Competitive performance of *Cabomba caroliniana*

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Summary *Cabomba caroliniana* A.Gray (cabomba) is an invasive aquatic species causing serious environmental and socio-economic impacts. In particular, cabomba has a tendency to create large monospecific stands once introduced and appears to negatively affect native macrophyte diversity.

Experiments have shown that cabomba, when cultured in isolation, grew significantly faster than any of the other macrophytes tested. However, competitive superiority over other macrophytes declined with increasing pH. Contrary to this, cabomba seemed to be a weak competitor in co-culture and few macrophytes showed signs of being affected by negative competitive interactions with cabomba.

The reduction in growth performance at pH >7.5 and the fact that cabomba appears to be a weak competitor means that cabomba might not be able to establish everywhere and displace other plants. This weakness of cabomba could potentially be exploited in future management and rehabilitation efforts.

Keywords *Cabomba caroliniana*, competition, aquatic plant ecology, aquatic weed management.

INTRODUCTION

Cabomba, a submersed macrophyte native to South American freshwaters, was introduced worldwide through the aquatic plant trade. From there, cabomba entered natural waterways through disposal of aquarium material and escape from commercial culture to become a serious aquatic weed in Australia, USA, and China (Mackey and Swarbrick 1997, Wilson *et al.* 2007). In Australia, cabomba is naturalised in Victoria, New South Wales, Queensland and the Northern Territory (Mackey and Swarbrick 1997). While cabomba is banned from trade in all Australian states, it continues to expand its range and has the potential to establish in suitable habitats Australia wide.

Cabomba reproduces predominantly through vegetative propagules (stem fragments) that are dispersed through human aquatic activities, such as boating and fishing (Wilson *et al.* 2007). Once established cabomba causes serious environmental and socio-economic impacts (Hogsden *et al.* 2007, Mackey and Swarbrick 1997, Wilson *et al.* 2007) and limited effective control options available in Australia hinder its management (Schooler *et al.* 2006, Hunt *et al.* in press).

Cabomba's most prominent environmental impact is the tendency to displace native macrophyte communities in lakes and reservoirs with mono specific stands (Lyon and Eastman 2006), thereby reducing native plant biodiversity (Hogsden *et al.* 2007). Competitive interactions between macrophytes are frequently influenced by habitat quality, such as substrate or water quality properties (e.g. Martin and Coetzee 2014, James *et al.* 1999). Consequently, variation in environmental conditions can strongly affect the competitiveness of macrophytes and shift competitive advantage from one species to another (James *et al.* 1999).

Currently our understanding of the ecology and the environmental impacts of cabomba are limited (Schooler *et al.* 2006, Bickel 2012) and in particular we do not know the mechanisms that allow cabomba to outcompete other aquatic macrophytes. Detailed knowledge about the competitive ability of cabomba and environmental factors that influence its competitive advantage will be invaluable for future management and restoration efforts that involve native aquatic macrophytes.

MATERIALS AND METHODS

Competition experiments were carried out with two exotic macrophytes cabomba (*Cabomba caroliniana* A.Gray, Cabombaceae) and egeria (*Egeria densa* Planch., Hydrocharitaceae) and four native species hydrilla (*Hydrilla verticillata* (L.f.) Royle, Hydrocharitaceae), vallisneria (*Vallisneria nana* R. Br., Hydrocharitaceae), potamogeton (*Potamogeton crispus* L., Potamogetonaceae) and myriophyllum (*Myriophyllum salsugineum* Orchard, Haloragaceae). The competitor species were chosen for their similar growth form, their abundance in South East Queensland and their potential to compete with cabomba: all of these species display invasive habits outside their native range. For each experiment, fresh macrophytes were collected in the greater Brisbane area and immediately transported to the lab in the Ecosciences Precinct, Brisbane. The experiments were either carried out in 110 L aquaria in the lab, or in 800 L outdoor mesocosms. Both systems were filled with a culture solution suitable for macrophyte growth and the pH was regulated through CO_2 injection. In the aquaria, water temperature was kept constant at 25°C with aquarium heaters; 14 h of daily light was supplied with fluorescent lights at ~80 mmol m^{-2} s^{-1}. The outdoor mesocosms were located in full sun throughout the day and they were subject to ambient conditions.

Competitive performance Similar sized stem fragments (~10 cm) of four macrophytes (cabomba, egeria, hydrilla and potamogeton) were planted individually in small pots (150 mL) filled with a mix of alluvial topsoil and fine sand (1 mm, 5% organic content). Nutrients were added to the substrate in the form of slow release fertiliser (Osmocote®: 2 g kg^{-1} substrate). The pots were topped up with a one centimetre layer of washed sand to prevent nutrient leaching. Pots were randomly allocated to aquaria with the pH electronically regulated at 6.5 or 7.5 through CO_2 injection. Subsequently, developing plants were successively harvested at days 5, 8, 13, 20, 27, and 34 (seven replicates for each species on each harvest day). At time of harvest, plant material was dried at 55°C for at least 48 h to assess final biomass (shoot and root dry mass) to the nearest 0.01 g. Stem length was measured to the nearest 1 mm.

Competitive interactions Fragments (cabomba, egeria, hydrilla, potamogeton, myriophyllum) or individual plants (vallisneria) (all 20 cm length) were planted in pots (630 mL) that were filled with an identical substrate mixture as for the previously described experiment with the exception of the fertiliser addition (Osmocote: 3 g kg^{-1} substrate). The macrophytes were planted as single species at two different densities (two and four stems per pot) or planted together with cabomba (two stems for each plant). There were 10 replicate pots for each density-species combination. Pots were cultured outdoors in mesocosms from autumn (April 2012) to spring (September 2012). Water temperature ranged from 27.3 to 13.7°C (mean = 20.7 ± 4.1 SD). The pH was regulated at pH 6.5 through CO_2 injection. At the end of the experiment, all plants were harvested and we determined wet mass to the nearest 0.01 g.

Statistics Parameters were compared among treatments using one way ANOVAs and TukeyHSD tests, carried out in R ver. 3.1.0, and were deemed significantly different at the 5% level.

RESULTS

Competitive performance Growth performance of the four macrophyte species differed widely and were affected by the pH of the water (Figure 1a–c), with all species, apart from potamogeton, preferring the lower pH. At pH 6.5, cabomba grew faster than any of the tested species. While the majority of cabomba fragments were rooted in the substrate within five days of planting, the competitors did not establish fully until 13 (egeria and hydrilla) and 23 days (potamogeton) after planting. By the end of the experiment (day 34), cabomba shoot dry mass, root dry mass and shoot length exceeded that of any competitor (Figure 1a–c).

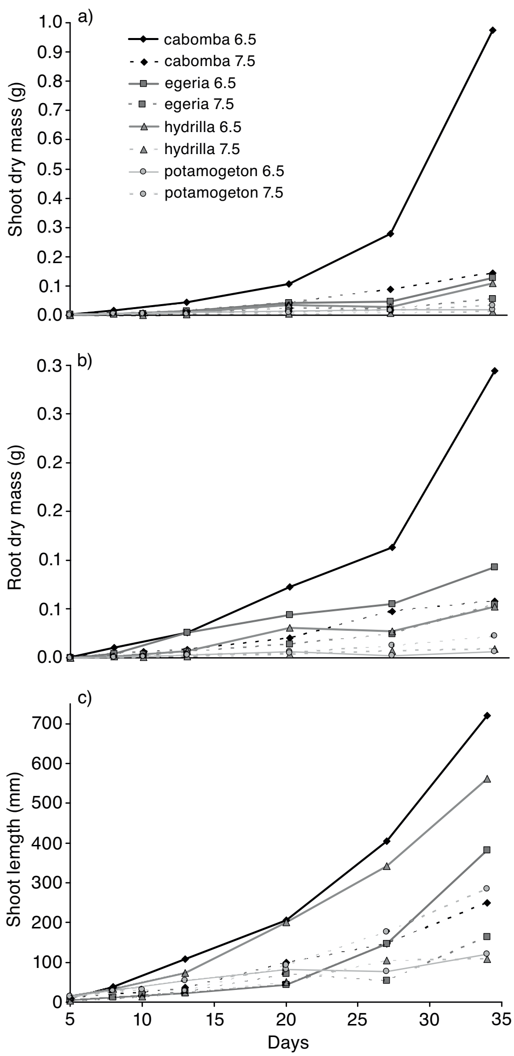

Figure 1a–c. Competitive performance of cabomba and three other macrophytes grown at two pH levels.

Cabomba growth was particularly remarkable in terms of the rapid biomass accumulation (Figure 1a). Cabomba growth performance was greatly reduced at pH 7.5 and shifted to a similar level to that of the other species. Nevertheless, at the end of the experiment, cabomba was still able to accumulate a biomass comparable to that achieved by the two next best competitors (egeria and hydrilla) under their optimum growth at pH 6.5.

Competitive interactions Few of the species showed any signs of negative competitive interactions, but the experiments indicated that there were density related effects on growth; i.e. final relative wet mass was lower in the four compared to the two stem treatments of the mono cultures (Figure 2a–e).

Potamogeton biomass differed significantly between treatments (ANOVA: $F = 3.832$, $P = 0.0343$) and was the only native species that showed a significant drop in relative biomass when cultured together with cabomba (Figure 2e). Similarly, cabomba relative biomass was reduced when co-cultured with potamogeton, but this was not significant (ANOVA: $F = 0.617$, $P = 0.547$).

Egeria and vallisneria showed a reduced biomass when co-cultured with cabomba (Figure 2c and d) compared to the 2 stem treatment, but the differences were not significant (Egeria: ANOVA: $F = 1.184$, $P = 0.321$; vallisneria: ANOVA: $F = 1.83$, $P = 0.18$). There was no indication that cabomba growth was influenced by egeria (ANOVA: $F = 1.665$, $P = 0.208$) or vallisneria (ANOVA: $F = 2.003$, $P = 0.154$).

Myriophyllum and hydrilla were unaffected by cabomba (myriophyllum: ANOVA: $F = 0.41$, $P = 0.667$; hydrilla: ANOVA: $F = 3.286$, $P = 0.0528$). Equally, cabomba was not influenced by myriophyllum (ANOVA: $F = 1.206$. $P = 0.315$ or hydrilla (ANOVA: $F = 0.737$, $P = 0.488$).

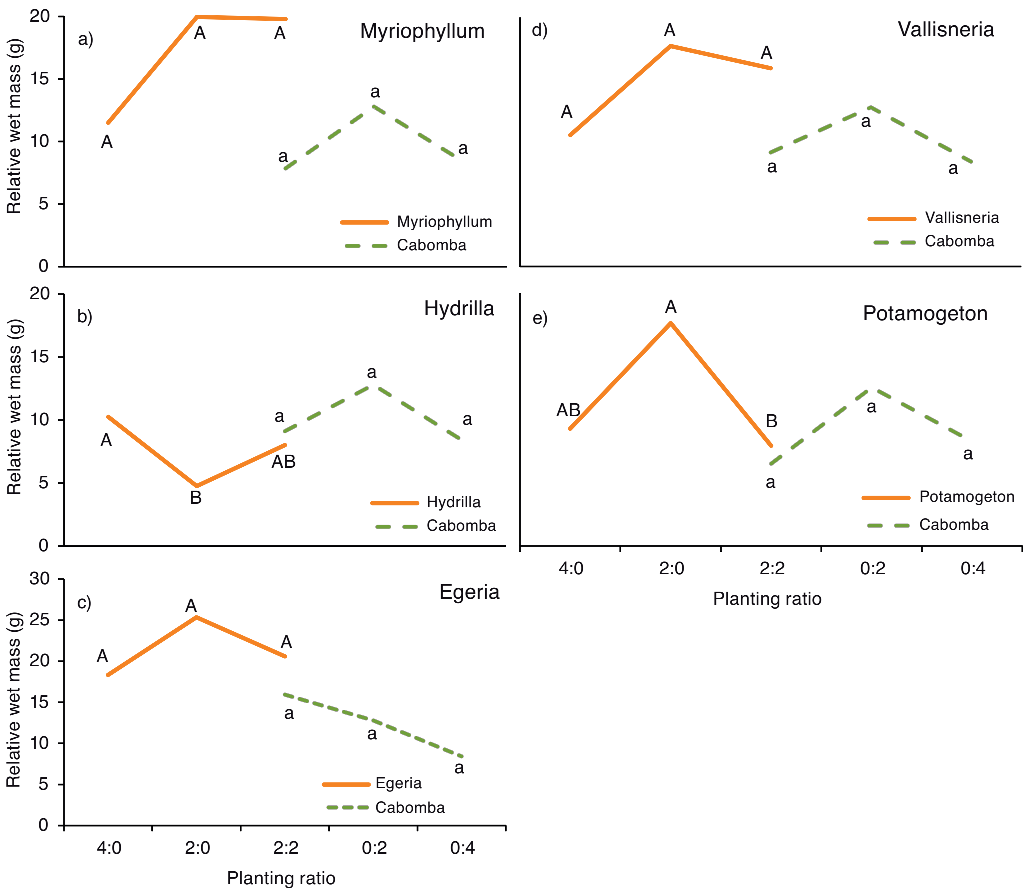

Figure 2a-e. Average relative wet mass achieved by each macrophyte in mono and co-culture. Significant differences are indicated at the 5% level by lettering. Note scale difference for egeria plot.

DISCUSSION

Similar to observations made with other invasive macrophytes (e.g. Hofstra *et al.* 1999), cabomba grew faster than any of the tested competitors. The rapid setting of roots gave it a head start, allowing it to outgrow potential competitors when introduced into a novel environment. Once it has formed a thick mono-specific canopy, the shading effect most likely reduces the growth of other macrophytes and eventually displaces them. This rapid growth rate explains the observed dominance of cabomba in the field.

However this might only be the case if cabomba can establish in disturbed areas that do not have an intact plant cover, or arrives at the same time as potential competitors in previously unoccupied habitat. This is corroborated by the fact that we found little evidence of cabomba having any direct competitive effects on the tested macrophytes. On the contrary, cabomba was a weak competitor when grown in mixed communities with other plants. Density dependent effects appeared to be stronger than species-specific interactions. This means that if cabomba is introduced into a healthy aquatic ecosystem with an intact macrophyte community, the risk of establishment might be greatly reduced.

Macrophytes are known ecosystem engineers that can alter their surrounding environment. An intact macrophyte community will increase the pH through photosynthesis in the surrounding water column (James *et al.* 1999), thereby potentially suppressing species that are sensitive to raised pH levels such as cabomba.

Future research should address the effects of macrophyte diversity on alien invasive species establishment in aquatic ecosystems and also investigate density dependent effects of competition in more detail.

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