AQUATIC MACROPHYTES IN THE TROPICS: ECOLOGY OF POPULATIONS AND COMMUNITIES, IMPACTS OF INVASIONS AND HUMAN USE

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Keywords: Aquatic biodiversity, nutrient cycling, food webs, nuisance species, assemblages

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Aquatic macrophytes are key components of waterscape because they provide food (both as leaf matter and detritus), affect nutrient cycles and mainly because they increase the habitat complexity, which enhances biodiversity in littoral regions. All species of macrophytes belonging to high plants returned to water along their evolutionary history and several strategies to cope with limitations in this medium were selected along their natural history. These adaptations are especially apparent in submerged plants, which changed their physiology and anatomy to survive in a habitat where inorganic carbon is scarce and anoxia is common in sediments. In congruence with what is described for other groups of organisms, tropical areas are recognized by having the highest number of species of macrophytes, in spite of the limited information about the mechanisms underlying this pattern. Different to what was thought by the first ecologists, most tropical ecosystems have clear seasonality, in general associated with rain versus dry periods, leading to water level fluctuations and in oscillations of other physicochemical factors such as nutrients, underwater light and CO_2. In conjunction, these factors affect macrophyte populations and the organization of assemblages. Biotic interactions are also important and strong herbivory (especially by buffalos) has been demonstrated to change dramatically aquatic plant communities all over the tropics. However, the high temperatures, typical of tropical areas, usually lead to increased rates of primary production and fast decomposition of macrophytes. High temperatures may also facilitate the development of these plants, and several native species have caused trouble for water usage in tropical areas. On the other hand, the commonest of macrophytes together with their fast biomass production make these plants very useful by man in the tropics, where they are used in religious rituals, food and waste treatment, among other purposes.

1. Introduction

The term ‘aquatic macrophytes’ refers to large plants visible to the naked eye and having at least their vegetative parts growing in permanently or periodically aquatic habitats. These plants colonize a variety of aquatic habitats and can be divided into the following life forms: rooted submerged – plants that grow completely submerged and are rooted into the sediment (e.g. elodea, *Elodea canadensis*); free-floating – plants that float on or under the water surface (e.g. water hyacinth, *Eichhornia crassipes*); emergent – plants rooted in the sediment with foliage extending into the air (e.g. cattail, *Typha domingensis*); and floating-leaved – plants rooted in the sediment with leaves floating on the water surface (e.g. water lilies, *Nymphaea* spp). An additional two life forms have been proposed: epiphytes – plants growing over other aquatic macrophytes (e.g. *Oxycarium cubense*); and amphibious – plants that live most of their life in saturated soils, but not necessarily in water (e.g. *Polygonum* spp).

Macrophytes include macroalgae of the divisions Chlorophyta (green algae), Xanthophyta (yellow-green algae) and Rhodophyta (red algae) and the “blue-green algae” (more correctly known as Cyanobacteria); Bryophyta (mosses and liverworts); Pteridophyta (ferns); and Spermatophyta (seed-bearing plants). However, most of the literature devoted to freshwater macrophytes has investigated three major groups: the Charales (an order of Chlorophyta comprising large – up to 2 m – and relatively complex multicellular algae), together with the vascular plant groups, Pteridophyta and Spermatophyta.

Macrophytes colonize virtually all freshwater habitats, from the tiny "living ponds" provided by Bromeliaceae (e.g. *Utricularia* spp), to thermal springs (e.g. *Najas tequefolia*) and waterfalls (e.g. members of the Podostemaceae colonize even the giant Iguaçu Falls, Brazil/Argentina). Most rivers, lakes, lagoons and reservoirs are colonized to differing degrees by macrophytes, whilst wetlands are characterized as areas where macrophytes dominate.

Studies on aquatic macrophytes, and especially their ecology, were few in number before the 1960s. The reasons are historical because the science of limnology primarily originated in north-temperate countries, where deep lakes are characteristic: such freshwater systems are amongst the least favorable of habitats to support aquatic macrophytes. Consequently, phytoplankton was considered (correctly) as the main primary producer and pelagic food webs were prioritized in those studies. A great increase in the literature concerning macrophytes occurred after 1960, caused probably by the recognition that a great number, if not most, aquatic ecosystems were in fact shallow, with extensive littoral regions favorable for supporting aquatic macrophyte communities. A second factor was increasing recognition of the role played by macrophytes in the biodiversity-support functioning of freshwater systems: vital for many animal communities, such as aquatic invertebrates, fish and aquatic birds.

In this article it is not possible to cover all relevant topics in depth: the literature on tropical macrophyte ecology and management is too large for this to be possible. We utilize Neotropical ecosystems (which support the highest macrophyte diversity) for many of our examples but also include data from tropical and sub-tropical Australasia, Africa and Asia. Following the publication guidelines for this book, we cited only the 20 most used literature items for the article. However, we also used numerous other references which are provided in a separate table (see Appendix 1). The link of these references to each specific topic considered in our article will be provided by the first author (smthomaz@nupelia.uem.br) upon request.

2. General Features of Macrophytes

2.1. Evolution

Although still controversial, the origin of terrestrial plants is generally agreed to be from green algae of the order Charales, known as stoneworts. After colonizing the land, representatives of numerous different families returned to water, colonizing both freshwater and marine ecosystems, with good evidence for at least 211 (but probably more) independent colonization events of this nature having occurred.

It is interesting to note that angiosperms began the return to water very early in their evolutionary history. An analysis of the angiosperm phylogenetic tree shows the terrestrial shrub *Amborella trichopoda* as the first diverging lineage from the main branch of the angiosperm phylogenetic tree, but the families Cabombaceae, Nymphaeaceae and Hydatellaceae, which comprise only aquatic species, occupy the second basal lineage. Fossil material collected in the Vale de Agua locality (in a complex of clay pits situated in the Beira Littoral, Portuguese Basin) and in Crato (Northeast Brazil) confirms that water lilies have colonized this region since the Early Cretaceous (125-115 Mya). Thus, some adaptations found in extant submerged species, like aerial pollination and presence of stomata (see below), are interpreted only under an evolutionary perspective.

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Biographical Sketches

Sidinei M. Thomaz received the BSEE degree in Biology in 1987 and the Ph.D. in Ecology in 1995 from the Federal University of São Carlos (São Paulo State, Brazil). He was president of the Brazilian Society of Limnology from 1999 to 2001 and Coordinator of the Committee for Pos-graduation in Ecology (Brazilian Ministry of Education) from 2002 to 2004. He is currently Associate Editor of 4 journals, including Hydrobiologia. Dr. Thomaz is Adjunct Professor in Ecology and Limnology at the Maringá State University since 1995 and he advised 12 Master and Ph.D. students in the last 10 years. He published c. 90 peer review papers and book chapters and edited 4 books. He has been interacting with individual researchers and groups from at least 5 other Brazilian universities, as well as from Canada, USA and UK. His work approaches ecology of macrophytes, patterns of aquatic diversity and its main determinants. The main environments studied by Dr. Thomaz include tropical and sub-tropical floodplains and reservoirs.

Francisco de A. Esteves received the BSEE degree in 1973 from the Federal University of Rio de Janeiro (Brazil) and the Ph.D. in 1978 from Max-Planck Institute für Limnologie (Kiel – Germany) under advisement of Dr. Harald Sioli. In 1978 he started his academic career in the Federal University of São Carlos (São Paulo state, Brazil) where he worked as adjunct professor until 1989. At that time he was invited to work in Federal University of Rio de Janeiro where he has assumed a full professor position in 1993. Due to his leadership he has created in 2006 the Núcleo de Desenvolvimento Sócio-Econômico de Macaé (NUPEM/UFRJ) in Macaé-RJ, the first campus of Biological Sciences outside Rio de Janeiro downtown, where he has been the director so far. Prof. Dr. Francisco de A. Esteves has published more than 150 scientific studies and edited and written several books on general aspects of Limnology. He has advised more than 40 Master and Ph.D. students and worked as consultant in several scientific Brazilian funding agencies during his career. His work has been also characterized by a strong commitment regarding societal and political aspects of science development and how scientific knowledge can alleviate poverty and promote conservation and sustainable development in Brazil.

Kevin J. Murphy holds a B.Sc. (Hons.) degree in Botany, and a Ph.D, both from the University of Liverpool, England. He has been a faculty member of the University of Glasgow, Scotland since 1984. He is editor of the standard text on aquatic plant management ("Aquatic Weeds", Oxford University Press, 1993), and co-author of a student textbook on "Ecosystems" (Routledge, London: 1st edn 1997, 2nd edn. 2007). His research emphasizes plant and freshwater ecology, and particularly the role of vegetation in the biodiversity support functioning of ecosystems. He has longstanding experience in applied ecological work on sustainable development issues in a range of temperate, tropical and sub-tropical habitats (primarily in Europe, Africa, and South America), plus applied studies of vegetation management and eutrophication management in aquatic habitats.

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