



Competitive abilities of invasive *Lagarosiphon major* and native *Ceratophyllum demersum* in monocultures and mixed cultures in relation to experimental sediment dredging

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ABSTRACT

Competitive abilities of *Lagarosiphon major* (Ridley) Moss (invasive in Belgium) and native *Ceratophyllum demersum* L. were assessed experimentally in relation to sediment dredging. We mimicked these conditions by taking undisturbed sediment ('before dredging' treatment) and by using restored sediment where the uppermost nutrient rich top layer was removed ('after dredging' treatment). Both the species were allowed to grow for seven weeks in monocultures and mixed cultures at different planting densities. Overall, invasive *L. major* performed better than native *C. demersum* independent of the characteristics of the growth environment. *L. major* achieved a higher relative growth rate (RGR) in both treatments based on total length (0.17–0.21 week⁻¹) and weight (0.10–0.19 week⁻¹) compared to *C. demersum* (length: 0.04–0.07 week⁻¹; weight: 0.03–0.17 week⁻¹). The better performance of *L. major* was due to a high plasticity under stressful conditions of low free CO₂ and high pH. Intraspecific competition and niche partitioning were observed between the two species indicating that species coexistence is favoured instead of competitive exclusion. *L. major* performed better in the 'after dredging' treatment. Consequently, we deduce that sediment dredging will not lead to a decline of the invasive *L. major*.

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1. Introduction

Increased worldwide travel and trade has led to the introduction of many invasive plant species beyond their native range (Westphal et al., 2008). The invasion of freshwater ecosystems by highly competitive new species is a global phenomenon with ecological and economic consequences, especially with the high vulnerability of these environments to invasion (Pimentel et al., 2000; Shea and Chesson, 2002; Strayer, 2010). New species interact with native species and competition is one of the most important biotic interactions. Competitive capacity determines the establishment success of newly introduced species as well as resistance to invasion (Lockwood et al., 2007). In aquatic ecosystems, the most intense competition is expected to occur between plants of similar growth form occupying the same position in the water column (Gopal and Goel, 1993).

Invasive *Lagarosiphon major* (Ridley) Moss and native *Ceratophyllum demersum* L. occur potentially in similar habitats as they both have a wide ecological range. *L. major*, a rooted, submerged aquatic species native to southern Africa, is recognized as a noxious, invasive aquatic weed in several European countries (DAISIE,

2009) with few isolated populations in Belgium (Branquart et al., 2009). As observed for most alien Hydrocharitaceae species, this submerged perennial aquatic plant develops dense monospecific stands which often occupy the entire water volume from the bottom to the surface, restrict water movement, cut off light and interfere with recreation activities (McGregor and Gourlay, 2002). *L. major* has been reported to outcompete native submerged aquatic vegetation (e.g. Charophytes, *Myriophyllum* spp., *Potamogeton* spp.) and affect associated assemblages of aquatic invertebrates and vertebrates (Rattray et al., 1994; Keenan et al., 2009). *C. demersum* is a submerged free-floating species native to Europe and widely distributed in Belgium (Van Landuyt et al., 2006). *C. demersum* however is considered as a pest in New Zealand, where it has spread rapidly and outcompeted other invasive plants (Wells et al., 1997). Like *L. major*, *C. demersum* has been observed to displace native aquatic vegetation by shading due to the formation of a closed canopy and to present problems in lakes and waterways. Also in its native range *C. demersum* can be locally abundant and dominate entire water bodies. This suggests that both species have a high competitive ability. In Flanders (northern Belgium) we visited three meso-eutrophic ponds (two private ponds: N 51°12'; E 4°40' and N 51°02' E 4°05'; one pond in a nature reserve: N 51°01'; E 4°52') where both species co-occur. In the nature reserve *L. major* was the dominant macrophyte with some patches of *C. demersum*. In the two private ponds both species were equally abundant and formed

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dense canopies. Therefore competitive interactions for resources seem inevitable, particularly because both species are canopy forming submerged hydrophytes that inhabit shallow as well as deep littoral habitats (Wells et al., 1997), and can grow in a wide range of aquatic habitats (Vestergaard and Sand-Jensen, 2000; National Heritage Trust, 2003).

Today, many European lakes and ponds suffer from eutrophication as a result of increased agricultural intensification and urbanization, which has led to a considerable accumulation of phosphorus in the sediment. High nutrient loading is thought to increase ecosystem invasibility (Davis et al., 2000) and lend competitive advantage of invasive species relative to native species (Daehler, 2003). In pond ecosystems, sediment dredging has been shown to be a successful restoration measure in reducing internal nutrient load (Søndergaard et al., 2000) and restoring local biodiversity (Louette et al., 2009). However, little is known on how pond restoration by dredging would affect the performance of invasive species relative to native species. Previous studies on the influence of eutrophication on aquatic weeds invasiveness have mainly focused on manipulation of nutrient levels by adding fertilizers (Van et al., 1999; Kercher and Zedler, 2004; Mony et al., 2007; Kennedy et al., 2009).

In the present study, we have investigated experimentally the impact of sediment conditions before and after dredging on the interference competition between *L. major* and *C. demersum*. We mimicked these conditions by using sediments which were (a) undisturbed with a high amount of organic sediments ('before dredging' treatment) and (b) restored – removal of upper layer – with a lower amount of nutrients in the remaining soil ('after dredging' treatment). The objectives were (1) to compare growth of *L. major* and *C. demersum* and (2) to examine the possible competitive effects between *L. major* and *C. demersum*, both in monocultures and mixed cultures at various planting densities under the two different sediment conditions.

2. Materials and methods

2.1. Experimental design

The experiment was carried out at the Vrije Universiteit Brussel, Belgium over 7 weeks in July–August 2008. Plants of *Ceratophyllum demersum* and *Lagarosiphon major* were collected in a private pond (N 51°12'; E 4°40') where they co-occur and were kept in tap water of 20 °C for one night before planting. Apical shoot tips, of 10 cm in length, were deposited without roots and ramifications into 2.5 L plastic pots (18 cm diameter, 14 cm deep) filled with sediment (either sediment condition (a) or (b)) to a depth of approximately 5 cm. To avoid soil loss and to stabilize the plants, a 0.5 cm layer of gravel was placed at the top. The pots were placed in filled 20 L outdoor plastic tanks (30 cm diameter, 31 cm deep, one pot per tank). Two-thirds of the aquarium water was replaced each other day to reduce the potential for algal growth and to replenish nutrients in the water column. All tanks were randomly rearranged each day to reduce the variation of light climate. Pond sediments and overlying water were collected from the Tenreuken pond (N 50°48'; E 4°25'), a peri-urban hypereutrophic pond in the Brussels Capital Region where *C. demersum* is the dominant macrophyte (Peretyatko et al., 2007). Intact sediment cores between 30 and 50 cm long were taken with a hand-held coring tube. Undisturbed cores were used as the 'before dredging' treatment. For mimicking the 'after dredging' treatment, the uppermost 10–15 cm sediment layer from undisturbed cores was removed. The most essential sediment components of the two sediment types are given in Table 1.

We used a complete additive design (Spitters, 1983) with *L. major*/*C. demersum* planting densities as 0/4; 0/8; 4/0; 8/0; 4/4;

Table 1

Main nutrients of the aquarium water (range) and of the two sediment types.

Water				
TP (mg P l ⁻¹)	SRP (mg P l ⁻¹)	NO ₃ ⁻ (mg N l ⁻¹)	NH ₄ ⁺ (mg N l ⁻¹)	
0.018–0.087	0.001–0.007	0.044–0.139	0.088–0.188	
Sediment				
	C _{org} (%)	N-Kj (mg g ⁻¹)	P (mg g ⁻¹)	NO ₃ ⁻ (mg N g ⁻¹)
Before dredging	2.7	2.68	0.12	0.028
After dredging	2.7	2.28	0.10	0.006

Abbreviations: SRP, soluble reactive phosphorus; TP, total phosphorus; N-Kj, Kjeldahl nitrogen; C_{org}, organic carbon.

8/8; 4/8 and 8/4 plants per pot (following Barrat-Segretain and Elger (2004)). Each density had four replicates. Monocultures and mixed cultures of *L. major* and *C. demersum* were grown for seven weeks. The mean individual plant dry weight measured at the start of the experiment (20 stem apices of 10 cm length for each species) after drying at 70 °C for 48 h was 0.180 ± 0.012 g (mean ± SE) for *L. major* and 0.140 ± 0.009 g (mean ± SE) for *C. demersum*. Two weeks after the start of the experiment the plants of both species were established. From this date (week 3 = sampling week 1), the total cumulative length of four plants (including ramifications) of each species in each tank was measured weekly. At the end of week seven, all the plants were harvested, the number of roots was counted and the plants were dried at 70 °C for 48 h. The dry weight of shoots, roots and whole plants (all g plant⁻¹) was measured. Water temperature (range 20.3–26.0 °C), pH (range 7.00–9.71) and light intensity (2 cm under water surface, range 882–3615 μmol m⁻² s⁻¹ PAR) were measured weekly. Chemical characteristics of the aquarium water were measured at weeks 3, 5 and 7 and revealed meso- to eutrophic conditions (UNEP, 1999) (Table 1).

2.2. Statistical analysis

The relative growth rate (RGR) of the two species was calculated at the end of the experiment by the formula $RGR = (\ln X_2 - \ln X_1) / (t_2 - t_1)$, where X_1 and X_2 are the plant mean length (L) or plant dry weight (W) at time t_1 and t_2 , respectively (Hunt, 1990). Before all statistical analyses, data were log-transformed if required to ensure normality and homogeneity of variance (Sokal and Rohlf, 2003).

The difference between the growth curves of the two species and between treatments within species was tested with ANCOVA with sampling week as covariate and species and pond management condition as fixed factors. The different RGR mean values were compared using t -tests or ANOVA (followed by Tukey post-hoc tests after significant ANOVA).

Competitive abilities of each species were estimated using the reciprocal yield model (Spitters, 1983). This procedure uses linear multiple regressions of the form:

$$\frac{1}{X_L} = b_{L0} + b_{LL}N_L + b_{LC}N_C$$

$$\frac{1}{X_C} = b_{C0} + b_{CC}N_C + b_{CL}N_L$$

where X_L and X_C are the mean length or mean dry weight per plant and N_L and N_C are densities of *L. major* and *C. demersum*, respectively. The intercepts (b_{L0} and b_{C0}) estimate the reciprocal of the maximum weight of individual plants. The regression coefficients b_{CC} and b_{LL} are measures of intraspecific competition, while b_{LC} and b_{CL} measure interspecific competition in mixed cultures. In

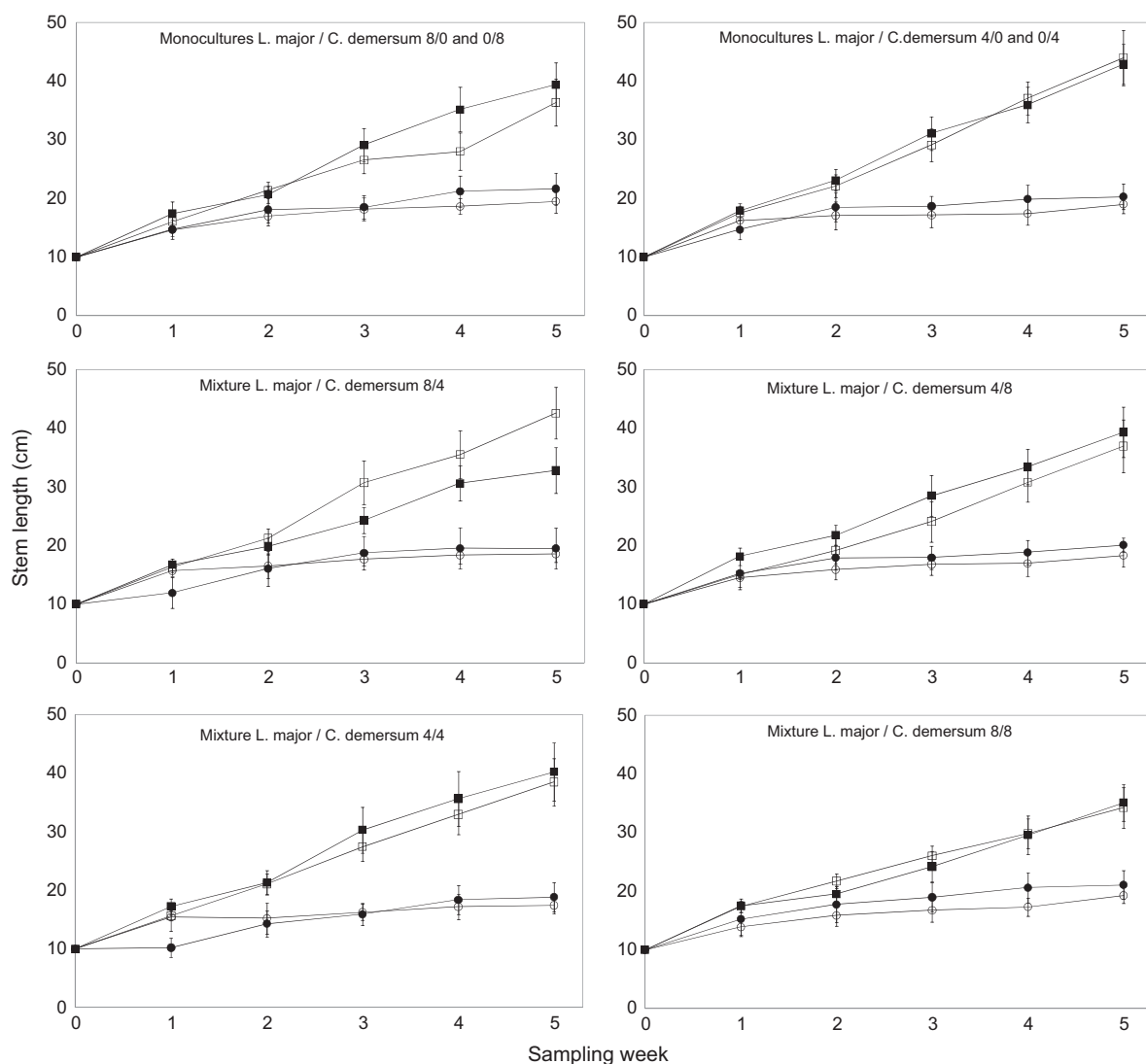


Fig. 1. Growth curves (mean \pm SE) of *L. major* and *C. demersum* under two different sediment conditions at different planting densities. Squares: *L. major*; circles: *C. demersum*; filled symbols: 'before dredging' treatment; open symbols: 'after dredging' treatment.

two species mixed cultures, the coefficients provide quantitative estimates of the reduction in growth of an individual of species 1 due to the addition of individuals of species 1 or species 2. The significance of these coefficients was tested with *F*-tests. All analyses were performed using STATISTICA v8.

3. Results

3.1. Stem elongation and biomass

In all experimental conditions the stem length of *C. demersum* was significantly lower than the stem length of *L. major* (ANCOVA, $P < 0.001$, Fig. 1), and for each species the sediment condition had no effect on the stem elongation. *L. major* reached the water surface within a week, then started to grow laterally and formed a canopy near the surface, while *C. demersum* stayed subsurface. Two-way ANOVA showed that the significant difference in stem length between the two species increased with time in monocultures and mixed cultures (significant effect of sampling week \times species interaction, $P < 0.001$).

Averaged across all planting densities, *L. major* accumulated significantly more total biomass (mean \pm SE) compared to *C. demersum* under the 'after dredging' treatment ($0.91 \pm 0.04 \text{ g plant}^{-1}$ versus

$0.49 \pm 0.06 \text{ g plant}^{-1}$, $P < 0.001$) as well as under the 'before dredging' treatment ($0.67 \pm 0.03 \text{ g plant}^{-1}$ versus $0.37 \pm 0.05 \text{ g plant}^{-1}$, $P < 0.001$). Mean individual shoot biomass (\pm SE) of *L. major* was higher under the 'after dredging' treatment than under the 'before dredging' treatment ($0.78 \pm 0.03 \text{ g plant}^{-1}$ versus $0.54 \pm 0.02 \text{ g plant}^{-1}$, $P < 0.001$), while mean individual root mass and number of roots did not change. For *C. demersum* there was no significant difference in accumulated biomass for the two sediment conditions.

3.2. Relative growth rate (RGR)

The RGR based on length of *L. major* was significantly higher than the length RGR of *C. demersum* both in monocultures and mixed cultures at the different densities under both sediment conditions (Fig. 2a). A comparison between the before and after dredging treatment indicate that neither species length RGR were influenced by sediment condition. The small variations in length RGR of both *L. major* and *C. demersum* plants when comparing monocultures versus mixed cultures were not significant (Fig. 2a).

The RGR based on weight of the two species calculated after seven weeks in monoculture did not differ significantly, but *L. major* had a significantly higher weight RGR than *C. demersum* in the

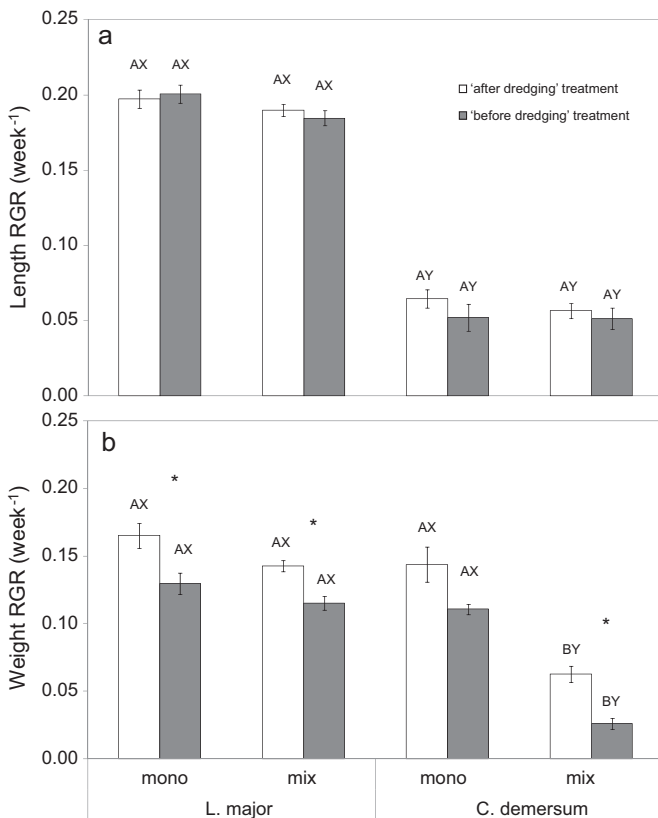


Fig. 2. The mean RGR \pm SE (week^{-1}) based on (a) total length and (b) dry weight of *L. major* and *C. demersum* cultivated in monocultures and mixed cultures under two different sediment conditions. Data were pooled for *L. major*:*C. demersum* mono planting densities and mixed planting densities at each sediment condition, respectively. Statistical differences are indicated by the following symbols: * (*L. major* plants or *C. demersum* plants, grown under the two different sediment conditions); A and B (*L. major* plants or *C. demersum* plants, grown in monocultures versus mixed cultures); X and Y (*L. major* plants versus *C. demersum* plants, grown in monocultures and mixed cultures, respectively).

mixed cultures with plants at different densities (Fig. 2b). The different sediment conditions influenced the weight RGR, especially for *L. major*. The weight RGR of *L. major* plants was significantly higher in the 'after dredging' treatment both in monocultures ($P < 0.05$) and mixed cultures ($P < 0.001$). For *C. demersum* this was only the case in the mixed cultures (Fig. 2b). A comparison of the weight RGR between monocultures and mixed cultures indicate that *C. demersum* performed better when growing with a conspecific than a heterospecific neighbour in both sediment conditions ($P < 0.001$). For *L. major* no significant difference between monocultures and mixed cultures was found.

3.3. Inter- and intraspecific effects (Spitters model)

Under the 'after dredging' treatment, analysis following Spitters model calculated on dry weight indicated reduced growth due to intraspecific interactions for both species ($P < 0.001$):

$$\frac{1}{W_L} = 0.606 + 0.083N_L + 0.024N_C, \quad R^2 = 0.67 \quad (1)$$

$$\frac{1}{W_C} = 1.307 + 0.430N_C - 0.042N_L, \quad R^2 = 0.57 \quad (2)$$

For *L. major* (Eq. (1)), the ratio of the coefficients comparing the intensity of intraspecific to interspecific interactions (b_{LL}/b_{LC}) was 3.5. When excluding interspecific competition the R^2 only declines to 0.62. This confirms that intraspecific competition from other *L. major* plants was more important than interspecific competition

from *C. demersum* plants in mixed cultures. The addition of one *L. major* plant to the mixture reduces the mean *L. major* weight to the same extent as 3.5 *C. demersum* plants. This is interpreted to mean that, *L. major* is 3.5 times stronger a competitor than *C. demersum*.

For *C. demersum* (Eq. (2)), the ratio of the species intra- and interspecific effects (b_{CC}/b_{CL}) was 10.2 indicating that one *C. demersum* plant and 10.2 *L. major* plants would have the same impact on *C. demersum* average plant weight. When excluding interspecific competition the R^2 only declines to 0.56. Hence, for both species the intraspecific competition is greater than the interspecific competition, so they are only partly limited by the same resource or they partly avoid each other. This is interpreted as niche separation (Spitters, 1983). In general, there is niche differentiation when the double quotient ($b_{LL}/b_{LC})/(b_{CL}/b_{CC})$ exceeds unity. In this case, we obtained a value of 35.7.

Interspecific interactions had a smaller effect on the competition outcome as we detected only a small change in R^2 when excluding interspecific competition and some marginally significant interspecific interactions ($0.05 < P < 0.1$) of *L. major* on both length and weight of *C. demersum* in the 'before dredging' treatment. Other multiple regressions showed no significant competitive effect for either species.

4. Discussion

The co-occurrence of the invasive *L. major* and the native *C. demersum* is expected to lead to competitive interactions for resources, particularly because both species are canopy forming submerged hydrophytes that inhabit shallow as well as deep littoral habitats (Wells et al., 1997), and can occupy a wide range of aquatic habitats (Vestergaard and Sand-Jensen, 2000; National Heritage Trust, 2003). We have investigated the effect of a common management practice against eutrophication in shallow waters on the performance of invasive species relative to native species. The new species *L. major* possesses traits that classify it as a 'good invader' such as vegetative growth habit, broad environmental tolerance and high relative growth rate (Sutherland, 2004). Due to its high RGR, *L. major* develops a dense canopy near the surface, which enables it to shade and overgrow co-occurring, lower stature species (Hofstra et al., 1999). Rattray et al. (1994) showed that *L. major* has a greater ability to increase both height and biomass during the initial colonization phase than native *Myriophyllum triphyllum*. These findings are confirmed by our results which show that, compared with the native species *C. demersum*, the stem elongation and length RGR of *L. major* are twice as high, both in monocultures and mixed cultures and in both sediment conditions; even when initial abundance of *L. major* is low (e.g. mix 4/8). Furthermore, this species has high light requirements so it is advantageous to allocate more resources to length growth. In this experiment the length RGR of *L. major* is higher than the weight RGR, which supports the theory that *L. major* growth resources are channeled to shoot extension (Rattray et al., 1994). However, length RGR of both species in this experiment is lower compared to other studies. Our plants have length RGR values between 0.17 and 0.21 week^{-1} for *L. major* and between 0.04 and 0.07 week^{-1} for *C. demersum*, lower than those found by Best and Meulemans (1979) (up to 0.31 week^{-1}), by Larson (2007) (up to 0.09 day^{-1}) for *C. demersum* and by James et al. (2006) (0.063 day^{-1}) for *L. major*. This difference in growth rate may be due to the experimental conditions: any treatment used for manipulating the plants can be a potential stress factor to the plants and cause loss of vitality. This phenomenon was also observed by Larson (2007) for *Ranunculus circinatus* and by Angelstein et al. (2009) for *Myriophyllum spicatum*. Another possible explanation is the maximum pH value recorded in our experiment (up to 10). High pH can cease net pos-

itive photosynthesis (Allen and Spence, 1981; James et al., 1999) consequently affecting growth and this may explain the lower RGR values observed. Initial plant density has also been reported to influence the growth (Barrat-Segretain and Elger, 2004). The high initial plant density in this study (160–640 plants m⁻²) can therefore have caused the lower growth rates. No differences are observed between the two species for the RGR calculated on weight when they are grown in monocultures for both sediment conditions. This might be explained by the ability of *C. demersum* to grow at relatively low light intensities (Wells et al., 1997) and therefore is expected to produce short, dense shoots under the water surface with an equal weight to the long, thin shoots of *L. major*. The RGR based on weight for *C. demersum* in the monocultures (0.10–0.17 week⁻¹) is similar with what was reported by Larson (2007) (0.02 day⁻¹). We could not find comparable values for *L. major* but the weight RGR observed in this experiment (0.10–0.19 week⁻¹) was similar with the growth rates reported by Angelstein et al. (2009) for *Elodea nuttalli* (~0.03 day⁻¹) but lower than what was reported by Barrat-Segretain and Elger (2004) for this species (~0.28 day⁻¹).

When examining the inter- and intraspecific competition using the model of Spitters, we find strong intraspecific effects for the 'after dredging' treatment for RGR calculated on weight. This indicates an effect of the species' initial density on its own biomass, suggesting a separate niche for this species. These results imply that instead of competitive exclusion, coexistence is favoured. Several traits of the studied species support the niche separation theory by Chambers and Prepas (1990) who concluded that interspecific competition plays a minor role in structuring submerged plant communities and that the species coexistence is due to differential utilization of resources (niche separation). First, because of lack of true roots, nutrient uptake by *C. demersum* is almost entirely foliar (Denny, 1972), while for rooted macrophytes (such as *L. major*) sediments can be the main source of both phosphorus and nitrogen (Barko and Smart, 1980). Second, *L. major* grows best under conditions of high light intensity (National Heritage Trust, 2003), while *C. demersum* is classified as a shade-adapted species (Wells et al., 1997). A strong intraspecific competition effect and niche differentiation have been reported in other competition experiments. Barrat-Segretain and Elger (2004) found a higher sensitivity to intraspecific neighbours for *Elodea canadensis*, probably due to competition for some micro-elements. Similarly, Njambuya et al. (2011) found stronger intra- than interspecific interferences in a competition experiment conducted with *Lemna* species. However, other studies reported equal or stronger interspecific effects (Aguar et al., 2001; Huckle et al., 2002; Spencer and Rejmánek, 2010). Another explanation, besides niche partitioning, is that light and nutrients of the water column are not limiting. The experiment was conducted in full summer with mean high light intensity measures and chemical analyses of the water showed no decrease of N and P nutrients during the experiment.

Although there is little evidence for interspecific competition, the growth of *C. demersum* in the mixed cultures is significantly reduced in both sediment conditions. The negative effect of *L. major* on the growth of *C. demersum* in the mixed cultures can be attributed to elevations of the pH by *L. major*. Many eutrophic waters have pH values in the range of 7–8, where the concentration of free CO₂ for photosynthetic activity becomes limiting (Kalf, 2002). A mechanism that enables species to overcome such limiting conditions will provide an aquatic plant with an advantage in alkaline waters. One such mechanism is the efficient utilization of bicarbonate ions as a dissolved inorganic carbon source, which has been described for other Hydrocharitaceae (e.g. *Elodea* sp.) (Prins et al., 1979). Macrophytes adapted to utilize bicarbonate are able to raise pH to 10 (O'Sullivan and Reynolds, 2004). In this experiment, photosynthesis by *L. major* raises the pH to values of almost

10 at the water surface. The limit is 10.4 for bicarbonate uptake. Furthermore, a calcium carbonate marl was formed rapidly on the upper surface of the leaves of *L. major* (I. Stiers, personal observation), a consequence of bicarbonate uptake by plants (Kalf, 2002). In a study conducted by James et al. (1999), *L. major* was reported to have the ability to photosynthesize and grow under very stressful conditions of high pH and low free CO₂, perhaps due to more efficient bicarbonate utilization than other species. It seems that this feature is the key to its success in dominating mixed plant communities as prolonged periods of high pH will suppress the photosynthetic performance of less aggressive submerged macrophytes.

Sediment dredging as a restoration technique is usually performed in shallow water bodies that suffer from internal phosphorus loading, need water deepening, require removal of toxic material and have excessive plant growth (Peterson, 1982). Several studies indicate that sediment removal is successful in the first three cases (Hovenkamp-Obbema and Fiegeen, 1992; Van der Does et al., 1992; Søndergaard et al., 2000; Mackie et al., 2007), but the effectiveness of dredging to control aquatic plants has not been well documented. Dredging removes aquatic plants and thereby reduces aquatic weed problems, however, their re-invasion rate will depend on a combination of depth, light, sediment texture and sediment nutrient content (Barko and Smart, 1986; Lauridsen et al., 1993). In our study, the experimental sediment dredging only has a small effect on lowering the nutrient level probably because the thickness of the nutrient-rich top layer that we removed was limited. However, *L. major* performs better in the 'after dredging' treatment which is lower in nutrients. The species accumulates more total biomass and a higher weight RGR both in monocultures and mixed cultures. Lauridsen et al. (1993) showed that the influence of sediments on growth of submerged aquatic plants might be due to physical properties rather than chemical composition. In our experiment, the top layer, used for the 'before dredging' treatment, consisted of a dark unconsolidated fluid mud layer containing fine-grained material. *L. major* has been reported to be favoured by sandy soil (National Heritage Trust, 2003). The sediment used to simulate the 'after dredging' conditions may have been more favourable for the initial anchoring and hence lead to a more successful growth of *L. major*. This may explain the better performance in the 'after dredging' condition (lower nutrient) relative to 'before dredging' condition (higher nutrient). For *C. demersum* it is not clear why there is a reduced weight RGR in the 'before dredging' treatment in the mixed cultures as this species does not depend on sediment for anchoring or nutrient uptake. A possible explanation can be differences in net diffusion into the overlaying water.

Based on the results of this experimental study, sediment dredging would not be a solution to reduce performance of invasive *L. major*. Although experimental studies are an important and essential method for interpreting and understanding species performance, they might represent an over-simplification of reality, which limits the ability to extrapolate the results to natural ecosystems. Therefore, care has to be taken when using experimental results for management decisions and the monitoring of the effects of management practices in natural conditions is essential to gain full knowledge on the ecology and performance of invasive exotic species.

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References

- Aguiar, M.R., Lauenroth, W.K., Peters, D.P., 2001. Intensity of intra- and interspecific competition in coexisting shortgrass species. *J. Ecol.* 89, 40–44.
- Allen, H.L., Spence, D.H.N., 1981. The differential ability of aquatic plants to utilize the inorganic carbon supply in freshwaters. *New Phytol.* 87, 269–283.
- Angelstein, S., Wolfram, C., Rahn, K., Kiwel, U., Frimel, S., Merbach, I., Schubert, H., 2009. The influence of different sediment nutrient contents on growth and competition of *Elodea nuttalli* and *Myriophyllum spicatum* in nutrient-poor waters. *Fundam. Appl. Limnol. Arch. Hydrobiol.* 175 (1), 49–57.
- Barrat-Segretain, M.-H., Elger, A., 2004. Experiments on growth interactions between two invasive macrophyte species. *J. Veg. Sci.* 15, 109–114.
- Barko, J.W., Smart, R.M., 1980. Mobilization of sediment phosphorus by submerged freshwater macrophytes. *Freshwater Biol.* 10, 229–238.
- Barko, J.W., Smart, R.M., 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology* 67, 1328–1340.
- Best, E.P.H., Meulemans, J.T., 1979. Photosynthesis in relation to growth and dormancy in *Ceratophyllum demersum*. *Aquat. Bot.* 6, 53–66.
- Branquart, E., Verreycken, H., Vanderhoeven, S., Van Rossum, F., other members of the Belgian Forum on Invasive Species, 2009. ISEIA, a Belgian non-native species assessment protocol. In: Segers, H., Branquart, E. (Eds.), Belgian Biodiversity Platform: Proceedings of a Scientific Meeting on Invasive Alien Species.
- Chambers, P.A., Prepas, E.E., 1990. Competition and coexistence in submerged aquatic plant communities: the effects of species interactions versus abiotic factors. *Freshwater Biol.* 23, 541–550.
- Daehler, C.C., 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annu. Rev. Ecol. Evol. Syst.* 34, 183–211.
- DAISIE, 2009. Handbook of Alien Species in Europe. Springer, Dordrecht.
- Denny, P., 1972. Sites of nutrient absorption in aquatic macrophytes. *J. Ecol.* 60, 819–829.
- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88, 528–534.
- Gopal, B., Goel, U., 1993. Competition and allelopathy in aquatic plant communities. *Bot. Rev.* 59, 155–210.
- Hofstra, D.E., Clayton, J., Green, J.D., Auger, M., 1999. Competitive performance of *Hydrilla verticillata* in New Zealand. *Aquat. Bot.* 63, 305–324.
- Hovenkamp-Obbema, I.R.M., Fieggan, W., 1992. The effects of dredging and fish stocking on the trophic status of shallow, peaty ditches. *Hydrobiologia* 233, 225–233.
- Huckle, J.M., Marrs, R.H., Potter, J.A., 2002. Interspecific and intraspecific interactions between salt marsh plants: integrating the effects of environmental factors and density on plant performance. *Oikos* 96, 307–319.
- Hunt, R., 1990. Basic Growth Analysis. Unwin Hyman, London, UK.
- James, C.S., Eaton, J.W., Hardwick, K., 1999. Competition between three submerged macrophytes, *Elodea canadensis* Michx., *Elodea nuttalli* (Planch.) St John and *Lagarosiphon major* (Ridl.) Moss. *Hydrobiologia* 415, 35–40.
- James, C.S., Eaton, J.W., Hardwick, K., 2006. Responses of three invasive aquatic macrophytes to nutrient enrichment do not explain their observed field displacements. *Aquat. Bot.* 84, 347–353.
- Kalff, J., 2002. Limnology: Inland Water Ecosystems. Prentice-Hall, Inc., USA.
- Keenan, E., Baars, J.-R., Caffrey, J.M., 2009. Changes in littoral invertebrate communities in Lough Corrib in response to an invasion by *Lagarosiphon major*. In: Pieterse, A., Rytkönen, A.-M., Hellsten, S. (Eds.), Proceedings of the 12th EWRS International Symposium on Aquatic Weeds.
- Kennedy, T.L., Horth, L.A., Carr, D.E., 2009. The effects of nitrate loading on the invasive macrophyte *Hydrilla verticillata* and two common, native macrophytes in Florida. *Aquat. Bot.* 91, 253–256.
- Kercher, S.M., Zedler, J.B., 2004. Multiple disturbances accelerate invasion of reed canary grass (*Phalaris arundinacea* L.) in a mesocosm study. *Oecologia* 138, 455–464.
- Larson, D., 2007. Growth of three submerged plants below different densities of *Nymphoides peltata* (SG. Gmel.) Kuntze. *Aquat. Bot.* 86, 280–284.
- Lauridsen, T.L., Jeppesen, E., Andersen, F.O., 1993. Colonization of submerged macrophytes in shallow fish manipulated Lake Vaeng: impact of sediment composition and waterfowl grazing. *Aquat. Bot.* 46, 1–15.
- Lockwood, J.L., Hoopes, M.F., Marchetti, M.P., 2007. Invasion Ecology. Blackwell Publishing, UK.
- Louette, G., Declerck, S., Vandekerckhove, J., De Meester, L., 2009. Evaluation of restoration measures in a shallow lake through a comparison of present day zooplankton communities with historical samples. *Restor. Ecol.* 19, 629–640.
- Mackie, J.A., Natali, S.M., Levinton, J.S., Sanudo-Wilhelmy, S.A., 2007. Declining metal levels at foundry cove (Hudson river New York): response to localized dredging of contaminated sediments. *Environ. Pollut.* 149, 141–148.
- McGregor, P., Gourlay, H., 2002. Assessing the prospects for biological control of *Lagarosiphon* (*Lagarosiphon major* (Hydrocharitaceae)). DOC Science Internal Series 57, Department of Conservation, Wellington, New Zealand.
- Mony, C., Koschnick, T.J., Haller, W.T., Muller, S., 2007. Competition between two invasive Hydrocharitaceae (*Hydrilla verticillata* (L.f.) (Royle) and *Egeria densa* (Planch.) as influenced by sediment fertility and season. *Aquat. Bot.* 86, 236–242.
- National Heritage Trust, 2003. *Lagarosiphon – Lagarosiphon major*. Weed Management Guide.
- Njambuya, J., Stiers, I., Triest, L., 2011. Competition between *Lemna minuta* and *Lemna minor* at different nutrient concentrations. *Aquat. Bot.* 94, 158–164.
- O'Sullivan, P.E., Reynolds, C.S., 2004. The lakes handbook. Limnology and limnetic ecology, vol. 1. Blackwell Publishing, Oxford, 699 pp.
- Peretyatko, A., Teissier, S., Symoens, J.-J., Triest, L., 2007. Phytoplankton biomass and environmental factors over a gradient of clear to turbid peri-urban ponds. *Aquat. Conserv. Mar. Freshwater Ecosyst.* 17, 584–601.
- Peterson, S.A., 1982. Lake restoration by sediment removal. *Water Res. Bull.* 18, 423–435.
- Pimentel, D., Lach, L., Zuniga, R., Morrison, D., 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50, 53–65.
- Prins, H.B.A., Snel, J.F.H., Helder, R.J., Zanstra, P.E., 1979. Photosynthetic bicarbonate utilization in the aquatic angiosperms *Potamogeton* and *Elodea*. *Hydrobiol. Bull.* 13, 106–111.
- Rattray, M.R., Howard-Williams, C., Brown, J.M.A., 1994. Rates of early growth of propagules of *Lagarosiphon major* and *Myriophyllum triphyllum* in lakes of differing trophic status. *N. Z. J. Mar. Freshwater Res.* 28, 235–241.
- Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17, 170–176.
- Sokal, R.R., Rohlf, F.J., 2003. Biometry: The Principles and Practice of Statistics in Biological Research. W.H. Freeman and Company, New York.
- Søndergaard, M., Jeppesen, E., Jensen, P.J., Lauridsen, T., 2000. Lake restoration in Denmark. *Lake Reservoir Manage.* 5, 151–159.
- Spencer, D.F., Rejmánek, M., 2010. Competition between two submersed aquatic macrophytes *Potamogeton pectinatus* and *Potamogeton gramineus*, across a light gradient. *Aquat. Bot.* 92, 239–244.
- Spitters, C.J.T., 1983. An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. *Neth. J. Agric. Sci.* 31, 1–11.
- Strayer, D.L., 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biol.* 55, 152–174.
- Sutherland, S., 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologia* 141, 24–39.
- UNEP (United Nations Environment Program), 1999. Planning and management of lakes and reservoirs: an integrated approach to eutrophication, Technical Publication Series 11, Shiga, Japan.
- Van, T.K., Wheeler, G.S., Center, T.D., 1999. Competition between *Hydrilla verticillata* and *Vallisneria spiralis* as influenced by soil fertility. *Aquat. Bot.* 62, 225–233.
- Van der Does, J., Verstraelen, P., Boers, P., Van Roestel, J., Roijackers, R., Moser, G., 1992. Lake restoration with and without dredging of phosphorus-enriched upper sediment layers. *Hydrobiologia* 233, 197–210.
- Van Landuyt, W., Hoste, I., Vanhecke, L., Van den Bremt, P., Verduyck, E., De Beer, D., 2006. Atlas van de Flora van Vlaanderen en het Brussels Gewest. Instituut voor Natuur- en Bosonderzoek en Nationale Plantentuin van België, Brussel.
- Vestergaard, O., Sand-Jensen, K., 2000. Alkalinity and trophic state regulate aquatic plant distribution in Danish Lakes. *Aquat. Bot.* 67, 85–107.
- Wells, R.D.S., De Winton, M.D., Clayton, J.S., 1997. Successive macrophyte invasions within the submerged flora of Lake Tarawera, Central North Island New Zealand. *N. Z. J. Mar. Freshwater Res.* 31, 449–459.
- Westphal, M.L., Browne, M., MacKinnon, K., Noble, I., 2008. The link between international trade and the global distribution of invasive alien species. *Biol. Invas.* 10, 391–398.