

Clonal integration in *Ludwigia hexapetala* under different light regimes



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ABSTRACT

Physiological integration among ramets of invasive plant species may support their colonization and spread in novel aquatic environments where growth-limiting resources are spatially heterogeneous. Under contrasting light conditions, we investigated how clonal integration influences growth, biomass allocation and morphology of *Ludwigia hexapetala*, an emergent floating-leaved macrophyte that is highly invasive in a range of wetland habitat types. In aquatic mesocosms, stolons of offspring ramets were either connected or severed from parent plants, with the pairs exposed to homogenous or heterogeneous combinations of sun or 85% shade. Morphological traits of all ramets were strongly influenced by light environment, and low light availability decreased plant growth, regardless of integration status. Allocation patterns varied with light regime; shaded plants increased allocation to leaf biomass while sun plants allocated more resources to belowground growth. Offspring ramets integrated with parents produced more biomass, suggesting a fitness advantage through integration. However, parent ramet performance declined with stoloniferous integration; integrated parents produced fewer ramets and allocated more resources to belowground biomass. For most response variables measured, there was no significant interactive effect between light treatment and integration, although parents growing in the shade attached to an offspring in the sun increased root mass ratio. The ability to establish and spread into new environments is a key trait of invasive plants, and physiological integration of resources may improve the establishment of juvenile ramets across variable light environments during early colonization. Physiological integration in patchy light environments may contribute to the invasiveness of *L. hexapetala*.

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1. Introduction

Clonality is a common growth pattern and asexual reproductive strategy of aquatic plants, facilitating their rapid dispersal and colonization throughout watersheds (Pyšek and Prach, 1993; Santamaría, 2002). Across spatially heterogeneous environments, clonal plants can share nutrients, carbohydrates, and water through physiological integration of connected ramets (Alpert and Mooney, 1986). This flexibility in growth form provides many benefits to clonal plants, including improved ability to grow and colonize in low resource environments (Stuefer et al., 1994; Alpert, 1996). Under severe growing conditions or high environmental variability, clonal plants may have increased survivorship (Xu et al., 2010) because clones can respond plastically by dividing labor and sharing resources (Alpert, 1996, 1999a,b; Xiao et al., 2007). However,

the benefits of clonal integration among ramets can vary among wetland plant species (Pennings and Callaway, 2000). Clonal integration also incurs maintenance costs related to stolon tissue, loss of internal resources due to resource sharing, and high genet or ramet mortality (Jónsdóttir and Watson, 1997). Under homogeneous conditions, clonal integration may be disadvantageous because the cost of the connection outweighs the resources gained (Alpert et al., 2003).

Light is a key resource that can be spatially heterogeneous, and thus may influence the growth and development of clonal plants. Floating-leaved species of macrophytes are the most competitive for light relative to other functional groups of aquatic plants and can dominate plant communities when nutrient availability and turbidity in the water column are high (Bornette and Puijalon, 2011). In shade, aquatic plants experience both decreased light quantity and quality (Méthy et al., 1990). Whereas the quantity of light in the environment supports plant growth, light quality has more influence on the morphology of plant leaves (Gratani, 2014). Clonal growth may be favored in heterogeneous light

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conditions, because rhizome or stolon production may help plants avoid the stress of limited light by directing ramet growth toward regions with more light (Méthy et al., 1990), potentially allowing resource sharing with clones growing in low light. In integration experiments with *Fragaria chiloensis* (L.) Duchesne in sand dunes, light deficient clones connected to ramets with access to sunlight accumulated more biomass than ramets in homogeneous high or low light conditions (Stuefer et al., 1994; Alpert, 1999a). Similarly, the aquatic plant *Alternanthera philoxeroides* (Martius) Grisebach shared resources between ramets growing in the sun and in the shade, and connection with an unshaded ramet improved establishment success of new ramets (Xu et al., 2012).

Due to the potential benefits that clonal growth has on plant establishment and spread, particularly in patchy or low resource environments, clonality may promote colonization of novel habitats by invasive plant species. Because of prolific ramet production and its positive impacts on survivorship (Barrat-Segretain et al., 1998), clonal growth may be favored in areas of high disturbance (Grace, 1993). In fact, non-native and invasive plants are more likely to be clonal than native plants, as clonal plants are more successful at expanding outside of their native range than non-clonal species (Thompson et al., 1995).

Surprisingly little research has focused on the benefits of clonal integration for aquatic invasive weeds (see Xiao et al., 2007, 2011). Aquatic systems are prone to disturbance events, such as flooding, which may provide gaps in the riparian zone for rapidly establishing species (Pyšek and Prach, 1993). Additionally, patchy resource availability in aquatic environments (Santamaría, 2002) may favor species with weedy, ruderal growth (Grime, 1977). Thus, clonal growth may be beneficial as a means of resource acquisition and rapid dispersal. For example, light availability along waterways and in riparian zones can be patchy (Gregory et al., 1991), and the success of non-native, clonal species in these environments may be linked to their ability to successfully forage for light and share resources.

In this study, we investigated the effect of clonal integration on ramets of *Ludwigia hexapetala* (Hook & Arn) Zardini, H. Gu & P.H. Raven (Onagraceae: syn. *L. grandiflora* ssp. *hexapetala*, Wagner et al., 2007) in contrasting light environments. *L. hexapetala* is a perennial, emergent floating-leaved aquatic plant native to South America that forms dense, buoyant mats over the water surface. Introduced as an ornamental plant, it has long been an invasive species in France, and more recently it has invaded watersheds elsewhere in Europe and in the United States (Thouvenot et al., 2013b). The primary mode of spread is hydrochorous dispersal of floating asexual shoot fragments, although the species also reproduces sexually via buoyant fruit capsules with viable seeds (Okada et al., 2009). Dispersal of rhizome fragments by hydrochory following bank erosion events is also possible, but not common. This flexible species has colonized a wide range of wetland habitats in both the native and invasive range and appears to tolerate both aquatic and seasonally wet environments (Thouvenot et al., 2013b).

Experiments suggest the quantity of sunlight available to *L. hexapetala* plays a dominant role in its growth, biomass production, and invasion success (Thouvenot et al., 2013a). It is possible that light heterogeneity along the river edge makes the riparian zones a suitable habitat for clonal species such as *L. hexapetala*, promoting its spread, as its ability to grow both stoloniferously and rhizomatously may encourage resource sharing among clones. Currently, there is no known study on clonal integration in response to light availability with *L. hexapetala*, and little is known about its sensitivity to light and how clones respond to reduced light in shaded habitats. This information could be useful in understanding the growth and morphology of *L. hexapetala* and in the development of control mechanisms for this and other invasive aquatic clonal plants.

This study addressed two questions: (1) Does low light decrease plant performance in the clonal aquatic plant *L. hexapetala*? and (2) How does clonal integration influence plant performance under differing light environments? We hypothesized that low light availability would decrease plant performance, regardless of the target plant's integration status. Second, we predicted that offspring performance, regardless of light environment, would increase when integrated with a parent ramet. In contrast, parent ramets, regardless of light environment, would be negatively impacted by integration with an offspring ramet. Third, we hypothesized that the relative benefit or cost of integration, for either offspring or parent ramets, would depend on whether the light environment was homogenous or heterogeneous.

2. Materials and methods

2.1. Experimental design

Source material of *L. hexapetala* for experimental treatments was collected from a 2 km reach of the Russian River near Asti, California, USA (38° 764–122° 968). Forty-five, 1.5 m long clippings of *L. hexapetala* were taken approximately 5–10 m apart in the river and transported on ice to the USDA-ARS Aquatic Weed Research Facility at the University of California, Davis. Cuttings were placed in deionized water in shallow plastic tubs indoors until transplanting (<48 h). Ramets were planted in pots (19.5 cm height, 14 cm inner diameter) with a modified University of California soil mix (described in Spencer and Anderson, 1986) containing a 50:50 ratio of sand to topsoil, micronutrients, and 15 g of Osmocote® slow release fertilizer (Scotts Miracle Grow Co., Marysville, Ohio, USA) with 0.17% N, 0.027% P, and 0.0036% K per pot. Pots were placed in 75 L plastic mesocosms (Utilatub, Model 14, Cleveland, Ohio, USA) containing approximately 70 L of deionized water. Mesocosms were paired, allowing connection between ramets for integrated treatments (Fig. 1). The clipped stem was buried in the soil 21 nodes from the apical tip and was considered the parent plant. The offspring plant was rooted 9 nodes from the buried end of the parent plant using an 8.8 cm galvanized wire support stake to secure it in the soil mix. Consequently, the offspring plant contained the apical meristem. Growmore® Eco Pond Clear (organic bacterial product, Growmore Inc., Gardena, California, USA) was added to mesocosms every other day to control potential algal growth, and water levels were maintained by replacing evaporated water in the mesocosms every 2–3 days. Plants were allowed to establish for 5 days prior to treatment initiation.

In order to understand how integration influences clonal plants under different light regimes, 6 replicates of 2 target *L. hexapetala* plants (parent and offspring) were randomly assigned to one of three different light treatments (Sun/Sun Shade/Shade, Shade/Sun) and one of two integration treatments (integrated or severed). In the treatments, both ramets were in ambient light (Sun/Sun), both

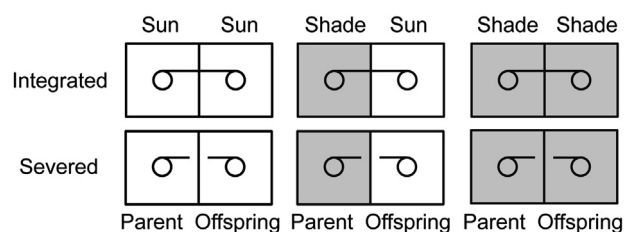


Fig. 1. One replicate of the experimental design, where the squares represent the water-filled tubs in which pots (circles) were placed. Each pair of squares consists of one experimental parent/offspring unit subjected to one of three light treatment combinations (Sun/Sun Shade/Sun; Shade/Shade) and with the ramet connection either integrated (solid line) or severed (broken line).

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