini (1998) indicates that a cynobacteria bloom in Itaipu Reservoir reduced the euphotic zone from 1.85 m to 0.61 m which led to a reduction in the dry weight of *E. najas* from 207 g m^{-2} to 48 g m^{-2}.

In its native range, *E. densa* forms beds having a complex underwater structure that provides habitat for epiphytic algae, zooplankton and fish (Pelicice & Agostinho 2006). Although it tends to form monospecific stands, *E. densa* appears to support relatively diverse communities of phytoplankton, zooplankton and fish (Mazzeo et al. 2003, Pelicice & Agostinho 2006). *E. densa*, like any

TABLE 2

Standing *E. densa* biomass in four study sites.

Biomasa de *E. densa* en cuatro sitios de estudio

Reference	Location	Average biomass (g dry wt m^{-2})	Biomass Range (g dry wt m^{-2})
Roberts et al. 1999	New South Wales, Australia	650 (estimate from graphs)	180 - 3000
Carrillo et al. 2003	High altitude lake, Colombia	522	83 - 1155
Boettcher 2007	Vadivia, Chile	477	189 - 841
Oliveira et al. 2005	São Francisco River, Brazil	497	-

important macrophyte, can have a strong, positive effect on the resource base of epiphytic macroinvertebrates and many if not most benthic macroinvertebrates (Diehl & Kornijów 1998). Thus, with an increase of macrophyte biomass, the biomass of macroinvertebrates tends to increase, but also the proportion of macroinvertebrates that are epiphytic increases. Although submerged macrophytes shelter macroinvertebrates from fish, as the biomass of macroinvertebrates increases with macrophyte growth, eventually fish density will increase as well (Diehl & Kornijów 1998).

Little is known about the use by avifauna of *E. densa* stands in its native range. A study from Florida shows that native birds utilized *E. densa* mats primarily as foraging sites (90 % of birds were observed actively feeding during weekly observations over a 2.5 month period; Bartodziej & Weymouth 1995). Nevertheless, this study doesn't show comparative behavioral and density data for similar communities dominated by native plants. *E. densa* stands in the Río Cruces wetland of Southern Chile played a key role in supporting the avifaunal community. Up to 92 % of the black-necked swan's diet in 1993-1995 was made up of *E. densa* (Corti & Schlatter 2002). These authors indicate that the intense grazing by the black-necked swan on *E. densa* limited standing biomass and potentially impacted the accrual rate of plant biomass in the wetland sediment. In addition to the black-necked swan, numerous other species of aquatic birds either grazed on *E. densa* or utilized the macrophyte beds as foraging sites (Lopetegui et al. 2007).

It is interesting to note that many macrophytes produce allelopathic substances that target epiphytic or planktonic algae and cyanobacteria, including various species of the genus *Elodea* (Hilt (nee Körner) 2006). The one study found in the scientific literature that looks at the allelopathic effects of *E. densa* shows that it has a species-specific effect on cultures of three species of blue-green algae (Nakai et al. 1999). It had a strong effect on the growth of *Anabaena flosaquae* (Lyngb.) Breb., a moderate effect on *Microcystis aeruginosa* (Kutzing) Lemmermann and no effect on *Leptolyngbya tenuis* (Gom.) Anag. and Komar. According to Søndergaard & Moss (1998) the impact of the allelopathic effects of macrophytes has yet to be understood at an ecosystem level given that it is hard to distinguish them from other competitive interactions. Nevertheless, in addition to the importance of increased turbidity in causing regime shifts (Scheffer & Van Nes 2007), high epiphytic algal growth could also contribute to such a shift through shading and competing for nutrients with macrophytes (Brönmark & Vermaat 1998). This highlights the importance of grazers, such as snails, in reducing the periphyton and thereby lending stability to the macrophyte (clear water) state. More work is needed to establish the importance of this mechanism in *Egeria densa* beds.

Impacts and management of an invasive species

As an invasive species, *E. densa* can negatively affect ecosystem functions and services. For example, large quantities of *E. densa* biomass frequently cause problems with irrigation systems and hydroelectric generation infrastructure (Thomaz & Bini 1998, Roberts et al. 1999). The dense canopies of *E. densa* favor mono-specific stands which can lower biodiversity through competition and exclusion (Roberts et al. 1999). The presence of invasive submerged macrophytes in New Zealand led to significant decrease in size and diversity of the sediment seed bank. This in turn can decrease the resilience of aquatic system to disturbances that could remove the one or few dominant species (Winton & Clayton 1996).

Experiences with *E. densa* as an invasive exotic species have differed according to region. In Australia, New Zealand and parts of the United States, much work has been done to understand the invasive potential of *E. densa*, find eradication methods, and inform the public so as to avoid further introductions (Roberts et al. 1999, Cal-IPC 2006). In California, it has been classified in the highest categories for invasiveness and impact (Cal-IPC 2006). In other parts of the world, its presence has been accepted or has passed unnoticed by the general public. Interestingly, much of the research on the genus *Egeria* in Brazil deals with its expansion into reservoirs and problems with blockage of hydroelectric equipment (Thomaz & Bini 1998, Barreto et al. 2000). As an example, there are now over 130 dams with a height over 10 m in the upper Paraná River basin (Thomaz & Bini 1998). *E. densa* and *E.*

najas have expanded into many of the reservoirs created by these dams (Pelicice & Agostinho 2006). Several characteristics of *E. densa* underlie its invasiveness and ability to colonize reservoirs: relatively fast growth rate, acclimatization to different light regimes, flexible nutrients uptake from water column and sediments, high productivity in low-medium nutrient environments, high phenotypic plasticity, high dispersal via vegetative fragments and high potential to colonize disturbed areas (Barko & Smart 1981, Feijoó et al. 2002, Pistori et al. 2004, Mony et al. 2007).

The invasiveness of *E. densa* in some systems has led to much research in eradication and control methods. Methods include physical removal, herbicide use, biological control, and water draw-downs. Mitchell (1980) stocked different densities of carp in two lakes in an effort to control emergent macrophyte growth. At low densities, the fish preferentially selected species other than *E. densa*. At higher densities, all vegetation was removed. Subsequent removal of carp from the lakes was challenging. In Florida, copper was used in the 1980s as an herbicide to manage aquatic weeds (including *E. densa*). However, after evidence of copper accumulation in sediment and bioaccumulation in fauna from mollusks to manatees came to light, the use of copper was discontinued (Leslie 1992). *E. densa* removed from plots in the shallows of a Brazilian reservoir regained its original biomass in about three months, even when removal was repeated five times consecutively (Oliveira et al. 2005). Mechanical removal of *E. densa* thus appears utterly ineffective under good growing conditions and with nearby propagule sources. Drawdown of reservoirs or other water bodies appears to be more effective against species of the genus *Egeria*. The Itaipú reservoir was allowed to drop to 5 m below its usual level for 3 months and the effect on *E. najas* biomass and distribution was studied (Thomaz et al. 2006). These authors indicate that although the species was not eliminated from the reservoir, *E. najas* had not begun to recover 10 months after drawdown. The combination of cold temperatures and low water levels associated with a drawdown could be especially lethal for *E. densa* (Marer & Garvey 2001). When not submerged, the shoot and leaf tissues of *E. densa* are vulnerable to drying and freezing in a matter of hours, while a prolonged drawdown will readily kill roots. Furthermore, Dos Santos & Thomaz (2007) analyzing data from the upper Paraná river floodplains, have shown that for floodplains connected through the river, drawdown periods have a negative effect on species richness and diversity as resulting from "habitat contraction". Interestingly, Van Geest et al. (2007) analyzing stable states in shallow lakes of The Netherlands show that when a native macrophyte seed bank is available, drawdown events indeed increase the likelihood of macrophyte dominance.

DISCUSSION: IS *E. DENSA* AN ECOSYSTEM ENGINEER?

We argue that *E. densa* should be considered an ecosystem engineer that is capable of modifying or regulating important ecosystem processes. However, a careful reading of the literature underlies the importance of a nuanced view that recognizes the variability in impact of this ecosystem engineer. It is possible to paint two distinct portraits of this species. On one hand, we see an aquatic competitor with a long list of traits that allows it to adapt to and potentially dominate the littoral zone of lakes, reservoirs and rivers: fast growth, vegetative propagation, ability to use nutrients from both the sediments and the water column, capacity to tolerate high levels of iron, induction of C_4-like metabolism under low CO_2 availability, capacity to grow under low light conditions. These characteristics allow it to inhabit a wide range of aquatic systems, as can be seen in the success of invasive populations in North and South America having extremely little genetic distances, i.e. success is not due to local selection and formation of biotypes (Carter & Sytsma 2001).

On the other hand, we see a species that does not fit this depiction of a highly competitive invader. *E. densa* is highly vulnerable to drawdown and the resulting exposure to air and extreme temperatures. Hauenstein (1981) indicates that individuals of this species did not survive for more than an hour when exposed to air. Marín et al (2009) have shown, via a numerical model of the Río Cruces wetland in Chile, how vulnerability to desiccation and low temperatures could potentially wipe out an entire population of *E. densa*, leading to a shift in ecosystem state. Some authors have noted that the distribution of *E. densa* can be explained, in large part, by light attenuation (Bini & Thomaz 2005). Compared to *E. najas*, the probability of *E. densa* occurrence decreased more steeply at high light attenuation values in Itaipú Reservoir. Concurrently, *E. densa* is negatively affected when the concentration of suspended solids is higher than 30 mg m^{-3} (Tanner et al. 1993). Nevertheless, Barko & Smart's (1981) finding of low light tolerance seems to contradict *E. densa*'s intolerance to high turbidity. However, this may be due to the distinct nature of laboratory versus field methods.

Low genetic variation in introduced populations of *E. densa* may also make this species vulnerable to attacks by pathogen or fungi, although no direct evidence of this has been found in the literature. Lastly, Ramírez et al. (2006) proposed that the thin leaves of *E. densa* make it vulnerable to high UV-B radiation. Casati et al. (2002) found evidence that extreme exposure of *E. densa* to UV-B can damage the enzymes involved in photosynthesis, impacting photosynthetic ability. This could be a factor at the surface of the water column but humic material in the water absorbs UV-B and can remove 90 % of UV-B in as little a few centimeters to a few meters (Kirk 1994).

Jones et al. (1994) classic paper defines ecosystem engineers as "organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials." Autogenic engineers change the environment with their own physical structures. This paper mentions submerged macrophytes as autogenic engineers that attenuate light, affect water flow, enhance sedimentation and oxygenate the rhizosphere. In the case of *E. densa*, we can add to this list of impacts: sequestration of nutrients from the water column and provision of habitat for zooplankton and fish. It is clear that *E. densa* fulfills these functions and should thereby be considered an autogenic ecosystem engineer.

Exploring the ecosystem engineering concept further, it is instructive to look at feedback loops arising from engineered physical change that in turn affects the engineer (Fig. 3). In the case of *E. densa*, positive feedback (or "extended phenotype engineering" from Jones et al. 1994) results from the attenuation of wave action or flowing water that can resuspend sediments. This regulates the turbidity of the water and helps ensure that *E. densa* receives high PAR; it also stabilizes sediments which supports colonization of new areas (Barko & James 1998). Nutrient sequestration that regulates phytoplankton growth is another positive feedback mechanism. Negative feedback loops can be viewed as the costs or trade-offs associated with ecosystem engineering (Matsuzaki et al. 2009). *E. densa* gradually contributes to rise in sediment levels by promoting sedimentation and through its own rapid biomass production. This ultimately leads to burial of photosynthetic tissues and to exposure to air and extreme temperatures which have been shown to be fatal (Hauenstein 1981, Barko & James 1998).

Finally, we propose that *E. densa* belongs to a select group of ecosystem engineers that are able to modulate and/or influence regime shifts between stable ecosystem states. Past examinations of regime shifts in aquatic systems have often examined alloctonous abiotic drivers such as pollution or climate change. However, Matsuzaki et al. (2009) indicate that invasive ecosystem engineers often catalyze state changes. Sudden shifts between states seem to be most common at intermediate nutrient concentrations and when emergent macrophytes have a significant presence in a given system, potentially over 40 % PVI (percent volume infested) according to Gasith & Hoyer (1998). There is evidence that as an invasive species, *E. densa* effectively modulated a regime shift observed in a lake in southern Chile, despite landscape factors that would have favored the continuation of a turbid water state (Urrutia et al. 2000). As a native or naturalized component of a system, *E. densa* may eventually auto-catalyze a shift from a clear water to a turbid water state as it builds sediment in shallow areas. Furthermore, the mono-specific nature of many *E. densa* stands exhibit vulnerability to the impact of allogenic ecosystem engineers such as carp or crayfish (Mitchell 1980, Matsuzaki et al. 2009). Ultimately, the central role that *E. densa* can play in regime shifts means that it should be a major focus of any attempts at ecosystem management.

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