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Environmental opportunities and constraints in the reproduction and dispersal of aquatic plants

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ABSTRACT

This paper focuses on the opportunities provided by aquatic environments for successful reproduction and effective dispersal of aquatic plants, and how the environment alters the reproductive and dispersal mechanisms of aquatic plants compared to their terrestrial predecessors. The removal of water stress allows aquatic plants to exhibit greater diversity in their reproduction systems. While aquatic environments reduce the success of sexual reproduction in aquatic plants, the dominance of asexual reproduction, as well as their continuous production, blurs the distinction between growth and reproduction in land plants. Asexual propagules should be included in reproductive allocation analysis of aquatic plants. Aquatic plants show special adaptations for water dispersal. Two different levels are suggested when discussing the reproduction and dispersal of aquatic plants: The evolutionary and ecological time scale. It is suggested that asexual reproduction in aquatic plants may assure population maintenance, thus work mainly at the ecological time scale. In contrast, sexual reproduction might in most cases be a luxury investment, responsible for population restoration from extreme events and primarily working at the evolutionary time scale. Different animals, especially birds, are able to disperse aquatic plants. Humans have a long-standing association with aquatic plant dispersal. Moreover, economic development also stimulates the long-distance dispersal of plants and increases the risk of biological invasions. There are few data about seed longevity but studies on seed banks and germination requirements suggest that many aquatic plants may possess special mechanisms to keep their seed viability under natural conditions. More research is needed on the allocation of resources between vegetative and sexual reproduction in aquatic plants. Propagule biology (vegetative and seeds) may provide new information about the adaption of plants to aquatic environments.

1. Introduction

Aquatic plants, an ecological group closely related with water, encompass only about 2% of the around 350,000 angiosperm species (Cook, 1990). The morphology of aquatic plants is shaped by the aquatic environment which makes them appear like a natural group. However aquatic plants are an extremely heterogeneous assemblage of species from different taxonomic families that have arisen as a result of fundamentally different evolutionary pathways (Sculthorpe, 1967; Hutchinson, 1975; Philbrick and Les, 1996). Cook (1990) estimated that the evolutionary processes that led terrestrial plants to evolve into aquatic plants have happened independently about 50–100 times.

As a special "fascination group" for naturalists and plant biologists (*sensu* Barrett et al., 1993), aquatic plants have inspired many and diverse interests and several journals are devoted to different kinds of research on aquatic plants. Aquatic plants are key components in shallow aquatic ecosystems and the details of their structuring roles in shallow freshwater lakes have been elucidated (Scheffer, 1998; Jeppesen et al., 1998). However, research on aquatic plants is still very limited compared to the huge number of studies on their terrestrial relatives. This can be illustrated by the fact that no book on aquatic plants with widespread influence has been published since Sculthorpe published his epoch-making book in 1967, *The Biology of Aquatic Vascular Plants*.

It is difficult to give a rigid and clear definition of aquatic plants (e.g. Sculthorpe, 1967; Den Hartog and Segal, 1964; Hutchinson, 1975) although they possess some characteristics that set them apart from the terrestrial plants. In this paper, I will use aquatic plants in its broad meaning (*sensu* Barrett et al., 1993), with special

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attention paid to submerged, floating-leaved and free floating plants whose life cycles are almost completely dependent on the water environment. According to the opinion of Best (1988), aquatic plants are herbaceous. Some special groups, such as mangrove, are not included in Cook (1990), who treated almost without exception only herbaceous plants, and this is followed here.

There are several reviews already summarizing the different biological and ecological aspects of aquatic plant reproduction and dispersal (e.g. Barrett et al., 1993; Philbrick and Les, 1996; Barrat-Segretain, 1996; Santamaría, 2002; Bornette and Puijalon, 2009). In this paper, the main focus will be paid on the opportunities provided by aquatic environment for successful reproduction and effective dispersal of aquatic plants, and the adaptation of aquatic plants to such conditions. It is argued that the nature of the aquatic environment alters the reproductive and dispersal mechanisms of aquatic plants compared to their terrestrial predecessors. This paper builds on several published reviews and provides a special focus of recent work undertaken by Chinese scientists.

2. From land to water: A completely different selective environment

From the time that plants successfully invaded land (http://www.timetree.org) to when angiosperms flourished all over the world (Janssen and Bremer, 2004; Bell et al., 2010), evolution produced plants that were adapted to various land habitats and so were fundamentally different from their aquatic ancestors (Maberly – this issue). For land plants, the atmospheric supply of CO_2 for photosynthesis is relatively constant, but water availability and temperature are considered to be the main driving forces controlling productivity. From this point of view, water and temperature can be considered the power behind the selective pressure in land plants.

When plants returned to water they did not just change their background environment but the selection pressures they faced. Water availability, one key factor that limits terrestrial plant life, disappeared as a limitation and temperature changes became more gradual. Water itself acts as a supporting medium for plants, but, unlike air, is highly variable in chemical composition. It is an active player in shaping the character of the aquatic environment and together with the rooting medium produces many different environmental gradients, such as depth, light quantity and quality, wave exposure, and substrate (Kalff, 2002). In water, the more rapid light attenuation and restricted supply of inorganic carbon (Maberly – this issue) are important factors limiting the productivity of submerged macrophytes. In summary, the selective forces for land plants changed completely in the aquatic environment, but aquatic plants have to face a rather more complicated physico-chemical and biological environment than their terrestrial ancestors. It is likely that the aquatic environment in general now is similar to the time when land plant returned to water. Although various groups of aquatic plants (in the meaning of systematics) evolved at different time (e.g. Les et al., 2003; Chen et al., 2012a,b), the aquatic environments they survived in at last should be mild enough to support their normal life. This relatively moderate environment might be responsible for the fact that aquatic vascular plants usually show limited taxonomic differentiation and low within-species genetic variation (Santamaría, 2002).

Although the biological features of aquatic plants are similar to their terrestrial relatives, the adaptive significance maybe different. One example relates to photosynthesis characteristics: It is generally accepted that C_4 land plants evolved in warm and high light areas (Hatch and Slack, 1966; Raghavendra and Sage, 2011), while CAM plants evolved in arid areas (Cushman and Bohnert, 1999; Silvera et al., 2010). But some aquatic plants also evolved similar biochemical features (Maberly and Madsen, 2002; Zhang et al., 2014; Keeley – this issue; Raven and Beardall – this issue), even if they live in a water-rich, light-limiting (especially for submersed plants) environment in order to minimize limitation of photosynthesis by inorganic carbon. We need to consider the different adaptive meaning of such characteristics of aquatic plants in general and also when considering aquatic plant reproduction and dispersal.

3. Reproduction of aquatic plants

Reproduction is the key process of a plant life cycle and aquatic plants exhibit a great diversity in their reproduction systems. As Barrett et al. (1993) suggested: "No other group of vascular plants displays such a wide diversity of reproduction systems as are found in aquatic plants". As in terrestrial plants, three broad categories of reproduction can be recognised: (i) asexual vegetative fragmentation; (ii) asexual production of specialized structures such as turions and (iii) sexual reproduction.

3.1. Asexual reproduction: Increased opportunity on release from water stress

The removal of water stress allows almost all vegetative parts of aquatic plants the possibility to become vegetative propagules. Considering the totipotency character of plant cells and organs, it is suggested that the removal of water stress increased greatly the possibility of vegetative parts of aquatic plants to become vegetative propagules. This is compounded by the density of the aquatic environment that greatly reduces the need for mechanical support in aquatic plants, especially in submersed species. Sculthorpe (1967) pointed out that the reduction in supporting tissue in aquatic plants makes them more easily broken by abiotic factors such as wind, waves and water currents and biotic factors such as herbivores. The high frequency of asexual reproduction in aquatic plants, especially the wide occurrence of shoot fragments as a major way of dispersal (e.g. Vari, 2013), conceals the normally clear distinction between growth and reproduction in land plants.

An interesting feature about the asexual reproduction of aquatic plants is that almost all species have more than one vegetative propagule, which is quite different from terrestrial species that usually have only one specialized vegetative propagule. Besides shoot fragments, the most common non-specialized vegetative propagule, many aquatic species also have multiple specified organs for vegetative reproduction, including corms, rhizomes, stolons, tubers, and turions (Sculthorpe, 1967; Hutchinson, 1975; Grace, 1993; Van Vierssen, 1993; Philbrick and Les, 1996). For example, *Potamogeton pectinatus*, a worldwide distributed species, can reproduce asexually using fragments, rhizomes and tubers (van Wijk, 1989; Chen et al., 2003).

Asexual reproduction is almost exclusively adopted by all aquatic plants, even in the few annuals such as *Najas* species, which may reproduce vegetatively during the growing season by extensive lateral growth, fragmentation, or the occasional production of turions (Sculthorpe, 1967; Agami et al., 1986; Philbrick and Les, 1996). However, there are some exceptions: In *Ottelia alismoides*, once a dominant annual species of the mid to lower reaches of the Yangtze River (Chen et al., 2008b), no signs of natural asexual reproduction have been observed. In contrast, *Ottelia accuminata* var. *jingxiensis*, with a similar rosette growth form, can be found to reproduce vegetatively by splitting into two at its shoot base, each of which can bear a separate plant (Yuan-Yuan Chen, personal observation, Fig. 1).

Why is asexual reproduction so common and important among aquatic plants, regardless of their evolutionary history? It is