This is the peer reviewed version of the following article: O'Hare et al. 2017 Plants in aquatic ecosystems: current trends and future directions. Hydrobiologia, on-line first, which has been published on 20 April 2017 DOI: 10.1007/s10750-017-3190-7.

Plants in aquatic ecosystems: current trends and future directions

Authors: Matthew T. O'Hare¹, Francisca C. Aguiar², Takashi Asaeda³, Elisabeth S. Bakker⁴, Patricia A. Chambers⁵, John S. Clayton⁶, Arnaud Elger⁷, Teresa M. Ferreira², Elisabeth M. Gross⁸, Iain D. M. Gunn¹, Angela M. Gurnell⁹, Seppo Hellsten¹⁰, Deborah E. Hofstra⁶, Wei Li¹¹, Silvia Mohr¹², Sara Puijalon¹³, Krzysztof Szoszkiewicz¹⁴, Nigel J. Willby¹⁵, Kevin A. Wood¹⁶.

1. Centre for Ecology & Hydrology, Bush Estate, Penicuik, Scotland, EH27 OQB, UK

2. Forest Research Centre, School of Agronomy, University of Lisbon, Tapada da Ajuda 1349-017 Lisbon, Portugal

3. Department of Environmental Science, Saitama University, 255 Shimo-okubo, Sakura, Saitama, 338-8570, Japan

4. Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands

5. Environment and Climate Change Canada, 867 Lakeshore Road, Burlington, Ontario, Canada L7R 4A6

6. National Institute of Water & Atmospheric Research, Gate 10 Silverdale Road, Hillcrest, Hamilton, New Zealand

7. EcoLab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France

8. Université de Lorraine, LIEC UMR 7360 CNRS, Rue Général Delestraint, Bâtiment IBISE, F-57070 Metz, Lorraine, France.

9. School of Geography, Queen Mary University of London, London E1 4NS, UK

10. Finnish Environment Institute SYKE, Freshwater Centre, Paavo Havaksen tie 3, FI-90570 Oulu, Finland

11. Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, 430074, China

12. Umweltbundesamt, Schichauweg 58, 12307 Berlin, Germany

View metadata, citation and similar papers at <u>core.ac.uk</u>

14. Poznan University of Life Sciences, Faculty of Environmental Engineering and Spatial Management, Wojska Polskiego 28, 60-637 Poznan, Poland

15. Biological & Environmental Science, Faculty of Natural Science, University of Stirling, Stirling, FK9 4LA, UK

16. Wildfowl & Wetlands Trust, Slimbridge, Gloucestershire, GL2 7BT, UK

3 LEHNA, F-69622

brought to you by 🗓 CORE

Key words: Angiosperms; Botany; Herbivory; Limnology; Macrophytes; Submerged aquatic vegetation; Trends in research

Running title: Plants in aquatic ecosystems

Abstract

Aquatic plants fulfil a wide range of ecological roles, and make a substantial contribution to the structure, function and service provision of aquatic ecosystems. Given their well-documented importance in aquatic ecosystems, research into aquatic plants continues to blossom. The 14th International Symposium on Aquatic Plants, held in Edinburgh in September 2015, brought together 120 delegates from 28 countries and six continents. This special issue of Hydrobiologia includes a select number of papers on aspects of aquatic plants, covering a wide range of species, systems and issues. In this paper we present an overview of current trends and future directions in aquatic plant research in the early 21st century. Our understanding of aquatic plant biology, the range of scientific issues being addressed and the range of techniques available to researchers have all arguably never been greater; however, substantial challenges exist to the conservation and management of both aquatic plants and the ecosystems in which they are found. The range of countries and continents represented by conference delegates and authors of papers in the special issue illustrate the global relevance of aquatic plant research in the early 21st century but also the many challenges that this burgeoning scientific discipline must address.

Introduction

In the early 21st century, researchers recognize the fundamental importance of plants that grow in and around water to the structure, functioning and service provision of aquatic ecosystems (Chambers et al., 2008). Aquatic plants interact with and influence the hydrological, geomorphological and physicochemical environments, and interact with a wide range of other organisms, from microbes to vertebrates, for example, by providing habitat and food (Brix, 1997; Engelhardt & Ritchie, 2001; Wood et al., 2017a). The current interest contrasts with the views of earlier limnologists a century ago who considered aquatic plants to be largely unimportant in aquatic ecosystems; for example, Shelford (1918) argued that "*One could probably remove all the larger plants and substitute glass structures of the same form and surface texture without greatly affecting the immediate food relations*". Over the past century the study of aquatic plants has expanded considerably, because of the increased recognition of their importance in fundamental system processes. Specialist journals have been established, such as Aquatic Botany (Den Hartog, 1975) and Journal of Aquatic Plant Management, as well as conferences devoted to aquatic plant research.

As a consequence of the growth of aquatic plant research over recent decades, our views on many key topics in aquatic botany have shifted (Vermaat & Gross, 2016; Phillips et al., 2016), and so this introduction to the special issue on plants in aquatic systems presents an overview of current trends and future directions in aquatic plant research in the early 21st century. It is a time of newly emerging fields and the advancement of long-established research areas. The research is set against a background of rapid environmental change that has been on-going for at least the last two centuries. The pace of change is unremitting with demands on water resources set to increase globally (Dudgeon et al., 2006; Vörösmarty et al., 2010). In the future the response of aquatic plant dominated systems

(e.g., shallow lakes and seagrass beds) to global temperature increases and climatic extremes may well become a focus of research efforts. The in-depth understanding aquatic botanists possess can only contribute positively to our understanding of how climate change will perturb aquatic systems. Trends in aquatic plant research reflect the environmental pressures on freshwater systems, legislative drivers, technical advances and developments in the wider fields of ecology and environmental management.

Both national and international legislative drivers have had a clear impact on the direction of aquatic plant research. In Europe, the implementation of the European Union (EU) Water Framework Directive (WFD) (European Commission, 2000) led to a massive surge in research on monitoring methods, their inter-calibration and the analysis of the resulting large multi-site datasets (Hering et al., 2010). As the WFD implementation moves into its second phase, we now see a shift in focus to restoration projects. We have learnt much during the implementation of this directive and it is likely that we will see knowledge transfer from European scientists to colleagues in countries across the globe. We see many countries in Asia and Africa now adopting reference based systems for freshwater assessment (e.g., Kennedy et al., 2016).

The global financial crash in 2008 has exacerbated the difficulty in obtaining research funding in many countries, and immediate output in terms of results reigns over the long-term understanding of complex interactions and processes (Krugmann, 2012). In Europe we have also seen a reduction in core funding for national research organizations and university researchers who work on aquatic plant management issues and there are concerns that there will be a slow erosion of the research base. The United Kingdom's decision in 2016 to leave the EU will likely have implications for site-level conservation of aquatic plants under the EU Habitats Directive (Council of the European Communities, 1992), although it is not yet clear what will replace the EU Directives in UK law. In the USA, the Department of Energy has been planning to increase hydropower output by retro-fitting turbines to pre-existing dams that are currently only used for flood control or water supply. While the election in the USA of President Trump in 2016, who is a climate change sceptic and pro-fossil fuel advocate, makes the implementation of this policy much less certain, it is worth noting that it did have substantial cross-party support. If this work is undertaken it could reduce the USA's carbon production and reduce its requirement to buy in fossil fuels from abroad, but careful assessment of downstream impacts on aquatic plants and other taxa will need to be undertaken. In China the current five-year plan, which has significant green policies, has energized the environmental sector and led to substantial efforts to exchange knowledge with western countries. We hope this exchange will lead to greater international collaboration between aquatic botanists in the future. In developing countries there is a need too for the services of aquatic botanists where rapid population expansion and the intensification of resource use have increased demands on water supplies and other natural resources. A striking example is the numerous hydropower plants constructed in South America that have caused profound changes in aquatic ecosystems, including macrophyte community composition and patterns of colonization (e.g., Martins et al., 2013). Yet at the same time as these enormous ecological changes, many developing countries also face reduced research funding and weakened environmental legislation, which limits conservation efforts (Azevedo-Santos et al., 2017). The conference attracted delegates from many developing countries and we would strongly encourage their future participation.

While global financial trends and legislative drivers have affected the direction of research, technical advances in survey and analytical methodologies have also been influential. Some established techniques have become increasingly used in aquatic botany, for example, molecular biology and stable isotope analysis. Recent reductions in the cost of stable isotope analysis have facilitated their use. Developments in ecological modelling and computational biology have allowed aquatic plants to be incorporated into models that can predict interactions between macrophytes and other organisms (e.g., Wood et al., 2014; Stillman et al., 2015). The continued development of remote sensing, drone technology and the software to interpret aerial photography, now allows new types of spatial analysis.

Moreover, the potential for drones to carry Light Detection and Ranging (LIDAR) equipment could facilitate aquatic plant-sediment interaction studies. The rise of 'citizen science' represents greater public participation in scientific research and has the potential to aid data collection (McKinley et al., 2017). Similarly, the emergence of R (the free statistical software environment) has encouraged the development and sharing of new analytical techniques (R Core Development Team, 2016).

Aquatic botanists work from an especially strong position where the physiology of the plants is well described and there is a deep knowledge of the plants' roles in system function. Aquatic plants have many advantages over other aquatic biota as study organisms: they are sessile, they can be accurately mapped, rapidly surveyed and cultured easily in the laboratory, and they are increasingly being used by a wide variety of researchers. Although, historically, there was an assumption that publishing aquatic botany studies in high impact journals was challenging, there is anecdotal evidence that this is no longer the case.

Against this background of environmental and societal change, aquatic botanists met recently to take stock of their discipline at the 14th International Symposium on Aquatic Plants, held in Edinburgh in September 2015. The symposium series originally began as an aquatic weeds meeting but over time the focus of the symposia changed as research and management interests altered. As our understanding and appreciation of the different roles that macrophytes play has increased, so too have the breadth of topics addressed at the symposia. The conference continues to attract delegates involved in the practical management of aquatic systems and those working directly in research. The synopsis which follows is based primarily on the conference output. The 14th International Symposium was attended by 120 delegates from 28 countries and six continents, and featured 79 oral presentations in addition to over 30 poster presentations. Although the 2015 symposium and the 13 preceding symposia were held in Europe, henceforth, every second symposium will be held outside Europe to reflect the global nature of the subject and the attendees. Global regions often diverge in approaches and attitudes towards macrophytes, for instance, weed management with herbicides is well accepted in the United States yet largely prohibited in Europe. Therefore, truly international conferences are vital in order to provide opportunities for global debates on such key issues. The next conference will take place in February 2018 in New Zealand and it will be jointly held with the Aquatic Plant Management Society of North America. The conference will also be supported by our colleagues from China, where there has been an upsurge in research interest in aquatic plants in recent years.

Traditionally, authors of conference presentations elaborated their contributions as full papers published in a special issue of Hydrobiologia (e.g., Caffrey et al., 1996; Caffrey et al., 1999; Caffrey et al., 2006; Pieterse et al., 2010; Ferreira et al., 2014). Thus, in this special issue of Hydrobiologia, we present a number of studies of aquatic plants that comprise the peer-reviewed proceedings of the 14th International Symposium on Aquatic Plants. In the remainder of this paper, we present an overview of current trends and future directions in aquatic plant research in the early 21st century. We focus on the following key areas of study, each of which represented a key session during the conference: (i) physical habitat interactions, (ii) riparian processes, (iii) ecological stoichiometry and nutrient cycling, (iv) trophic interactions – focused on plant herbivore interactions, (v) community responses to environmental change in space and time, (vi) aquatic plant monitoring, (vii) ecotoxicology, (viii) restoration, (ix) the future of invasive species management and (x) fundamental science.

Overview of current trends and future directions in aquatic plant research

Physical habitat interactions and riparian processes

The interactions between plants and water flow and sediments has been championed sporadically for over forty years, but in the last decade work has accelerated as the importance of the interactions for

ecology, hydrology and fluvial geomorphology were fully realized. Plants influence physical processes: transport of solutes, sediment deposition/resuspension, hydraulic conditions and light transmittance (O'Hare, 2015; Klančnik et al., 2017). In turn the physical environment affects macrophytes. Its effects are induced by mean velocity, turbulence and water level (O'Hare, 2015). Macrophytes can be affected at scales, from individual plants to populations and communities. This is exemplified by plant growth which is known to be influenced from the microscale, for example, cell ultrastructure (Atapaththu et al., 2015), to macroscale, for example, biomechanical traits (Puijalon et al., 2011; Schoelynck et al., 2014). Current developments in our understanding of these complex two-way interactions between aquatic vegetation and physical factors are tightly linked to fluid dynamics modelling (Marjoribanks et al., 2014; Verschoren et al., 2016).

While aquatic botanists have tended to focus on aquatic macrophytes, geographers have been examining both instream and riparian vegetation. An especially exciting development is the realization that vegetation fringing a river's edge has a substantial influence on fluvial geomorphological processes. In effect, nearshore plants (emergent and submerged) help engineer river form (Gurnell, 2014; Gurnell et al., 2016). This has significant practical implications as alterations to hydrology and fluvial geomorphology are as widespread as nutrient pollution in Europe, effecting approximately half of all water bodies (Kristensen, 2012). We speculate that this reflects an unmeasured but global trend as evidenced by the contributions from Africa and Asia to this session on impacts of flow disturbance and regulation. Regulation by hydropower dams influences the colonization rates of aquatic and riparian vegetation, with synergic impacts when rivers are subjected to sediment removal or impaired by storage reservoirs (Aguiar et al., 2016). Such disturbances create ecosystems prone to alien plant invasions, and regulation alters the growth trajectories, composition and complexity of native communities (Bunn & Arthington, 2002). During the conference the concerning case of Podostemaceae in West-Africa (strictly aquatic angiosperms) was highlighted, where six species are critically endangered and four species have become extinct due to altered flows (personal communication). Such issues can be overcome: for example, implementing environmental flows that inundate geomorphological structures and create slack waters helped with the restoration of regulated rivers by enhancing recruitment and colonization (Rivaes et al., 2015; Souter et al., 2014). While most research in this field focuses on rivers, data from the UK and Denmark indicate artificial water-level fluctuations in lakes affects macrophytes (e.g., Baastrup-Spohr et al., 2015; May & Spears, 2012; Smith et al., 1987), and that shoreweed (*Littorella uniflora* (L.) Asch.) has potential as a model species in ecological studies of both lake productivity and morphometry (e.g., Baastrup-Spohr et al., 2016; Robe & Griffiths, 2000).

In due course, this field of research has the potential to produce novel tools for management, especially nature-based solutions to flooding, and fresh insights into the ecology of aquatic plants. A research effort equivalent to that which elucidated the basic mechanisms of lake eutrophication (Vollenweider, 1968) will likely be required to resolve these major research questions. With this realization will come a far greater appreciation of the role of both instream and riparian vegetation in engineering physical habitats. Further collaborative research between geographers and ecologists will emerge.

Ecological stoichiometry and nutrient cycling

Ecological stoichiometry bridges ecology and ecosystem functions or processes at various levels, from individuals to communities. Despite clear theories (Elser et al., 2000), elemental requirements and the influence of environmental factors on nutrient uptake seem more complex for aquatic plant systems. At a global scale, silica is a nutrient which is in surprisingly short supply in marine environments requiring frequent inputs from freshwater systems. The role of macrophytes and other primary producers in influencing silica delivery is gaining increasing interest and its accumulation in

macrophytes may be a functional trait that enables them to adapt to environmental conditions (Schoelnyck & Struyf, 2016). At local scales, macrophytes strongly influence their physico-chemical environment. Aquatic weed mats may constitute important hotspots for greenhouse gas emissions in temperate shallow lakes, but wetland vegetation can also assist in nitrogen assimilation (Ribaudo et al., 2017; Volkmann et al., 2016). Yet, the relation between environmental nutrient availability and macrophyte nutrient content is often less clear. For example, research, presented during the conference, showed that upland streams with proliferations of pond water-crowfoot (*Ranunculus peltatus* L.) tend to have a low N:P ratio at overall very high nitrogen and phosphorus concentrations (personal communication). Although intra-specific C:N:P stoichiometry of submerged macrophytes correlates to sediment and water nutrient availability, inorganic carbon availability may also play a strong role in their nitrogen-based metabolism (Hussner et al., 2016). Further research, presented during the conference, found that macrophyte tissue nutrient concentrations appear more closely related to plant growth form than to phylogeny (personal communication).

Trophic interactions – focused on plant herbivore interactions

Since the seminal paper by Lodge (1991) on herbivory of aquatic plants, researchers have been devoting considerable attention to plant-herbivore interactions in aquatic ecosystems. Now, in the early 21st century, it has now been demonstrated, unequivocally, that herbivores can provide strong top-down regulation of macrophyte beds (Bakker et al., 2016; Wood et al., 2017a). These top-down mechanisms can interact with recovery from stress; for example, recovery of macrophyte beds after eutrophication attracts herbivorous water birds, but the colonization process can be hampered by strong vertebrate herbivory. In contrast, smaller invertebrate grazers may assist recovery of eutrophic systems. They stimulate submerged macrophyte growth and establishment by consuming periphyton (instead of the tougher macrophytes) that would otherwise reduce light availability for macrophytes (Bakker et al., 2016; Wood et al., 2017a).

Recognizing the importance of herbivory opens new research avenues by scaling up from macrophyte beds to aquatic ecosystem functioning, as herbivores affect methane emission, carbon cycling and regime shifts (Hidding et al., 2016). Furthermore, there is an urgent need to predict how global change will alter trophic interactions as a result of exotic species invasions (Redekop et al., 2017), temperature rises (Zhang et al., 2017) or changes in hydrological patterns (Wood et al., 2017b). Finally, current and future conservation challenges lay in predicting and managing the consequences of recovery of larger vertebrate herbivores, through re-introductions such as the Eurasian beaver (*Castor fiber* L.) in Europe (e.g., re-wilding), as well as by strong local herbivore population increases in species such as mute swans (*Cygnus olor* Gmelin).

Community responses to environmental change in space and time

The study of the responses of aquatic plant communities to environmental change in space and time is both a mature field of research and one with critical new questions being asked. Current research effort has seen a continued focus on the role of bottom-up regulation through environmental drivers (e.g., Fernández-Aláez et al., 2017) and competitive processes between macrophyte species (e.g., Gérard & Triest, 2017; Nunes & Camargo, 2017) in shaping aquatic plant community composition. Our understanding of how connectivity can influence floodplain macrophyte populations has now matured to the point where scenario modelling is feasible, for example, on the Murray-Darling system in Australia where species richness of floodplain plant communities can be predicted as a function of channel connectivity in the watershed (Campbell et al., 2014). Furthermore, recent studies of aquatic plant responses to floods in large floodplains have offered support for the flood homogenization hypothesis (Thomaz et al., 2007). Floodplain inundation has received less attention on smaller systems; however, comparative assessments of the importance of different aquatic habitats to a Scottish regional flora confirmed the importance of riverine backwaters (Keruzoure et al., 2013), a habitat that

had been previously neglected. That study illustrated an increasing awareness of spatial processes operating beyond individual sites, and the associated issue of scale-dependent responses. Thus, for example, the effects of land use on macrophyte richness in lakes are scale-dependent and are of greater importance at small spatial scales relative to the influence of hydrological connectivity (O'Hare et al., 2012). Looking beyond the immediate is one of the most powerful approaches of space and time analyses, and frequently produces insightful findings. Not only do we see this in relation to hydrological connectivity young due to their glacial origins, with the signal of glaciation still evident in the composition of their flora (Alahuhta et al., 2017).

Aquatic plant monitoring

Changes in the abundance or composition of an aquatic plant community are often obvious signals of alteration in the ecological condition of a lake or stream. In fact, a recent review of assessment methods used to implement the EU Water Framework Directive showed that the majority of methods are based on macroscopic plants (28% of all methods), followed by benthic invertebrates (26%) (Birk et al., 2012). Moreover, unlike many other biological indicators, macrophytes are equally good at detecting eutrophication/organic pollution and hydrological/morphological changes (Birk et al., 2012). Historically, surveys of abundance and composition were challenging in terms of both field effort and taxonomic ability. As identified at this symposium, improved methods for mapping abundance and composition of aquatic vegetation are now becoming available: high-resolution aerial images of lake and rivers taken with unmanned aircraft systems permit identification, mapping and abundance estimates of non-submerged species while near-infrared-sensitive DSLR cameras can be used to map spatial distribution and depth of submerged species (e.g., Visser et al., 2015).

Research is continuing to show that community metrics (e.g., cover, diversity and richness) and species frequency of occurrence are often related to water quality, lending support for the development of macrophyte-based indices for classification of fresh waters and brackish water ecosystems and seagrass beds (Spears et al., 2016). Although many macrophyte indices are based only on hydrophytes due to their dependency on the quality of the aquatic environment, the importance of helophytes has been demonstrated as indicators of the eutrophication process, for example, in the bioassessment of lowland lakes (Kolada, 2016). Biochemical measurements may also provide a new tool for bioassessment: for example, during the conference evidence was presented that 15N and C:N values from caged duck weed (*Spirodela* sp.) were found to relate to the proximity and timing of sewage manure or fertilizer inputs into rivers in South Africa (personal communication). Despite encouraging advances in both methods for mapping aquatic vegetation and approaches for assessing water quality, physical factors such as hydrological modifications to water courses or inter-annual variation in water levels can confound the relationship between macrophyte occurrence and water quality, necessitating caution when deciding the status of a water body based on limited (temporal or spatial) macrophyte data.

Ecotoxicology

The banning of herbicides for use in aquatic systems across the EU resulted in a shift in research away from studies on the efficacious use and impacts of pesticides in controlling aquatic plants. A strong research focus remains, however, on the effects of pesticides and other pollutants derived from terrestrial systems on aquatic plants (Coutris et al., 2011; King et al., 2016).

This was the first time an ecotoxicology session was held at the conference and it focused on linking ecological studies with chemical risk assessment, with the overarching aims to make assessment methods more realistic and to identify emerging plant-contaminant issues. The work presented in the

session indicated a continuing shift toward the use of more realistic test species. To refine risk assessments, laboratory studies used more realistic exposure conditions than standard techniques; an example was presented at the conference in which pesticide exposure pulses, typical of running water bodies, caused less harm to gibbous duckweed (*Lemna gibba* L.) than standard exposure conditions (personal communication). A higher tier approach, using mesocosms, proved effective when investigating indirect effects of chemicals on plant populations and communities. On plant-contaminant issues, the interaction between chemical contaminants and other stressors was evident; for example, evidence presented at the conference showed that the stoichiometry (C:N:P) of Eurasian water milfoil (*Myriophyllum spicatum* L.) was not only influenced by light and nutrients, but also by herbicides and the metalloid arsenic (personal communication). Field monitoring and biomarker assays revealed a significant relationship between the decline of dwarf eelgrass (*Zostera noltei* Hornem.) in the Vaccarès lagoon in France and its exposure to chemical contaminants including metals and pesticides (personal communication).

Restoration

Management of aquatic macrophytes is an essential part of freshwater restoration projects (Phillips et al., 2016). Macrophyte restoration can have multiple benefits, for example, supporting endangered waterfowl and fish species or limiting the spread of invasive species, such as Nuttall's waterweed (*Elodea nuttallii* (Planch.) H. St. John), in Europe. To successfully restore macrophytes, consideration of the following factors can be helpful: the genetic background of macrophyte population used, native seed bank viability, control of herbivores and, in the case of eutrophic lakes, the use of geo-engineering tools which reduce internal P loading, (Combroux et al., 2001; Guittonny-Philippe et al., 2015; Hussner et al., 2017). Restoration science is still under development and new data are desirable; monitoring using macrophyte growth forms can provide a cost-effective tool for evaluating the effect of individual restoration projects while long-term records of macrophyte dynamics can provide valuable information for assessment of broader, global scale change (Ecke et al., 2016).

Throughout the history of this symposium the loss of lake macrophytes due to eutrophication has been a core issue. Now, in the 21stcentury, research on the mechanisms of eutrophication continues but with a somewhat different emphasis; we now see more work presented on systems that are in recovery. Research has turned to drivers that influence the recovery trajectory; for example, trophic interactions involving herbivores, which have been somewhat neglected in the past, and issues associated with the role of invasive species.

The future of invasive species management

The spread of invasive species and decline in biodiversity is associated with accelerating globalisation, human migration and increasing pressures on freshwater supplies; however, whilst challenging, successful invasive species management has been demonstrated using combinations of lake and aquatic plant-based approaches matched with appropriate management tools (Havel et al., 2015). In some cases, regime shifts amongst aquatic flora, such as floating to submerged vegetation, may follow from the use of classical biological control (Cuda et al., 2008; Bakker et al., 2016). Yet in other cases invasive aquatic plants may not be considered the primary drivers of change, adding to debate surrounding the anthropocentric interpretation of benefits (*vs* detriments) for many non-native species in impacted habitats. Increasingly, there is a focus towards, arguably, bigger more 'threatening' issues such as climate change in the management of invasive species that could result in greater impacts from existing nuisance aquatic plants at a global level. For example, alien aquatic species can reduce the diversity of native seedbanks, thereby, jeopardising future restoration. Targeted

experimental work in both field and laboratory conditions is allowing researchers to understand competitive interactions between native and invasive species (Gérard & Triest, 2017). Continued research investment is required to manage the spread of invasive species. The development of new knowledge and techniques will likely provide new opportunities in the future for more effective invasive species management and aquatic restoration (e.g., Lozano & Brundu, 2017).

Fundamental science

Applied aspects dominate much of current aquatic plant research, such as aquatic plant populations' restoration, monitoring and ecological quality assessment, and different forms of response of aquatic plants to human disturbance or novel ways to control plant overgrowth. Nonetheless, fundamental science is often the basis for management actions, and indeed many failures relate to the lack of taxonomic resolution, the misunderstanding of species autecology and role in the ecosystem, or undefined tolerance responses over the disturbance gradient. Fundamental science, thus, provides, in large part, the key to successful plant management.

In spite of the development of genetic and cytoplasmic tools, morphological traits are still relevant as well as the role of population traits, for example, for dispersal and survival. Many ecosystem processes are also driven by vegetation, shaping succession of both plant and animal communities, in the shortand long-terms, in which interspecific competition and environmental constraints determine the end point. Understanding such processes is fundamental for biomanipulation, ecosystem restoration and the proper management of both constructed and natural wetlands.

Conclusions

Both the conference presentations and this resulting special issue of Hydrobiologia reflect the broad discipline that aquatic botany has become over the last century. Research interest in aquatic plants range from the use of aquatic plants as model organisms, to the roles of aquatic plants within ecosystems and to the conservation of aquatic plants themselves. Furthermore, the range of countries and continents represented by conference delegates and authors of papers in this special issue illustrate the global relevance of aquatic plant research in the early 21st century.

Currently, the International Symposia on Aquatic Plants are dominated by research on freshwater taxa, and in particular those found in shallow lakes. However, greater integration of freshwater macrophyte and marine seagrass research efforts, and their associated literatures, would benefit our overall understanding of aquatic plant biology, management and conservation. Whilst aquatic plant species may differ across ecotones, the processes that shape aquatic plant assemblages, such as bottom-up and top-down control and competitive processes, will share common elements. For example, recent research into herbivory on aquatic plants has synthesized information from freshwater, brackish and marine ecosystems (e.g., Bakker et al., 2016; Wood et al., 2017a).

Our understanding of aquatic plants, the range of scientific issues being addressed and the range of techniques available to researchers, have all arguably never been greater. This is to be welcomed, as the challenges facing researchers and practitioners have also never been more pressing. Climate change, rising human demand for resources including water, pollution of freshwater resources, the spread of invasive non-native species, land-use changes and intensification, together with the degradation, fragmentation and loss of aquatic habitats, all present huge challenges to the conservation and management of both aquatic plants and the ecosystems in which they are found (Dudgeon et al., 2006; Vörösmarty et al., 2010; Short et al., 2016). The 15th International Symposium on Aquatic Plants, to be held in New Zealand in February 2018, will be an excellent opportunity to assess our progress in meeting these challenges and to identify the areas in which we need to do more.

Acknowledgements

We are grateful to André Padial, Baz Hughes, and two anonymous reviewers for their helpful comments on earlier drafts of this manuscript.

References

Aguiar, F. C., M. J. Martins, P. C. Silva & M. R. Fernandes, 2016. Riverscapes downstream of hydropower dams: Effects of altered flows and historical land-use change. Landscape and Urban Planning 153: 83–98.

Alahuhta, J., S. Hellsten, M. Kuoppala & J. Riihimäki, 2017. Regional and local determinants of macrophyte community compositions in high-latitude lakes of Finland. Hydrobiologia. doi: 10.1007/s10750-016-2843-2

Atapaththu, K. S. S., A. Miyagi, K. Atsuzawa, Y. Kaneko, M. Kawai-Yamada & T. Asaeda, 2015. Effects of water turbulence on variations in cell ultrastructure and metabolism of amino acids in the submersed macrophyte, *Elodea nuttallii* (Planch.) H. St. John. Plant Biology 17: 997–1004.

Azevedo-Santos, V. M., M. P. Fearnside, C. S. Oliveira, A. A. Padial, F. M. Pelicice, D. P. Lima Jr, D. Simberloff, T. E. Lovejoy, A. L. B. Magalhães, M. L. Orsi, A. A. Agostinho, F. A. Esteves, P. S. Pompeu, W. F. Laurance, M. Petrere Jr, R. P. Mormul & J. R. S. Vitule, 2017. Removing the abyss between conservation science and policy decisions in Brazil. Biodiversity and Conservation. doi: 10.1007/s10531-017-1316-x

Baastrup-Spohr, L., K. Sand-Jensen, S. V. Nicolajsen & H. H. Brunn, 2015. From soaking wet to bone dry: predicting plant community composition along a steep hydrological gradient. Journal of Vegetation Science 26: 619–630.

Baastrup-Spohr, L., C. L. Møller & K. Sand-Jensen, 2016. Water-level fluctuations affect sediment properties, carbon flux and growth of the isoetid *Littorella uniflora* in oligotrophic lakes. Freshwater Biology 61: 301-315.

Bakker, E. S., K. A. Wood, J. F. Pagès, G. F. Veen, M. J. A. Christianen, L. Santamaría, B. A. Nolet & S. Hilt, 2016. Herbivory on freshwater and marine macrophytes: a review and perspective. Aquatic Botany 135: 18–36.

Birk, S., W. Bonne, A. Borja, S. Brucet, A. Courrat, S. Poikane, A. Solimini, W. van de Bund, N. Zampoukas

& D Hering, 2012. Three hundred ways to assess Europe's surface waters: An almost complete overview of biological methods to implement the Water Framework Directive. Ecological Indicators 18: 31–41.

Brix, H., 1997. Do macrophytes play a role in constructed treatment wetlands? Water Science and Technology 35: 11–17.

Bunn, S. E. & A. H. Arthington, 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30: 492–507.

Caffrey, J. M., P. R. F. Barrett, K. J. Murphy & P. M. Wade (Guest Editors), 1996. Management and ecology of freshwater plants. Hydrobiologia 340: 1–354.

Caffrey, J. M., P. R. F. Barrett, M. T. Ferreira, I. S. Moreira, K. J. Murphy & P. M. Wade (Guest Editors), 1999. Biology, ecology and management of aquatic plants. Hydrobiologia 415: 1–339.

Caffrey, J. M., A. Dutartre, J. Haury, K. J. Murphy & P. M. Wade (Guest Editors), 2006. Macrophytes in aquatic ecosystems: from biology to management. Hydrobiologia 570: 1–263.

Campbell, C. J., C. V. Johns & D. L. Nielsen, 2014. The value of plant functional groups in demonstrating and communicating vegetation responses to environmental flows. Freshwater Biology 59: 858–869.

Chambers, P. A., P. Lacoul, K. J. Murphy & S. M. Thomaz, 2008. Global diversity of aquatic macrophytes in freshwater. Hydrobiologia 595: 9–26.

Combroux, I., G. Bornette, N. J. Willby & C. Amoros, 2001. Regenerative strategies of aquatic plants in disturbed habitats: the role of the propagule bank. Archiv für Hydrobiologie 152: 215–235.

Council of the European Communities, 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Communities L206: 7–50.

Coutris, C., G. Merlina, J. Silvestre, E. Pinelli & A. Elger, 2011. Can we predict community-wide effects of herbicides from toxicity tests on macrophyte species? Aquatic Toxicology 101: 49–56.

Cuda, J. P., R. Charudattan, M. J. Grodowitz, R. M. Newman, J. F. Shearer, M. L. Tamayo & B. Villegas, 2008. Recent advances in biological control of submersed aquatic weeds. Journal of Aquatic Plant Management 46: 15–32.

Den Hartog, C., 1975. Aquatic botany — Aims and scope of a new journal. Aquatic Botany 1: 1–2.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny & C. A. Sullivan, 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81: 163–182.

Ecke, F., S. Hellsten, J. Kohler, A. W. Lorenz, J. Raapysjarvi, S. Scheunig, J. Segersten & A. Baattrup-Pedersen, 2016. The response of hydrophyte growth forms and plant strategies to river restoration. Hydrobiologia 769: 41–54.

Elser, J. J., W. F. Fagan, R. F. Denno, D. R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, S. S. Kilham, E. McCauley, K. L. Schulz, E. H. Siemann & R. W. Sterner, 2000. Nutritional constraints in terrestrial and freshwater food webs. Nature 408: 578–580.

Engelhardt, K. A. M. & M. E. Ritchie, 2001. Effects of macrophyte species richness on wetland ecosystem functioning and services. Nature 411: 687–689.

European Commission, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Communities L327: 1–72.

Fernández-Aláez, C., M. Fernández-Aláez, F. García-Criado & J. García-Girón, 2017. Environmental drivers of aquatic macrophyte assemblages in ponds along an altitudinal gradient. Hydrobiologia. doi: 10.1007/s10750-016-2832-5

Ferreira, T., M. T. O'Hare, K. Szoszkiewicz & S. Hellsten (Guest Editors), 2014. Plants in Hydrosystems: From Functional Ecology to Weed Research. Hydrobiologia 737: 1–345.

Gérard, J. & L. Triest, 2017. Competition between invasive *Lemna minuta* and native *L. minor* in indoor and field experiments. Hydrobiologia. doi: 10.1007/s10750-016-2754-2

Gurnell, A., 2014. Plants as river system engineers. Earth Surface Processes and Landforms 39: 4–25.

Gurnell, A. M., D. Corenblit, D. García de Jalón, M. González del Tánago, R. C. Grabowski, M. T. O'Hare, & M. Szewczyk, 2016. A conceptual model of vegetation-hydrogeomorphology interactions within river corridors. River Research and Applications 39: 142–163.

Guittonny-Philippe, A., M. E. Petit, V. Masotti, Y. Monnier, L. Malleret, B. Coulomb, I. Combroux, T. Baumberger, J. Viglione & I. Laffont-Schwob, 2015. Selection of wild macrophytes for use in constructed wetlands for phytoremediation of contaminant mixtures. Journal of Environmental Management 147: 108–123.

Havel, J. E., K. E. Kovalenko, S. M. Thomaz, S. Amalfitano & L. B. Kats, 2015. Aquatic invasive species: challenges for the future. Hydrobiologia 750: 147–170.

Hering, D., A. Borja, J. Carstensen, L. Carvalho, M. Elliott, C. K. Feld, A. -S. Heiskanen, R. K. Johnson, J. Moe, D. Pont, A. L. Solheim & W. van de Bund, 2010. The European Water Framework Directive at the age of 10: a critical review of the achievements with recommendations for the future. Science of the Total Environment 408: 4007–4019.

Hidding, B., E. S. Bakker, M. J. M. Hootsmans & S. Hilt, 2016. Synergy between shading and herbivory triggers macrophyte loss and regime shifts in aquatic systems. Oikos 125: 1489–1495.

Hussner, A., T. Mettler-Altmann, A. P. M. Weber & K. Sand-Jensen, 2016. Acclimation of photosynthesis to supersaturated CO2 in aquatic plant bicarbonate users. Freshwater Biology 61: 1720–1732.

Hussner, A., I. Stiers, M. J. J. M. Verhofstad, E. S. Bakker, B. M. C. Grutters, J. Haury, J. L. C. H. van Valkenburg, G. Brundu, J. Newman, J. S. Clayton, L. W. J. Anderson & D. Hofstra, 2017. Management and control methods of invasive alien freshwater aquatic plants: A review. Aquatic Botany 136: 112–137.

Kennedy, M. P., P. Lang, J. T. Grimaldo, S. V. Martins, A. Bruce, S. Lowe, H. Dallas, T. A. Davidson, H. Sichingabula, J. Briggs & K. J. Murphy, 2016. The Zambian Macrophyte Trophic Ranking scheme, ZMTR: A new biomonitoring protocol to assess the trophic status of tropical southern African rivers. Aquatic Botany 131: 15–27.

Keruzore, A. A., N. J. Willby & D. J. Gilvear, 2013. The role of lateral connectivity in the maintenance of macrophyte diversity and production in large rivers. Aquatic Conservation: Marine and Freshwater Ecosystems 23: 301–315.

King, R. S., R. A. Brain, J. A. Back, C. Becker, M. V. Wright, V. T. Djomte, W. C. Scott, S. R. Virgil, B. W. Brooks, A. J. Hosmer & C. K. Chambliss, 2016. Effects of pulsed atrazine exposures on autotrophic community structure, biomass, and production in field-based stream mesocosms. Environmental Toxicology and Chemistry 35: 660–675.

Klančnik, K., I. Iskra, D. Gradinjan & A. Gaberščik, 2017. The quality and quantity of light in the water column are altered by the optical properties of natant plant species. Hydrobiologia. doi: 10.1007/s10750-017-3148-9

Kolada, A., 2016. The use of helophytes in assessing eutrophication of temperate lowland lakes: Added value? Aquatic Botany 129: 44–54.

Kristensen, P., 2012. European waters: assessment of status and pressures. Publications Office of the European Union, Luxembourg.

Krugmann, P., 2012. End this depression now! W. W. Norton & Company, London, UK.

Lodge, D. M., 1991. Herbivory on freshwater macrophytes. Aquatic Botany 41: 195–224.

Lozano, V. & G. Brundu, 2017. Prioritisation of aquatic invasive alien plants in South America with the US Aquatic Weed Risk Assessment. Hydrobiologia. doi: 10.1007/s10750-016-2858-8

Marjoribanks, T. I., R. J. Hardy, S. N. Lane & D. R. Parsons, 2014. Dynamic drag modeling of submerged aquatic vegetation canopy flows. River Flow 2014: 517–524.

Martins, S. V., J. Milne, S. M. Thomaz, S. McWaters, R. P. Mormul, M. Kennedy & K. Murphy. 2013. Human and natural drivers of changing macrophyte community dynamics over 12 years in a Neotropical riverine floodplain system. Aquatic Conservation: Marine and Freshwater Ecosystems 23: 678–697.

May, L. & B. M. Spears, 2012. Managing ecosystem services at Loch Leven, Scotland, UK: actions, impacts and unintended consequences. Hydrobiologia 681: 117–130.

McKinley, D. C., A. J. Miller-Rushing, H. L. Ballard, R. Bonney, H. Brown, S. C. Cook-Patton, D. M. Evans, R. A. French, J. K. Parrish, T. B. Phillips, S. F. Ryan, L. A. Shanley, J. L. Shirk, K. F. Stepenuck, J. F. Weltzin, A. Wiggins, O. D. Boyle, R. D. Briggs, S. F. Chapin, D. A. Hewitt, P. W. Preuss & M. A. Soukup, 2017. Citizen science can improve conservation science, natural resource management, and environmental protection. Biological Conservation 208: 15–28.

Nunes, L. S. C. & A. F. M. Camargo, 2017. Do interspecific competition and salinity explain plant zonation in a tropical estuary? Hydrobiologia. doi: 10.1007/s10750-016-2821-8

O'Hare, M. T., 2015. Aquatic vegetation—a primer for hydrodynamic specialists. Journal of Hydraulic Research 53: 687–698.

O'Hare, M. T., I. D. M. Gunn, D. S. Chapman, B. J. Dudley & B. V. Purse, 2012. Impacts of space, local environment and habitat connectivity on macrophyte communities in conservation lakes. Diversity and Distributions 18: 603–614.

Phillips, G., N. Willby & B. Moss, 2016. Submerged macrophyte decline in shallow lakes: what have we learnt in the last forty years? Aquatic Botany 135: 37–45.

Pieterse, A., S. Hellsten, J. Newman, J. Caffrey, F. Ecke, T. Ferreira, B. Gopal, J. Haury, G. Janauer, T. Kairesalo, A. Kanninen, K. Karttunen, J. Sarvala, K. Szoszkiewicz, H. Toivonen, L. Triest, P. Uotila & N. Willby (Guest Editors), 2010. Aquatic Invasions and Relation to Environmental Changes: Proceedings of the 12th International Symposium on Aquatic Weeds, European Weed Research Society. Hydrobiologia 656: 1–267.

Puijalon, S., T. J. Bouma, C. J. Douady, J. van Groenendael, N. P. R. Anten, E. Martel & G. Bornette, 2011. Plant resistance to mechanical stress: evidence of an avoidance-tolerance trade-off. New Phytologist 191: 1141–1149. R Core Development Team, 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Redekop, P., E. M. Gross, A. Nuttens, D. E. Hofstra, J. S. Clayton & A. Hussner, 2017. *Hygraula nitens* the only native aquatic caterpillar in New Zealand, prefers feeding on an alien submerged plant. Hydrobiologia. doi: 10.1007/s10750-016-2709-7

Ribaudo, C., V. Bertrin, G. Jan, P. Anschutz & G. Abril, 2017. Benthic production, respiration and methane oxidation in *Lobelia dortmanna* lawns. Hydrobiologia 784: 21–34.

Rivaes, R., P. M. Rodriguez-Gonzalez, A. Albuquerque, A. N. Pinheiro, G. Egger & M. T. Ferreira, 2015. Reducing river regulation effects on riparian vegetation using flushing flow regimes. Ecological Engineering 81: 428-438.

Robe, W. E. & H. Griffith, 2000. Physiological and photosynthetic plasticity in the amphibious plant, *Littorella uniflora*, during the transition from aquatic to dry environments. Plant Cell and Environment 23: 1041–1054.

Schoelynck, J., K. Bal, V. Verschoren, E. Penning, E. Struyf, T. Bouma, D. Meire, P. Meire & S. Temmerman, 2014. Different morphology of *Nuphar lutea* in two contrasting aquatic environments and its effect on ecosystem engineering. Earth Surface Processes and Landforms 39: 2100–2108.

Schoelynck, J. & E. Struyf, 2016. Silicon in aquatic vegetation. Functional Ecology 30: 1323–1330.

Shelford, V. E., 1918. Conditions of existence. In: Ward, H. B. & G.C. Whipple (eds), Freshwater Biology. John Wiley, New York: 21–60.

Short, F. T., S. Kosten, P. A. Morgan, S. Malone & G. E. Moore, 2016. Impacts of climate change on submerged and emergent wetland plants. Aquatic Botany 135: 3–17.

Smith, B. D., P. S. Maitland & S. M. Pennock, 1987. A comparative study of water level regimes and littoral benthic communities in Scottish lochs. Biological Conservation 39: 291–316.

Souter, N. J., T. Wallace, M. Walter & R. Watts, 2014. Raising river level to improve the condition of a semi-arid floodplain forest. Ecohydrology 7: 334–344.

Spears, B. M., E. B. Mackay, S. Yasseri, I. D. M. Gunn, K. E. Waters, C. Andrews, S. Cole, M. De Ville, A. Kelly, S. Meis, A. L. Moore, G. K. Nürnberg, F. van Oosterhout, J. -A. Pitt, G. Madgwick, H. J. Woods & M. Lürling, 2016. A meta-analysis of water quality and aquatic macrophyte responses in 18 lakes treated with lanthanum modified bentonite (Phoslock[®]). Water Research 97: 111–121.

Stillman, R. A., K. A. Wood, W. Gilkerson, E. Elkinton, J. M. Black, D. H. Ward & M. Petrie, 2015. Predicting effects of environmental change on a migratory herbivore. Ecosphere 6: 114.

Thomaz, S. M., L. M. Bini & R. L. Bozelli, 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia 579: 1–13.

Vermaat, J. A. & E. M. Gross, 2016. Aquatic botany since 1975: have our views changed? Aquatic Botany 135: 1–2.

Verschoren, V., D. Meire, J. Schoelynck, K. Buis, K. D. Bal, P. Troch, P. Meire & S. Temmerman, 2016. Resistance and reconfiguration of natural flexible submerged vegetation in hydrodynamic river modelling. Environmental Fluid Mechanics 16: 245–265.

Visser, F., K. Buis, V. Verschoren & P. Meire, 2015. Depth Estimation of Submerged Aquatic Vegetation in Clear Water Streams Using Low-Altitude Optical Remote Sensing. Sensors 15: 25287–25312.

Volkmann, C., S. Halbedel, M. Voss & H. Schubert, 2016. The role of dissolved organic and inorganic nitrogen for growth of macrophytes in coastal waters of the Baltic Sea. Journal of Experimental Marine Biology and Ecology 477: 23–30.

Vollenweider, R. A., 1968. Water management research. Scientific fundamentals of the eutrophication of lakes and flowing waters with particular reference to nitrogen and phosphorus as factors in eutrophication. Organization for Economic Co-operation and Development, Directorate for Scientific Affairs, Paris.

Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann & P. M. Davies, 2010. Global threats to human water security and river biodiversity. Nature 467: 555–561.

Wood, K. A., R. A. Stillman, F. Daunt & M. T. O'Hare, 2014. Can sacrificial feeding areas protect aquatic plants from herbivore grazing? Using behavioural ecology to inform wildlife management. PLoS One 9: e104034.

Wood, K. A., M. T. O'Hare, C. McDonald, K. R. Searle, F. Daunt & R. A. Stillman, 2017a. Herbivore regulation of plant abundance in aquatic ecosystems. Biological Reviews. doi:10.1111/brv.12272

Wood, K. A., R. A. Stillman, R. T. Clarke, F. Daunt & M. T. O'Hare, 2017b. Water velocity limits the temporal extent of herbivore effects on aquatic plants in a lowland river. Hydrobiologia. doi: 10.1007/s10750-016-2744-4

Zhang, P., B. A. Blonk, R. F. van den Berg & E. S. Bakker, 2017. The effect of temperature on herbivory by the omnivorous ectotherm snail *Lymnaea stagnalis*. Hydrobiologia. doi: 10.1007/s10750-016-2891-7