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Inhibition effects of daughter ramets on parent of clonal plant *Eichhornia crassipes*

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ABSTRACT

The aquatic invasive clonal *Eichhornia crassipes* was selected to study the effect of nutrients and stolon severing on clonal plants in less heterogenous aquatic environments. Under high nutrient conditions, parent ramets produced more daughter ramets and leaves with higher biomass, and, subsequent to severing daughter ramets, especially those in early stages; parents produced more daughter ramets and leaves with higher biomass. However, leaf number and biomass of individual daughter ramets did not differ from individuals with severed stolons and the control treatment. The biomass and leaves of the daughter ramets were lower than the control and other severing treatments that were carried out at later stages only when the nutrient level was low and the stolons of the daughter ramets were severed at early stages of growth. For this reason, the total number of ramets and leaves were lower in early stage severing treatments than severing treatments at later stages. After severing the connection with the daughter ramets, the root/shoot biomass ratio of the parent ramets increased, indicating that water hyacinths display morphological plasticity after stolon severing by increasing root growth. This study indicates that in aquatic environments where the nutrient distribution is less heterogenous in the same layer of water, daughter ramets of the water hyacinth can inhibit the growth and clonal reproduction of the parent, and this inhibition was strongest at early stages of ramet growth.

1. Introduction

The responses of clonal plants to heterogeneous resources have been extensively researched since the 1980s. In a heterogeneous habitat, clonal plants have two strategies, one is physiological integration and the other is phenotypic plasticity. Physiological integration can buffer clonal plants against spatial heterogeneity by greater resource availability through structures such as rhizomes and stolons (Pitelka and Ashmun, 1985). Phenotypic plasticity is the ability of a genotype to modify its growth and development in response to changes in the environment (Dorken and Barrettp, 2004).

The role of clonal integration and plasticity among clonal plants has been studied extensively in terrestrial environments. However, despite clonal growth being an important aspect of population biology in many aquatic and wetland plants (van Groenendael et al., 1996) studies focusing on clonal integration in aquatic plants are few (Tomasko and Dawes, 1989; Nielsen and Pedersen, 2000). Studies have shown that the vertical distribution of nutrients in aquatic microenvironments may not be uniform, but nutrient distribution in the same layer of open water is less heterogeneous than in soil environments (Sculthorpe, 1967; Cook, 1985; Les, 1988; Barrett et al., 1993; Santamaría, 2002). Ramets of submerged clonal plants may be distributed in different water layers under varying nutrient, light and other biological (e.g., microbial) conditions (Wallsten and Forsgren, 1989; Weisner et al., 1997; Van den Berg et al., 1998; Cronk and Fennessy, 2001; Scheffer, 2004; Liu et al., 2012). Due to these differences physiological integration occurs between ramets the leaf size and number of a submerged clonal plant, *Potamogeton malaianus* Miq., have changed significantly for physiological integration in different water sediments (Liu et al., 2007). Similarly, in different water CO_2 concentrations, *Potamogeton crispus* also has significant physiological integration in leaf size, number and mass (Xie et al., 2003). However, in plants that only grow in the same water layer, the physiological integration of clonal plants may not be found in uniform aquatic habitats, because it cannot improve the fitness of ramets in horizontal directions (Pitelka et al., 1985; Caraco and Kelley, 1991; Alpert, 1999). Studies have shown that clonal plants in homogeneous environments, often via stolon fragmentation among ramets to disseminate propagules,

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because in homogeneous environments, maintaining the connection among ramets and sharing resources among ramets have little significance (deKroon et al., 1996). In addition, when daughter ramets mature, fragmentation among ramets can greatly improve fitness (Zhang et al., 2002, 2003). The extent of ramet interdependence vs. independence may potentially be mediated by resource availability in specific habitats (Derner and Briske, 1998). Caraco and Kelley (1991) proposed that intraclonal ramets may be integrated to a lesser extent in environments with high resource availability compared to those with low resource availability. In heterogeneous habitats, the combined growth of connected ramets is greater than the sum of the growth of the two ramets when the stolon is severed (Friedman and Alpert, 1991; Hutchings and Wijesinghe, 1997), whereas in homogeneous habitats, the potential benefits of an intact clonal system may be nil or negative. In aquatic environments, the connection between mature ramets through rhizomes or stolons ("spacers") may restrict the amount of water-surface ramets can occupy. When the ramets were connected with parent, the older parts of the parent plants are rapidly abandoned in favour of new ramets (Noble et al., 1979; Schmid and Harper, 1985; Schmid and Bazzaz, 1987). The stolons between the parent and the daughter of aquatic clonal plants tend to be broken in uniform aquatic environments, and favour clonal growth and the occupation of more water space (Crowley et al., 2005), however a number of studies have produced contrasting effects on the artificial severing of stolons. A study by Hutchings and Wijesinghe (1997), for example, showed that severing the stolons between all the ramets of clonal plants had no impact on yield in homogeneous environments, whereas Teng et al. (2011) showed that after splitting the stolons or rhizomes, a clonal plant can grow and regenerate more vigorously. In addition, because aquatic environments have a fluid character, and their chemical and physical factors change easily, severing the stolons of floating aquatic clonal plants facilitates the spread of ramets over long distances in rivers or lakes (van Groenendael et al., 1996). In this way, aquatic clonal plants can avoid mortality by loss of physiological integration between ramets or by fragmentation (Hutchings, 1999). Many observations have also showed that if connected ramets all lie within a homogeneous patch of habitat, the morphology of the whole plant alters to enhance acquisition of the most limiting resource (Noble and Marshall, 1983; Slade and Hutchings, 1987; Friedman and Alpert, 1991; Stuefer et al., 1994). When nutrients or other soil-based resources are scarce, the Root/Shoot ratio increases, and when light is scarce the root/shoot ratio decreases (Hunt and Nicholls, 1986). However, it is not clear what this connectedness means for the growth and clonal reproduction of aquatic plants. Much of the relevant information on physiological integration comes from clonal plants, and physiological integration inevitably occurs early on in the ontogeny of ramets, because older ramets provide resources to support the establishment of their successors (Alpert, 1999; Hutchings, 1999). The level of support declines as new ramets acquire the capacity to obtain their own resources, but significant resource transfer can often be detected over very long periods (Jónsdóttir and Callaghan, 1989). However, most of these investigations have evaluated the relations between parent and daughter ramets only for terraneous clonal plants with few focusing on aquatic clonal plants. We test whether, in an aquatic environment, the daughter ramet restricts the growth and clone of the parent, and whether this restriction will continue after the stolon is severed.

We examined the responses in plasticity and integration to severing stolons in an aquatic clonal plant, *Eichhornia crassipes* (Mart.) Solms-Laubach, a perennial floating aquatic clonal species with the popular name "water hyacinth". Under greenhouse conditions, we considered whether: (1) in a uniform aquatic habitat, the daughter ramet can inhibit the growth of the parent via the stolon; (2) severing the stolon promotes the growth and clonal reproduction of the parent; (3) the inhibition of the parent ramet by the daughter changes with the growth of the daughter ramet, and a juvenile ramet exerts stronger inhibition than a mature ramet; and (4) this inhibition effect differs in response to nutrient levels after the stolons are severed.

2. Materials and methods

2.1. Study species

E. crassipes originated in the state of Amazonas, Brazil, spread to other regions of South America, and was carried by humans throughout the tropics and sub-tropics. It now occurs in at least 62 countries and causes extremely serious problems between 40°N and 45°S. It is the most damaging floating aquatic weed worldwide and much money has been spent in attempts to control it (Harley, 1994). *E. crassipes* is usually a free-floating species, whereas other species of *Eichhornnia* are rooted in the substrate (Wright and Purcell, 1995). It is an erect perennial herb, which reproduces from stolons and by seed. The leaves have either bulbous or slender petioles. The flowers are bluish-purple with yellow centres and are arranged spirally in spikes. The roots are fibrous, with many laterals trailing freely in the water to a depth of 1 m or more. With an average annual productivity of 50 dry (ash-free) tonnes per hectare per year, *E. crassipes* is one of the most productive (perhaps the most productive) plants in the world (Abbasi and Nipaney, 1986). *E. crassipes* ramets are root-bearing rosettes that form new rosettes in the leaf axil. Each new rosette is produced at the end of a stolon, which elongates with age and can eventually carry the rosette over 50 cm away from the parental ramet. The morphology and architecture of leaves, rosettes, and clonal groups are highly plastic (Richards, 1982; Watson and Cook, 1982).

2.2. Experimental procedures

E. crassipes was cultivated in a greenhouse. When enough ramets were produced, we chose ramets without new daughter ramets as the material for the experiment. Each ramet had 5–6 leaves. The compound fertilizer for water cultivation was produced by the Scotts Company of USA, trade name Osmocote I. The main elements of the fertilizer are total nitrogen 14% (ammonium nitrogen 6.8%, nitrate nitrogen 7.2%), water-soluble phosphoric acid 14%, water soluble potash 14%, and the valid microelements contain Fe 0.15%, Mn 0.16%, Cu 0.05%, B 0.02%, Mo 0.015%, and Zn 5%. We quantified the compound fertilizer at four levels: 25 g (Nutrient 1, N1), 50 g (Nutrient 2, N2), 100 g (Nutrient 3, N3), and 200 g (Nutrient 4, N4), together with a blank control (only tap water, without fertilizer) (N0). Each nutrient level was represented by 16 samples. Each fertilizer sample was put into a cubic plastic barrel (70 cm × 50 cm with 50 cm deep). Tap water was added to all the plastic barrels to a depth of 20 cm. Therefore, according to the above nutrient level design, the concentrations of nitrogen, phosphorus and potassium in different treatments were about N: 50 mg/L, P: 50 mg/L and K: 50 mg/L in N1 treatment, and accordingly, N: 100 mg/L, P: 100 mg/L, K: 100 mg/L in N2 treatment, N: 200 mg/L, P: 200 mg/L and K: 200 mg/L in N3 treatment, N: 400 mg/L, P: 400 mg/L and K: 400 mg/L in N4 treatment. However, the fertilizer of Osmocote is a kind of slow release fertilizer, and various nutrients will not immediately be released into the water.

Each selected ramet was then grown in a plastic barrel and regarded as a parent ramet. Severing treatments were carried out once daughter ramets were established. The stolon between the parent and the daughter ramet was severed at one of three levels: (1) severing treatment 1 (S1), the ramet was severed just after it had grown from the base of the bulbiform petiole, with