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Ecological and evolutionary consequences of sexual and clonal reproduction in aquatic plants☆

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ABSTRACT

Aquatic angiosperms have evolved from a diverse assemblage of terrestrial lineages and exhibit broad variation in morphology, life history, and reproductive systems. This variation reflects evolutionary modifications that have occurred following transitions to aquatic habitats, and adaptation to the wealth of ecological niches that occur in wetland environments. Despite this variation, nearly all perennial aquatic plants share one important feature: propagation through both sexual and clonal reproduction. These contrasting reproductive modes involve the formation of propagules that differ in size, resource status, and genetic identity. Accordingly, the balance between sexual and clonal reproduction has important ecological and evolutionary consequences for dispersal, recruitment, and spatial patterns of genetic diversity within and among populations. Here, we review the diversity of aquatic plant life histories and reproductive modes and consider: (1) their effects on patterns of dispersal across spatial scales ranging from the local population to inter-continental transport; (2) how clonality affects sexual fitness via trade-offs and mating patterns; (3) the roles of sexual versus clonal reproduction in population establishment and in the subsequent spread of invasive aquatic plants; (4) how the contrasting properties of sexually-versus clonally-derived propagules in terms of dispersal and competition potentially influence patterns of selection on reproductive mode; (5) the roles of phenotypic plasticity, somatic mutations and epigenetic inheritance in promoting invasion success in widespread clonal aquatic species. We conclude our review by identifying profitable areas for future enquiry in an effort to provide a robust agenda for future research on the ecology and evolution of aquatic plants.

1. Introduction

Life in and around water presents both challenges and opportunities for most plants. Despite the constraints to plant growth posed by many features of aquatic environments, including flooding, submergence, anoxia, and desiccation, the return to water from land is a widespread phenomenon among herbaceous taxa. Although aquatic plants constitute a relatively small percentage of vascular plants (~1–2%), evolutionary transitions from land to water are estimated to have originated on 50–100 separate occasions, with 396 genera in 78 angiosperm families containing aquatic species (Cook, 1990). Adaptive solutions to the colonization of aquatic environments are many and they have resulted in the evolutionary diversification of numerous unrelated aquatic lineages. Diversification can encompass entire angiosperm families (e.g. Alismataceae, Hydrocharitaceae, Podostemaceae, Pontederiaceae), whereas in other instances a few scattered aquatic species have arisen independently in predominantly terrestrial families (e.g. Apiaceae, Fabaceae, Phyllanthaceae, Rubiaceae). The heterogeneity of aquatic environments (Crawford, 1987; Santamaría, 2002) imposes varied selection pressures on aquatic plant populations (Barrett et al., 1993), and this has resulted in considerable variation in the structure and function of aquatic plants and a range of life histories and growth forms (Sculthorpe, 1967). A major challenge for aquatic botanists is to understand the ecological and evolutionary processes driving adaptation and speciation in aquatic plants.

A particularly striking feature of aquatic plants is their diverse reproductive systems. Indeed, it is probably the case that no other angiosperm functional group exhibits such a wide diversity of

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reproductive modes. Although annuals are a characteristic feature of many transient aquatic habitats such as vernal pools (e.g. *Veronica peregrina*; Linhart, 1988) and seasonal tropical ponds (e.g. *Eichhornia paniculata*; Husband and Barrett, 1991), the vast majority of aquatics are perennial with mixed reproductive strategies, including various combinations of sexual and clonal reproduction. Because aquatic plants are derived from terrestrial relatives they have commonly retained the sexual systems and mating patterns of their land-based ancestors. Indeed, there is no strong evidence that transitions to the aquatic realm favor particular sexual systems; all of the main angiosperm floral strategies and inbreeding avoidance mechanisms are represented among aquatic plants (e.g. cosexuality, monoecy, dioecy, self-incompatibility, heterostyly, herkogamy, dichogamy; reviewed in Richards, 1997). Similarly, with the exception of the evolution of hydrophily (Cox, 1988), most of the main pollination systems found in aquatic plants also occur in terrestrial plants, with facultative cleistogamy perhaps overrepresented (Sculthorpe, 1967) and wind-pollination underrepresented (Cook, 1988) among aquatic families. Thus, as far as sexual reproduction is concerned, patterns of mating in aquatic plants appears to be no different from that found in their terrestrial counterparts, although a rigorous comparative analyses is needed to confirm this hypothesis.

The most reproductively distinct feature of aquatic plants concerns their diverse methods of asexual reproduction and reliance on this form of reproduction, especially in deep-water habitats unsuitable for seedling establishment (Hutchinson, 1975; Grace, 1993). In addition to apomixis, which is occasionally reported (e.g. Hydatellaceae; Iles et al., 2012), there are diverse mechanisms for clonal regeneration in aquatic taxa including bulbils, rhizomes, runners, stolons, tubers and turions (Sculthorpe, 1967). The adaptive value of these mechanisms of clonal propagation is probably multifaceted (Grace, 1993) and should depend on features of the habitats occupied. For example, stem tubers in habitats that experience seasonal desiccation (e.g. *Pontederia subovata*; Puentes et al., 2013) and easily fragmented stems in rivers that experience flooding (e.g. *Eichhornia azurea*; Cunha et al., 2014) enable genet persistence. The ease with which clonal fragmentation occurs in many aquatic habitats enables the rapid multiplication and dispersal of genets promoting colonization of new sites. Although the particular mechanisms of clonal propagation in aquatic species probably reflect ecological selection resulting from local environmental conditions, the consequences of this variation for dispersal distinguishes many aquatic species from their terrestrial relatives.

The amount of sexually (seed) and asexually (clonal propagules) produced diaspores affects the character of gene dispersal in aquatic plants, influencing population genetic structure (Barrett et al., 1993; Eckert and Barrett, 1993) and biogeography (Cook, 1985, 1987). The various types of seeds and clonal propagules produced by aquatic plants vary widely in dispersal ability and this influences spatial patterns of genetic variation within and among populations (Yakimowski and Barrett, 2014). Determining the relative importance of sexual and clonal reproduction and their roles in short- and long-distance dispersal is necessary for interpreting patterns of genetic diversity across spatial scales ranging from local to regional levels. One of the major challenges in both terrestrial and aquatic plants is to determine the relative amounts of sexual and asexual reproduction occurring in populations and the contribution that seeds versus vegetative propagules make to short- and long-distance dispersal. It seems probable that the main difference between terrestrial and aquatic plant species may lie in the more important role that clonal propagules play in long-distance dispersal, colonization and gene flow. Genetic markers are beginning to offer some promise in studies of these processes but we are still some way from quantifying the number of new offspring that establish from sexual and asexual reproductive modes and the number of new recruits in populations that arise from between population dispersal.

Given that most aquatic species reproduce by both sexual and clonal means, this mixed reproductive strategy must have clear adaptive benefits. However, under particular circumstances functional antagonism between these reproductive modes can occur, with potential influences on fitness. Such an effect can take two forms. First, if there are strong trade-offs between investment in sexual and asexual reproduction prolific clonal propagation has the potential to limit flowering and seed production with demographic consequences (Van Drunen and Dorken, 2012). Under environmental conditions unfavourable for the recruitment of sexually produced progeny, selection on genetically based trade-offs could potentially result in the loss of sex in clonal species (Eckert, 2002). Under these circumstances asexual populations may depend entirely on vegetative propagules for colonization of new environments. Second, extensive clonal spread, particularly in species with polymorphic sexual systems, has the potential to interfere with cross-pollen dispersal leading to a reduction in seed set and the quality of sexually produced offspring as a result of geitonogamy (i.e. the dispersal of self-pollen among flowers on the same genetic individual, Eckert, 2000; Barrett, 2015). Such influences on fertility and mating will depend critically on clonal architecture and the mechanisms governing vegetative propagation in aquatic species.

The flexibility of reproductive systems in most aquatics is likely to be of adaptive significance in aquatic environments, which are often characterized by strong spatial and temporal heterogeneity. In particular, aquatic habitats often experience significant fluctuations in water level and rapid changes in the speed of water currents during flooding. Genets may only survive these forms of disturbance through clonal fragmentation and/or the dispersal of vegetative propagules. These hydrological changes may be part of a natural cycle [e.g. the annual flooding regimes of the Amazon river (Junk and Piedade, 1997) and Pantanal wetlands of Brazil (Hamilton, 2002)], with many species possessing adaptations that facilitate survival and reproduction in habitats subject to regular flooding. Today, many aquatic environments are also experiencing increased environmental change as a result of various forms of anthropogenic disturbance (e.g. dam building, draining of marshes, conversion of wetland to rice fields, building of canals). Moreover, global climate change is affecting local patterns of precipitation resulting in both an increased frequency and duration of droughts and more intense floods. Many of these forms of environmental change play an important role in the reproductive ecology and dispersal of aquatic plants. Flooding causes fragmentation of clones and serves to disperse vegetative propagules long distances in river systems, enabling the colonization of unoccupied environments (Fig. 1). Also, many aquatic species require changes in water level to stimulate seed germination and allow seedling establishment (e.g. *Eichhornia crassipes*; Barrett, 1980); however, the degree of water level fluctuation is often a delicate balance, with too much amplitude between wet and dry conditions resulting in mass seedling desiccation. Future global environmental change seems likely to have important consequences for the reproductive systems and dispersal of aquatic plants, although this topic has not received the attention we believe it deserves.

In this review, we examine sexual and clonal reproduction in aquatic macrophytes, with a particular focus on how they might influence the ecology and evolution of populations as result of dispersal. We begin by briefly reviewing the reproductive and growth strategies of aquatic plants and then compare the salient features of dispersal through seed and vegetative propagules highlighting both natural and human-mediated dispersal. We next consider functional interactions between clonal and sexual reproduction affecting resource allocation and mating and the conditions under which this may negatively affect sexual fitness. This is followed