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The amphibious invader: Rooted water hyacinth's morphological and physiological strategy to survive stranding and drought events

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ABSTRACT

Water hyacinth (*Eichhornia crassipes* Mart. Solms Pontederiaceae) mainly occurs as a free-floating aquatic plant, but can survive decreasing water levels when rooted in soil. This adaptation to seasonal fluctuations in hydrology may contribute to its invasive potential in natural and man-made water bodies, where stranded plants can take root. To understand how water hyacinth plants rooted in saturated-soil compared to floating conspecifics, we conducted a month long mesocosm growth experiment in a well fertilised outdoor pool (experiment one) comparing plant traits between treatments. Following this, we investigated the effect of water stress on the plants rooted in soil, by conducting a progressive and prolonged drought (experiment two). We simultaneously investigated the effect of nutrient depletion in the mesocosm, on both the floating plants and those in saturated-soil. Plant physiological parameters were measured on these treatments. Plants were re-watered after the drought to assess mortality at two different drought intensities. Floating plants produced a larger total leaf area compared to plants rooted in saturated-soil, however, plants in both treatments developed a similar number of leaves and ramets. Progressive drought reduced photosynthesis, which was attributed to both stomatal and metabolic limitations. Nutrient stress reduced photosynthesis more in floating plants than rooted plants, and these reductions in photosynthesis were solely attributed to metabolic limitations caused by a decreased chlorophyll content. Plants recovered from prolonged drought but not prolonged severe drought. Water-stressed water hyacinth exhibited a drought avoidance strategy, a trait which may contribute to its ability to persist in variable aquatic environments.

1. Introduction

Water hyacinth, native to South America, is a free-floating macrophyte which has heavily invaded numerous water bodies throughout tropical and subtropical regions worldwide (Hill, 2003). Once invaded, water hyacinth has various detrimental effects on the ecological (Midgley et al., 2006) and economic activities (Mailu, 2001) of a system. Within Africa, this invasion is largely attributed to the local hydrology of small water bodies, eutrophication through anthropogenic nutrient enrichment and climatic incompatibility of the biological control agents (Hill and Cilliers, 1999; Coetzee et al., 2011). In particular, South African water bodies and rivers maintain elevated nutrient levels (De Villiers and Thiart, 2007), which strongly favour the growth and proliferation of water hyacinth (Reddy et al., 1990; Julien, 2000; Gupta et al., 2012). Additionally, many of these rivers and man-made water bodies experience water level fluctuations due to seasonal changes and/or anthropogenic effects (Hill and Olckers, 2001).

Water hyacinth evolved in an environment, where seasonal changes in hydrology are common (Bechara, 1996; Neiff, 2001; Neiff et al., 2008). Due to these changes in hydrology, water hyacinth has adapted to different growth conditions, where it occurs as a free-floating plant or to a lesser extent as an emergent macrophyte (Penfound and Earle, 1948; Barret and Forno, 1982). This trait is also observed in other aquatic invasive plants; some persist despite severe declines in water level, even well below the soil surface (Hussner, 2009, 2010). Exposed soil is important for the germination of water hyacinth seeds, where seedlings or small plants persist in relatively dry soil awaiting favourable conditions, such as inundation, to then abscise and float freely (Penfound and Earle, 1948; Pérez et al., 2011). Contrastingly, receding water levels may also strand floating plants, which may take root in soil, possibly aided by their contractile roots (Mauseth, 1999) and persist, provided the soil does not fully dehydrate (Penfound and Earle, 1948; Barret, 1980). Then, much like the seedlings, these rooted plants can abscise when an inundation event occurs (Penfound and Earle, 1948). However, during periods of abnormally low soil moisture, either from reduced rainfall, drought or water abstraction, stranded water

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hyacinth plants would require a strategy to persist and survive until water levels return to normal.

Drought is typically defined as the depletion of soil moisture in response to the absence of significant rainfall, which results in plants sustaining injury (Kramer, 1982), whereas in aquatic systems, drought can also apply when reduced inflow and/or increased water abstraction depletes soil moisture. Although plants respond to drought differently, overall, water stress causes a decrease in photosynthesis (Lawlor, 2002) and plant growth (Boyer, 1982; Farooq et al., 2009). Aquatic plants also demonstrate strategies to cope with water deficits when they become stranded. These strategies are reflected in changes to morphology and physiology. Morphologically, these plants typically reduce leaf area whilst increasing relative root biomass (root:shoot ratio) (Touchette et al., 2007; Hussner et al., 2008; Hussner, 2010). Physiologically, plants may reduce transpiration rates to increase water use efficiency (Touchette et al., 2007; Lawlor, 2013). These responses are indicative of a drought avoidance strategy, which usually decrease the plant's overall water demands allowing persistence during temporary periods of water stress (Brock and Galen, 2005; Touchette et al., 2007; Lawlor, 2013). Interestingly, some aquatic plants demonstrate enhanced performance and water relations subsequent to short term drought events (Touchette et al., 2010).

Given the harm caused by water hyacinth in both natural and manmade water bodies, it is expected that changing hydrology will influence its growth, physiology, survival and ultimately its invasive potential. Therefore, the first aim of this study was to investigate the plant traits of water hyacinth grown in saturated-soil as a rooted plant compared to free-floating plants. This was done in a manner emulating a natural system with eutrophic conditions, like that seen in most invaded sites worldwide. The second aim of the study was to determine physiological parameters allowing sediment-rooted water hyacinth to respond to progressive drought and nutrient depletion. Based on a system where the nutrient-rich inflow into an impoundment has slowed or stopped, three micro habitats were simulated where plants were either: 1) free-floating, 2) rooted in water-saturated soil and 3) stranded progressively drought-stressed rooted plants. Further, a recovery from a prolonged drought and then a prolonged severe drought was investigated to identify the soil water content threshold that resulted in plant mortality.

2. Material and methods

Ramet plants were grown from parental water hyacinth plants (collected from an existing culture at University of the Witwatersrand Insectary nursery) in a well-fertilised outdoor pool under full sunlight conditions (~2000 μmol m^{-2} s^{-1}). The pool had a diameter of 200 cm, depth of 45 cm and a volume of 1400 L. Thirty-six ramet plants of similar size were detached from the parent plants, weighed and divided into three similar groups consisting of 12 plants each and then returned to the pool (parent plants removed). Twelve ramets were assigned as floating plants and 24 were each potted in 25 cm diameter pots containing ± 6 kg river sediment (clay-loam: sand = 29.4%, silt = 43.3%, clay = 27.3%). These plants were then used in experiments one and two that ran in succession. During the 31 day growth experiment (experiment one), two floating nutrient dispensers, each containing 300 g of granular 7:1:3 fertiliser (N = 95 g kg^{-1}; P = 14 g kg^{-1}; K = 41 g kg^{-1}) were replenished twice, and on two occasions, iron chelate (13%) (0.013 g l^{-1}) and 100 ml Seagro® (N = 53 g kg^{-1}; P = 7 g kg^{-1}; K = 7 g kg^{-1}) were added. Water samples were extracted for nutrient analysis at the start and end of experiment two, using a 0.45 μm syringe filter from five positions (samples pooled) within the pool. Ammonium (N-NH_4^+) and orthophosphate (P-PO_4^-) were measured using standard spectrophotometric methods (Parsons et al., 1984). Oxidised nitrogen (N-NO_x; NO_2^- + NO_3^-) was determined using the reduced copper-cadmium method (Bate and Heelas, 1975). Air temperature remained consistent during the two experiments with an average maximum and minimum of 26.2 °C (Range 17–36 °C) and 15.1 °C (Range 10–20 °C) respectively. Water temperature ranged between 20.1 and 26.2 °C.

2.1. Experiment one: growth comparison between floating and saturated-soil rooted plants

The first experiment compared water hyacinth plant traits between free-floating plants (n = 12 at the start, n = 19 after 31 days due to vegetative reproduction) and plants rooted in soil in pots (n = 12). The pots were immersed in water to the level of the soil surface. All plants were kept in the same pool under the same nutrient concentrations, temperature, humidity, and light conditions. The growth trial was conducted over a 31 day period from 12th January to 12th February 2016. On four sampling occasions (days 0, 16, 22 and 30), the total leaf number, leaf area (all leaves on a plant) and ramet production per plant was measured. Leaf area was calculated using a leaf width to area relationship which was developed at the end of the growth trial using a range of leaf sizes collected from floating (n = 42, R^2 = 0.985) and rooted (n = 42, R^2 = 0.976) plants. Leaf area was measured using a CI-202 Portable Laser Area Meter (CID Bio-Science, Inc. WA, USA 98607). Due to its destructive nature, total wet biomass and above and below ground biomass were only measured at the end of experiment two.

2.2. Experiment two: simulated progressive drought and nutrient depletion

Experiment two followed on from experiment one, where the same pool and plants were used. The experiment consisted of three treatments of 12 plants each: 1) free-floating plants (floating), 2) potted plants rooted in saturated-soil (saturated-soil) and 3) potted plants subject to progressively decreasing soil water content (drought). To understand the effects of water and nutrient stress on the plants, leaf physiological parameters were measured. This experiment was based on a closed system where reduced or stopped water inflow is accompanied by reduced nutrient input, therefore after the start of this experiment no additional nutrients were added to the pool.

Two treatments, floating plants and saturated-soil plants remained in the pool, while the drought treatment plants in pots were removed from the pool and the simulated progressive drought was conducted over a 24 day period (Fig. 1). Soil moisture for the drought treatment was measured daily in a minimum of two positions within each pot (values averaged). When necessary, water from the pool was poured evenly across the soil surface to maintain the desired soil dehydration rate. Volumetric soil water content (VSWC) was measured using a HS2 Hydrosense II (Campbell Scientific, Inc. Utah 84321-1784) with 12 cm probes (Range: 0%–50% VSWC). To determine the gravimetric soil water content (SWC) to VSWC relationship, three pots containing the same volume of experimental soil (no plants) had their SWC and VSWC measured daily while the soil dehydrated naturally over a two week

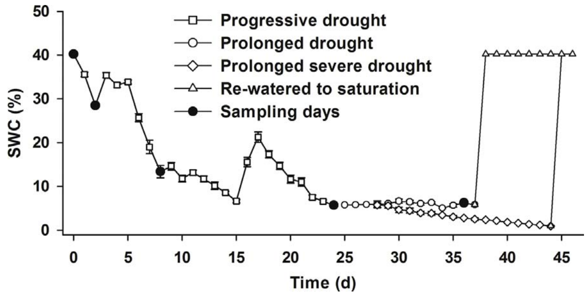

Fig 1. Soil water content (SWC) for drought-stressed rooted water hyacinth plants during the progressive, prolonged and prolonged severe simulated droughts and re-watering phases of experiment two. (n = 6–12 plants; mean ± SE). Solid circles (●) denote leaf physiology sampling occasions. Plants were re-watering to saturation on days 37 and 44. The peaks at day 4, 9, 11 and 17 indicate minor rainfall events.