Ecosystems around the world are experiencing an increase in invasions of alien macrophytes. Most alien freshwater macrophytes are transported for commercial purposes as attractive ornamental species for aquarium or garden pond use. These plants often escape or are released by humans in neighbouring water bodies, where they can cause serious ecological and economic impacts. Many freshwater bodies are highly eutrophicated due to phosphorus inputs resulting from human activities. Elevated phosphorus (P) loadings in freshwater ecosystems have often favoured invasive species, being able to use nutrients efficiently at high nutrient levels and showing high relative growth rates (RGR) and other important traits. There is no clear consensus on which traits promote invasiveness, especially for aquatic plants. This is probably due to the diversity of species and growth forms. Several studies have examined the performance of invaders in high nutrient levels, however few investigated the performance and traits of invaders in low nutrients, especially for aquatic plants. A low water column phosphorus supply could affect invasive species’ growth, nutrient uptake and competitive performance. Additionally, changes in morphology could reveal apparent variation in traits promoting invasiveness. Determining the role of nutrient availability in species invasiveness is therefore important for the management of invasive aquatic weeds and for revealing potential high-impact invaders.

We investigated competitive strategies and traits of invasive species in different levels of phosphorus (P) supply. To best determine invasive species’ strategies and traits, intense competition is essential. Competition was therefore investigated between invasive species, since invasive species often have high growth rates in high nutrient levels, and competition is presumed to be intense. Competition between invasive species is also related to field conditions since multiple invasions are expected to occur. Additionally, we compared invasive species with similar growth form and position in the water column, since this is when highest competition takes place. Chosen species were also closely related to reduce differences attributed to phylogeny.

We performed indoor experiments always using two related invasive species with the same growth form: free-floating lemnids, emergent Ludwigia and submerged myriophyllids. The lemnid species included Lemna minuta, a native to North and South America, and Landoltia punctata originating from Australia and Southeast Asia. The studied emergent plants were Ludwigia grandiflora and Ludwigia peploides, two invasive macrophyte species originating
from North and South America. For the submerged growth form, we considered *Myriophyllum aquaticum* and *Myriophyllum heterophyllum*, native to North and South America. *M. aquaticum* also appears as an amphibious plant but was grown under submerged conditions to obtain highest interference. All species considered in this work are highly invasive plants in Belgium except *L. punctata*, which occurs in the Netherlands.

In each experiment, we grew the two related species in monocultures and mixtures following a complete additive design under high and low phosphorus levels to answer the following research questions: (i) Does a low water column P supply have a negative effect on the invasive species growth rates? (ii) Does a different water column P supply affect the strategy of invasive species and change the competitive outcome? (iii) Do similar species have similar strategies when responding to different P levels? We then compared results from all the growth forms and discussed (1) Whether there is a better invader strategy in high and low water column P level. (2) Whether more successful invaders are characterized by trait plasticity or by high trait values. (3) Which growth form will perform best in low water column P. (4) Whether P reduction in the surface water could be an efficient management tool for reducing the performance of invasive species.

We also performed indoor and outdoor competition experiments between invasive and native related species with similar growth form that are common in high nutrient conditions: free-floating lemnids and submerged myriophyllids. For the lemnids we studied the invasive *Lemna minuta* and the native *Lemna minor*. We performed a field experiment in eutrophic condition and an indoor experiment in mesotrophic condition to study the possible effect of lower P on the performance of the invasive species versus native species and investigate the reintroduction potential of native related species. The *Myriophyllum* experiment was conducted with invasive *Myriophyllum aquaticum* and native *M. spicatum*. This native species is also a highly competitive invasive species itself in North America. The experiment was performed indoor in high nutrient conditions, hypothesizing that the native species could out-compete the invasive *M. aquaticum* in current nutrient-loaded conditions and therefore be a good candidate for reintroduction.

Our results of the invasive versus invasive species experiments showed that a low phosphorus supply had important impacts on the RGR of all species. Growing in a water column P concentration concurring with a eutrophic level already resulted in somewhat
lower growth rates for all species compared to values found in literature. An even lower P level concurring with mesotrophic condition instigated even lower RGRs. One exception was the slightly higher RGR for *Myriophyllum* in mesotrophic versus eutrophic condition, which was probably attributed to lower decomposition rates.

Our results showed that the competitive effect of invasive species highly depends on nutrient availability. In high (eutrophic) nutrient concentrations, plants with a high nutrient uptake ability and growth will often be the better competitors, while in low (mesotrophic) nutrient conditions however, being a better competitor seems of less importance, and being able to withstand low nutrient levels is more crucial. In low nutrient availability building structurally sound or heavily defended tissues may be more imperative in time than high RGR.

We did not find a common response in high or low P availability for species belonging to different growth forms. For the emergent *Ludwigia* species, *L. grandiflora* was the better competitor in both P levels. The species produced the highest biomass and had highest P accumulation in both P levels. Its tissue P% was higher than *L. peploides* in high P, but lower in low P. For Myriophyllids, *M. heterophyllum* was the better competitor in high P, but produced lower biomass and showed highest tissue P of the two species. Nevertheless, the two species accumulated similar amounts of P in their shoots. In low P, *M. heterophyllum* also had lowest biomass and highest tissue P, however there was no clear better competitor. The total P accumulation however was higher for *M. aquaticum*. These results indicate that competition for nutrients is a very complicated matter and that a uniform plant strategy concerning competition for nutrients across growth forms or related species with the same growth form does not exist. Consequently, strategies are species-specific. Fast nutrient uptake and high growth have often been found to be the superior competitive strategies. This seems applicable for the *Ludwigia* species, since the species with the highest growth was the better competitor. However, for the Myriophyllids, the species with the highest nutrient storage and lowest biomass in high P was the better competitor. *M. heterophyllum* allocated more P towards storage than growth compared to *M. aquaticum*. Fast growth, the fitness proxy often used, seems not necessarily the best strategy in every environment.
The effect of low P supply on species’ morphological traits did show a general trend for species with a similar growth form. Both free-floating lemnids showed similar reaction in traits to low P, by increasing the number of fronds per cluster. The emergent Ludwigia species also had similar strategies for coping with low P, both species showed an increase in number of leaves but a reduction in all other traits. It also seemed that the better free-floating and emergent competitor in low P, i.e. *L. punctata* and *L. grandiflora*, mostly had higher trait values than their neighbouring species. We found the submerged species to have different strategies to cope with low P. *M. aquaticum* possessed similar lateral spread and lower branching degree while *M. heterophyllum* showed an opposite pattern. This can be explained by the ability of *M. aquaticum* to grow emergent, therefore investing in vertical growth to quickly reach the water surface.

We can conclude that aquatic plant interactions and the role of nutrient availability is a very complex study and should be further investigated. No generalisations can be made across these three contrasting growth forms. The (potential) effect of invasive species is species specific and context dependent. It does however seem that very similar species (such as the studied lemnids and *Ludwigia*) respond in a similar way to low P. Also, plant performance of rooted plants seems to be more related to higher trait values than trait plasticity.

Given the promising results we obtained from our experiments, we advise a water column P reduction. Our experiments indicated that low P resulted in lower Ludwigia branch numbers, stem length and biomass. Additionally, low P changed both *Myriophyllum* species’ morphology: *M. aquaticum* showed lower branching degree and root/shoot ratio, while *M. heterophyllum* decreased its lateral spread. Even lemnid growth and invasiveness was severely reduced in low P. Our results show low water column P to affect species morphology, which could affect the extensive mat formation and fragmentation rates and enhance control efforts of the species. We believe that in current nutrient-loaded conditions lemnids are the better invaders. P management to low nutrient levels will probably have the least effect on Ludwigia due to its ability of nutrient uptake from the soil, possession of storage structures and difficult removal.

The experiments involving invasive and native species showed promising results for invasive species control. The eutrophic outdoor and mesotrophic indoor competition experiment
between invasive free-floating *Lemna minuta* and native *Lemna minor* showed that in field conditions, the alien and native *Lemna* species performed similarly and there was no better competitor. In the mesotrophic indoor condition however, the native *L. minor* was the better competitor. The species’ RGR were also lower in the indoor experiment. This indicates that the (re)introduction of *L. minor* in *L. minuta* invaded ponds could already have an effect after removal of the invader. However, our indoor experiment showed even more promising results in P level corresponding to mesotrophic condition, revealing higher competitive performance of the native compared to the invasive species. However field experiments in low phosphorus levels are needed to confirm our results.

The indoor experiment between invasive *Myriophyllum aquaticum* and native *M. spicatum* showed the biomass RGR of the latter to always be higher than the former. Even though *M. aquaticum* weight RGR was not affected by the presence of the heterospecific competitor, it did show reduced length RGR in mixtures. *M. spicatum* also produced more and longer branches and showed higher lateral spread. We believe *M. spicatum* to be a good candidate for reintroduction to control the spread of *M. aquaticum* in Belgian water bodies, being able to out-compete and shade control-induced fragments. We recommend a water column P reduction of freshwater ecosystems to reduce the performance and impact of invasive species, and facilitate removal efforts. Additionally for *M. aquaticum* invaded water bodies, we suggest the reintroduction of *M. spicatum* to be incorporated into future management plans, however after small field testing experiments since environmental conditions might influence the results.

Low P will thus have an effect on the performance of invasive species, RGR and traits, and likewise is a priority for water managers, to reduce algal blooms and enhance aquatic ecosystem diversity. Besides P-reduction, an active reintroduction of related native species from neighbouring systems can be considered to enhance the effect of reducing alien cover and reduce the ability of regeneration and recolonization of control-induced fragments of invasive species. Future perspectives therefore include indoor simulation of introduction as performed here, but in similar conditions as the invaded sites. Reintroduction should also be tested in the concerned sited in small patches to confirm indoor results.