Competition between *Lemna minuta* and *Lemna minor* at different nutrient concentrations

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ABSTRACT

We investigated the differential responses of invasive alien *Lemna minuta* and native *Lemna minor* to nutrient loading as well as the mechanism of competition between the species. The role of nutrients, species identity, species influence in determining the outcome of competition between the species was estimated using the Relative Growth Rate Difference (RGRD) model. The two species differed in their response to nutrient loading. The native *L. minor* responded indifferently to nutrient loading. The species Relative Growth Rate (RGR) was $0.10\,\mathrm{d}^{-1}$, $0.11\,\mathrm{d}^{-1}$ and $0.09\,\mathrm{d}^{-1}$ in high, medium and low nutrients, respectively. On the other hand, the invasive *L. minuta* responded opportunistically to high nutrient availability and had an RGR of $0.13\,\mathrm{d}^{-1}$, $0.10\,\mathrm{d}^{-1}$ and $0.08\,\mathrm{d}^{-1}$ in high, medium and low nutrients, respectively. As a result, the invasive species was dominant in high nutrient availability but lost to the native species at low nutrient availability. The invader formed approximately 60% and less than 50% of the stand final total dry biomass in high and low nutrient availability, respectively. Species RGR were reduced by both intra- and interspecific competition but intraspecific effects were stronger than interspecific effects. On the overall, the species significantly differed in their constant RGR. These differences in RGR between the species (species identity) and the differential response to nutrient loading were the main determinant of change in final biomass composition of these species in mixture. Species influence (competition) only had a small influence on the outcome of competition between the species. The observed species response to nutrient loading could be targeted in management of the invasive species. Lowering nutrients can be proposed to reduce the impact of the invasive *L. minuta*.

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1. Introduction

Invasive species are projected as the future most important drivers of change in freshwater ecosystems due to various reasons (Sala et al., 2000). When an alien plant species is introduced, competition for resources is possibly the first interaction the species has with the resident community. Previous studies have shown that high resource availability enhances the performance of invasive species (Van et al., 1999; Daehler, 2003; Adair et al., 2008). High growth-rate in favorable environments is linked to poor performance in more stressful environments across a range of plant taxa (Pugnaire and Valladares, 2007). In plant interactions, species robustness under unfavourable conditions and opportunism under favorable conditions may determine the success and abundance of species in a certain environment. If a species robust fitness is the key to its success, then it can be considered a 'Jack-of-all-trades' since the species is better able to maintain its fitness in unfavourable environments. On the contrary, if the success of a species that is

in competition with another is due to an ability to more rapidly take advantage of available resources, then this species shows a greater opportunism in favorable conditions and can be considered a 'Master-of-some' scenario. A species that is both a 'Jack' and 'Master' exhibits a relatively indifferent response to unfavourable conditions but is versatile enough to take advantage of favorable conditions and increase its performance relative to its competing counterparts (Richards et al., 2006). How a native or non-native species fits in this description has consequences in the management of invasive species.

Nutrient enrichment (both phosphorus and nitrogen) as a result of human activities has been implicated worldwide in massive changes in biological diversity and ecosystem services (Scheffer et al., 2003; Smith, 2003). High nutrient availability is one of the factors thought to render a habitat subject to invasion (Alpert et al., 2000) and increases competitive advantage of invasive species relative to natives (Daehler, 2003). Therefore, synergistic interactions between introduced plant species and nutrient enrichment pose a great threat to native plant biodiversity. Previous studies on the influence of nutrient enrichment on competition between invasive and native aquatic plants have mainly focused on submerged macrophytes (Van et al., 1999; Mony et al., 2007; Kennedy et al.,

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2009) with fewer studies on floating macrophytes (Tipping et al., 2009). *Lemna minuta* Kunth (*L. minuta*) and *Lemna minor* L. (*L. minor*) are free-floating macrophytes whose growths are greatly influenced by abiotic factors such as temperature and nutrient availability (Landolt and Kandeler, 1986; Scheffer et al., 2003). In aquatic ecosystems, the most intense competition is expected to occur between species of similar growth forms occupying identical positions in the water column (Gopal and Goel, 1993). However, even with apparent similarities these species may differ considerably in their robustness and opportunism to resource availability and fluctuation, as well as in their competitive abilities (Daehler, 2003; Doyle et al., 2003).

Historically, experimental systems have informed understanding of species interactions and the role of environmental conditions in enhancing invasiveness and invasibility. They have provided the basis for understanding ecological processes applicable at larger scales. Therefore, experimental systems have become widely used and accepted tools in ecology (Ives et al., 1996). However, they present various limitations (e.g. short time frame, small-scale, lack of a complex array of interaction found in natural conditions, laboratory conditions that do not fully reflect natural conditions) that may limit our ability to relate and extrapolate small-scale experiment to natural systems (Carpenter, 1996; Petersen et al., 1997; Schindler, 1998). Therefore, the extent and generalization from small-scale experiments to field conditions cannot be done without much care. In the present study we conducted a controlled experiment to investigate the degree to which the invasive *L. minuta* differs from the native *L. minor* in terms of robustness and opportunism to nutrient availability, as well as their tolerance to intra- and inter-specific competition. We also determined the role of species identity (species constant growth rate), species influence (intra- and inter-specific effects of a species on its Relative Growth Rate (RGR) and that of the other species), and nutrients on change in biomass composition of both species in mixtures. The relative importance of these factors in determining which species gains in a mixture will give insight on invasive species management and possible competitive impacts of the invasive *L. minuta* on the native *L. minor*.

2. Materials and methods

2.1. Laboratory experiment

The duckweeds (*L. minuta* and *L. minor*) used in this investigation were collected from a nature area 'Kalkense Meersen' in Belgium where the two species were found growing together. A single plant (single clone) for each species was cultured in the laboratory under full strength Hoagland's solution for rapid multiplication of fronds for use as our stock culture for this experiment. Before setting each experiment, we pre-cultured a few fronds for two weeks to generate new and young rapid growing fronds that are acclimatized to the experimental conditions. We used these newly formed fronds as mother fronds in our investigation.

We grew the two species both in monoculture and mixture in glass beakers (diameter: 90 mm) along a nutrient gradient under controlled conditions. The beakers were placed in a growth chamber at $25 \pm 2\,^{\circ}C$ with a 16:8 light:dark cycle. The irradiance measured at the level of culture medium ranged from 63 to 72 μmol m^{-2} s^{-1}. This was monitored not to fall outside the range of 55–80 μmol m^{-2} s^{-1} in the culture area (measured at several points at the level of culture medium). We used modified Hoagland E+ solution (approximately 250 mL per beaker) as our growth media. The full-strength concentration (0.34 g N L^{-1}, 0.15 g P L^{-1}) was chosen as a high-nutrient availability treatment and diluted (1) three times to achieve a transitional nutrient condition here referred to as

medium nutrient condition (0.11 g N L^{-1}, 0.05 g P L^{-1}) and (2) to one tenth of the original concentration to produce a low-nutrient availability treatment (0.03 g N L^{-1}, 0.01 g P L^{-1}). To reduce algae growth and competition with lemnids, we renewed the growth solution after every two days. In addition, we rinsed the lemnids in distilled water to remove any algae that might be attached on the fronds and roots prior to culturing in fresh medium.

The experimental design followed an addition series (Spitters, 1983) consisting of factorial combinations of different densities of the two competing plant species. The ratio of *L. minuta* to *L. minor* planting densities were 0:14, 0:28, 14:0, 28:0, 14:14, 14:28, 28:14, 28:28 fronds per beaker, equivalent to total densities ranging from 155 to 622 fronds m^{-2} at the start of the experiment. Each density treatment was replicated five times resulting in a total of 40 beakers at three nutrient treatments. After 20 days of growth, all plants were harvested, separated into species and the species total biomass was dried to a constant weight at 70 $^{\circ}$C. The initial dry biomass was measured by randomly sampling 30 sets of 14 and 28 fronds, from which six random sets of each density (per species) were averaged to represent the initial dry biomass of each of the five replicates for the three nutrient treatments. Therefore, a species total initial biomass per stand varied according to the initial planting densities of 14 and 28 fronds. The mean initial dry biomass at planting density 14:14 was 0.011 g and 0.015 g for *L. minuta* and *L. minor*, respectively.

2.2. Data analysis

We assessed the growth performance of *L. minuta* and *L. minor* by species final biomass and average Relative Growth Rate (RGR). Preliminary assessment for the relative response of each species to nutrient change was done by comparing the biomass output ratio of *L. minuta* to *L. minor* and examined for significant differences along the nutrient gradient. The effects of nutrient change on species RGR for each initial frond density and the differences between monocultures and mixtures were analyzed using one-way ANOVA in normally distributed data and Kruskal–Wallis ANOVA in nonnormally distributed data. In addition, differences between species in mixture per nutrient treatment were assessed using *t*-test and Mann–Whitney *U*-test in normally and non-normally distributed data, respectively. The RGR for *i*th species (for *i* = species 1 or 2) was calculated according to Connolly and Wayne (1996) as:

$$RGR_i = \ln \frac{(Y_i/y_i)}{t} \tag{1}$$

where Y_i is the species stand biomass at the end of the experimental period, y_i is the species stand biomass at the beginning of the experimental period, t is the duration of the experiment, and ln is the natural logarithm. The effect of the competitive interactions and nutrient treatment on a species RGR was investigated using multiple regressions. Linear equations for species average RGR were defined as follows; for species 1, in a mixture of species 1 and 2:

$$RGR_1 = a_{10} + a_{11}y_1 + a_{12}y_2 + a_{30}T \tag{2}$$

The corresponding equation for species 2 in a mixture of species 1 and 2:

$$RGR_2 = a_{20} + a_{21}y_1 + a_{22}y_2 + a_{30}T \tag{3}$$

The coefficients a_{11} and a_{22} are a measure of intraspecific effects of a species on its own RGR, while a_{12} and a_{21} are a measure of interspecific effects of species 2 and 1 on RGR of species 1 and 2, respectively. The constant a_{10} and a_{20} indicate a constant *RGR* for species 1 and 2, respectively, over the growth period while a_{30} measures the effect of nutrient treatment (*T*) on a species RGR. y_1 and y_2 are the stand initial biomass of species 1 (*L. minuta*) and 2 (*L. minor*).

Since in this experiment we are also interested in assessing the roles of species identity, species influence, and of nutrient treatment on the change in the relative proportional abundance of the species in mixture, we applied the RGRD model of Connolly and Wayne (2005) for two species. Change in the species relative proportions over time occurs if one species in a mixture gains at a faster per unit rate than another. Thus, a species with a significantly higher constant growth rate will be more abundant and its final proportion in a stand will be higher than that of the slower-growing species. Otherwise, if all species gain at the same rate the stand composition in terms of the biomass proportional abundance of a species will remain the same. Connolly and Wayne (2005) acknowledge that dynamics and shift in community composition depends on many process other than growth. However, their model focuses on relative importance of (1) species growth traits, which are reflected in the difference in average relative growth rate between species (species identity), (2) the difference between the intraspecific effects of a species on its own RGR and its interspecific effects on RGR of the other species (species influence), and (3) environmental variables (Treatment). We modeled RGRD (RGR minuta − RGR minor) as follows:

$$RGRD_{12} = b_0 + b_1 y_1 + b_2 y_2 + b_3 T + \varepsilon \tag{4}$$

The coefficients b_1 and b_2 measure the effects of changing the initial biomass of species 1 (L. minuta) or 2 (L. minor) on RGRD. A positive value of b_i (for i = 1 or 2) indicates that an increase in the ith species biomass in the initial community will enhance the RGRD in favor of species 1 and hence will bias the final composition towards that species. A negative value has the opposite effect. The coefficients b_1 and b_2 are also referred to as influence coefficients (Ramseier et al., 2005) as they reveal how changes in initial abundance of the species can influence the growth differential between species. The coefficient b_3 measures the effects of applied treatment (denoted by variable T). A positive value of b_3 means that increasing nutrient concentration enhances RGRD and hence increases the proportion of species 1 in the composition. If all the coefficients (b_1, b_2, b_3) are zero then RGRD is not affected by the initial composition nor applied treatment, and will be constant (b_0). This constant difference in average RGR reflects the differences in RGR of the two species over the growth period and will shift the stand composition towards the faster growing species. In the case where b_0 is also zero, the community composition will not change over the experimental period. Therefore, the model allows for the evaluation of the question of which species gains in mixture and the relative importance of species identity, species influence and nutrient treatment as separate determinants of community change.

3. Results

3.1. Relative response of each species to nutrient treatments

3.1.1. Biomass

Averaged across all density treatments L. minuta accumulated (mean ± SE) 22.1 ± 0.9, 13.8 ± 1.1, and 9.3 ± 0.6 g m^{-2} in high, medium and low nutrient treatment, respectively. On the other hand L. minor accumulated 14.5 ± 1.5, 15.9 ± 0.9 and 16.1 ± 0.7 g m^{-2} in high, medium and low nutrient treatment, respectively. The ratio of L. minuta to L. minor biomass output was used to compare the relative response of each species among nutrient treatments; the mean ratio of L. minuta to L. minor for high nutrient treatment (1.8 ± 0.2) was significantly higher than in medium (0.9 ± 0.01) and low nutrient treatments (0.8 ± 0.04) (Kruskal–Wallis test H (2, N = 90) = 40.89 p < 0.001).
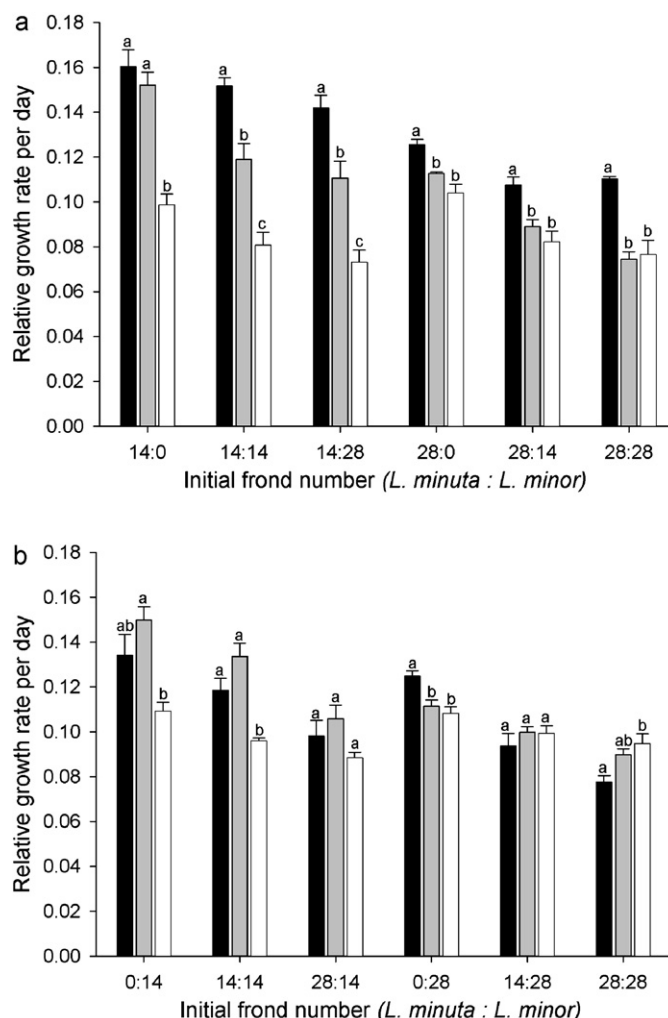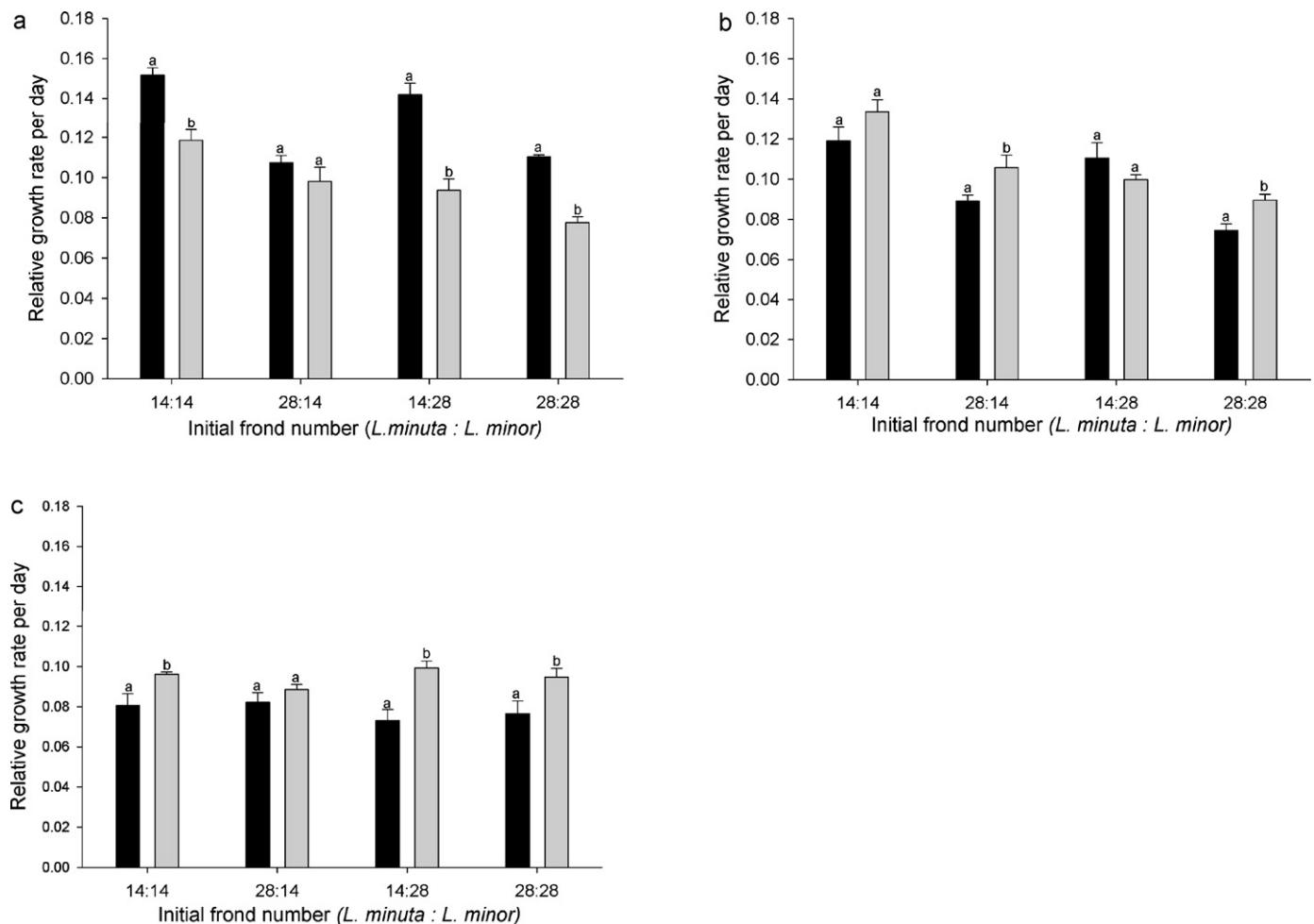

Fig. 1. Relative Growth rate along a density treatment for (a) L. minuta and (b) L. minor at high nutrient (black bars), medium nutrient (grey bars) and low nutrient (white bars) availability. Small letters indicate significant differences among nutrient treatments at P < 0.05. Error bars represent ±SE of the means.

3.1.2. Relative Growth Rate (RGR)

The RGR of L. minuta both in monocultures and mixtures shows a clear response pattern to nutrient change with significantly higher RGR in high than in medium and low nutrient treatments (Fig. 1a). The RGR of L. minor, however, did not show a distinct response pattern to nutrient change. Nevertheless, like L. minuta, the species RGR in high nutrient concentration was significantly higher than in low nutrient concentration (Fig 1b). Additionally, our results also show that monocultures performed better than mixed cultures (Mann–Whitney U-test; p < 0.001).

3.2. Species performance in mixture along a nutrient gradient

Generally, L. minuta grew faster than L. minor when they were both cultured at equal densities in high nutrient concentration. It slowly lost to L. minor as nutrient concentration was decreased such that, RGR of L. minor at medium and low nutrient concentration was higher than that of L. minuta (Fig. 2a–c; density 14:14 and 28:28). Some differences in RGR were also observed when the two species were cultured at unequal densities (Fig. 2a–c; density 28:14 and 14:28). Overall, L. minuta grew faster than L. minor in mixed culture in high nutrient availability but the reverse was true in low nutrient availability.

Fig. 2. Relative growth rate of *L. minuta* in mixture with *L. minor* along density treatment at (a) high, (b) moderate and (c) low nutrient availability. *Small letters* indicate significant differences between *L. minuta* (black bars) and *L. minor* (grey bars) at $P < 0.05$. Error bars represent ±SE of the means.

3.3. Intra- and inter-specific competition and nutrient concentration effects on a species RGR

The overall responses of each species RGR to a conspecific and/or hetero-specific neighbor and nutrient treatment are described in Table 1. A negative coefficient indicates a decrease in a species RGR because of increasing initial biomass of a species (y_1 or y_2) and/or nutrient concentration while a positive coefficient indicates the opposite. The magnitude of the coefficients and their significance indicate their relative influence on species RGR.

Regression analysis on species RGR indicates that both species had a higher constant growth rate in high than in low nutrient availability. However, high nutrients favored the invasive *L. minuta* relative to the native *L. minor* as the invader achieved a higher constant RGR. The opposite was observed in low nutrient conditions. Competition significantly influenced species growth. The RGRs of *L. minuta* and *L. minor* were suppressed by both intra- and interspecific competition. As such, increasing the initial biomass of either a conspecific or a heterospecific neighbor in the mixture negatively affected a species RGR (negative competition coefficient on species RGR, Table 1). This is an indication of intense intra- and interspecific competition. However, the overall magnitude of interspecific coefficients indicates that the competitive effects due to *L. minuta* on the RGR of *L. minor* were greater compared to those of *L. minor* on the RGR of *L. minuta*. Overall, both species experienced stronger intra- than interspecific effects on their RGRs.

Nutrient treatment had positive effects on both species RGR as indicated by the positive coefficient of treatment variable (T). However, the response of each species RGR to nutrient loading differed. The invasive *L. minuta* strongly responded opportunistically to high nutrient availability, while *L. minor* responded indifferently to nutrient treatment. This is indicated by the significance and non-significance of treatment variable (T) coefficient for *L. minuta* and *L. minor*, respectively (Table 1).

3.4. Change in species biomass composition

Our results from the RGRD model indicate that there was a change in biomass composition of the two species in mixture, since all the four coefficients were significantly different from zero (Table 2). Based on the constant, the shift in final biomass of the two-species in mixture was more towards *L. minor* (indicated by the negative and significant constant, Table 2 overall equation). However, the increase in final relative to initial abundance was only evident in medium and low nutrient conditions, but not in high nutrient condition as these conditions mainly favored *L. minuta*. As such, *L. minuta* was the dominant species in high nutrient availability and formed approximately 60% of the stand final total dry biomass. Conversely, *L. minor* was dominant in medium and low nutrient conditions making up over 50% of the stand final total dry biomass.

Table 1
Estimated coefficients of species intra- and inter-specific competition in high, moderate, low and overall nutrient treatment. The constant reflect species constant growth rate while intra-effects and inter-effects reflect reduction in species growth rate due to a con-specific and hetero-specific neighbor, respectively. T reflects the effects of nutrient treatment on a species RGR. Values in bold indicate significant coefficient at t statistics greater than/equal to 2.

Species	Variable	Nutrient regime	Estimates of the coefficient in the model				R^2
			Constant	Intra-effects	Inter-effects	T	
L. minuta	RGR	High	**0.1279**	**−3.7552**	−0.3709	–	0.89
		Moderate	**0.0983**	**−3.5034**	**−1.1705**	–	0.85
		Low	**0.0782**	**−3.5055**	−1.2492	–	0.67
		Overall	**0.0517**	**−3.6220**	**−0.7944**	**0.0249**	0.92
L. minor	RGR	High	**0.0970**	**−2.3378**	**−1.7417**	–	0.70
		Moderate	**0.1073**	**−2.6122**	**−1.8241**	–	0.79
		Low	**0.0946**	**−1.0298**	−0.5336	–	0.11
		Overall	**0.0973**	**−2.3836**	**−1.6301**	0.0012	0.60

3.5. Determinant of change in species final biomass composition

Based on the magnitude of the coefficients of the RGRD model (Table 2), the change in biomass composition of these two species in mixture was mainly driven by nutrient treatment and species identity (the constant difference in average growth rate of species in mixture). Species influence (effect of intra- and interspecific competition on a species own RGR and on RGR of the other species) had a minimal influence on the change in final biomass structure of these species in mixture. Changing the initial biomasses of a species either enhanced or reduced the RGR differential between the species. While increasing the initial biomass of *L. minor* enhanced the RGRD between the two species in mixture, increasing the initial biomass of *L. minuta* had the opposite effect. This was due to the stronger intraspecific effects on a species RGR, compared to the smaller interspecific effects. Additionally, increasing the nutrient concentration enhanced the RGRD and shifted the final biomass in favor of *L. minuta* (indicated by the positive coefficient of treatment variable (T) in Table 2). Low nutrient availability had the opposite effect.

4. Discussion

4.1. Biomass and RGR response to nutrient availability and competition

Species competitive ability or performance can be measured in various ways (Goldberg and Landa, 1991). Here, we used species biomass output and RGR as a measure of competitive ability or performance of invasive *L. minuta* and native *L. minor* in mixture. Many studies have been conducted to compare the performance of invasive species and their co-occurring native species to investigate whether invasive plants perform better than native species (Daehler, 2003).

In the present study, the invasive *L. minuta* outperformed the native *L. minor* in high nutrient but not in medium and low nutrient availability. We observed that the alien *L. minuta* accumulated more total biomass and had a higher RGR than the native *L. minor*

in high nutrient availability even when the initial abundance of native *L. minor* was twice that of the invasive *L. minuta*. However, in low nutrient availability, *L. minor* dominated the invasive *L. minuta* even when its initial abundance was only half that of *L. minuta*. The invasive *L. minuta* therefore responded opportunistically to high nutrient availability. Such opportunism by the invasive species in resource-rich conditions has been observed in other studies (Van et al., 1999; Daehler, 2003; Burns, 2006). However, some invasive species are found to dominate the natives in both resource-rich and resource-poor conditions (Kolb et al., 2002; Burns et al., 2007; Garcia-Serrano et al., 2007).

In competitive situations, the species with a higher RGR is deemed to be more efficient over the course of the experiment in the sense that it has a higher output per unit input (Connolly and Wayne, 2005). Therefore, such a species is able to dominate an area quickly. Clonal species such as *L. minuta* and *L. minor,* rapidly colonize, occupy, and preempt space through rapid clonal expansion. Clonal growth in *Lemnaceae* is primarily through budding of new fronds from mother fronds. In favorable environmental conditions, for example in nutrient rich conditions, the rapid generation of fronds often yields high mat densities, which result in overcrowding and overtopping. Overcrowding and overtopping was very common in our experiment and might have had negative effects on species performance. High population densities significantly limit growth of duckweeds and other free-floating macrophytes due to overcrowding (Driever et al., 2005; Frédéric et al., 2006) and shading effects (Dickinson and Miller, 1998; Tipping et al., 2009). Shading effects together with root foraging may have enhanced the relative performance of *L. minor* compared to *L. minuta* in low nutrient conditions. The native species often overtopped the invasive *L. minuta* and generally developed longer and more roots than the invasive species in low nutrient availability. This root plasticity in relation to nutrient availability was previously observed (Landolt and Kandeler, 1987; Cedergreen and Madsen, 2002). All in all, the better performance in high than in low nutrient treatments by both species indicates that the species can tolerate and respond to very high nutrient loading, a condition common in many ponds, canals and ditches in Belgium.

Table 2
Estimated coefficient of Relative Growth Rate Difference (RGRD) between *L. minuta* and *L. minor* in mixture in high, moderate, low and overall nutrient treatment. The constant (species identity) reflects the constant difference in relative growth rate between the two species in mixture. Species influence reflects the balance between intra- and inter-specific effects of a species on its own RGR and that of another species and thus on RGRD. T reflects the influence of nutrient treatment on RGRD. Values in bold indicate significant coefficient at t statistics greater than/equal to 2.

Variable	Nutrient regime	Constant	Species influence		T	R^2
			L. minuta	*L. minor*		
RGRD$_{minuta−minor}$	High	**0.0309**	**−2.0135**	**1.9659**	–	0.58
	Moderate	**−0.0090**	**−1.6793**	**1.4416**	–	0.48
	Low	**−0.0165**	**−2.9752**	−0.2207	–	0.31
	Overall	**−0.0456**	**−1.992**	**1.5890**	**0.0237**	0.71

4.2. Determinant of change in biomass proportion

The changes in biomass proportional abundances of two species in mixture over the duration of experiment is related to differences in RGR between species and thus change in species relative abundance depends on the performance of the species in a community (Connolly and Wayne, 2005). The results of our RGRD model on *Lemna* indicate that the change in final biomass composition of these species in mixture was primarily driven by species identity and nutrient treatment. We observed large differences in RGR between these species in mixture among the nutrient treatment. Such large differences in RGR between species in mixture (species identity) can lead to a considerable change in the relative abundance of a species, as differences in RGR between species is much the strongest element in modifying species biomass composition (Connolly and Wayne, 2005). Species influence (competition) although significant had a relatively small effect on RGRD between species and thus a small influence in changing the biomass proportion of these two species in mixtures. This importance of species identity relative to species influence in determining the change in biomass proportional abundance of a species in mixture was previously observed (Connolly and Wayne, 2005; Ramseier et al., 2005). In addition to species identity, environmental conditions (nutrient availability) enhanced the RGRD between species and thus influenced the biomass composition of a species in mixture.

In this analysis, although species influence (competition) had small effects on RGRD and thus on species final biomass proportion, their influence on species RGR was important. The stronger intra- than interspecific effects on both species growth rates had negative effects on species final proportion and these effects were more pronounced at high initial biomass of either species. Such stronger intra- than interspecific effects of competition have been reported by other studies (e.g. Johansson and Keddy, 1991 but see Huckle et al., 2002; Aguiar et al., 2001).

4.3. The importance of assessing the main determinant of change in biomass composition in invader–native species interactions

Assessing the main determinants of change in biomass composition is particularly relevant in studies involving invasive and native species. This is because decrease in abundance of a native species relative to a co-occurring invader is often attributed to intrinsic competitive effects of the invader on the native (Davis, 2009). Here we have shown that, although the competitive ability of the invasive *L. minuta* on the native *L. minor* was strong, the abundance of the invasive alien relative to the native was facilitated by species identity and response to nutrient loading. The opportunistic response of the invader to high nutrient loading enabled the species to dominate in high nutrient availability conditions. The native species robustness on the other hand, enabled the species to outperform the invader in low nutrient availability conditions. Hence, the conclusion by Daehler (2003) that alien invaders greater performance is largely context dependent is well demonstrated in our study.

The performance of invasive species may differ from natives if species interactions control plant performance. In this case an invasive alien with a novel growth or functional form could potentially have a competitive advantage over a native, or escape attack from native pathogens or herbivores (Levine and D'Antonio, 1999). When abiotic factors, such as nutrient availability, control plant performance the invasive alien may not differ from the native because the same factor will then determine performance of both native and non-native species. Thus, determining the relative importance of species growth traits (species identity), species influence and environmental conditions in enhancing the abundance of an invader relative to native species could be informative to invasive

species manager. The information on species growth traits and their response to environmental conditions can be targeted to minimize the effects of invaders on native species. In this study, lowering nutrients can be proposed to reduce the impact of the invasive *L. minuta*. However, such inferences cannot be made without much care since the laboratory conditions used here do not fully reflect the field conditions. The low irradiance used here may have influenced the species performance, although we do not expect species response to nutrient availability to change even at high irradiance. For management purposes, future manipulation of nutrient loading and effects on species performance should be conducted in field conditions to ensure ecological validity.

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