J. Aquat. Plant Manage. 51: 1–6

Do patterns of establishment support invasive status of five aquatic plants in New Zealand?

KARSTEN DOLLERUP, TENNA RIIS, AND JOHN S. CLAYTON*

ABSTRACT

In order to improve management of invasive aquatic plants, a Weed Risk Assessment Model (WRAM) on aquatic plant species in New Zealand was introduced in 2000. The model ranks different attributes such as habitat versatility, competitive ability, reproductive output, dispersal mechanisms, range of potential impacts, potential distribution, and resistance to management activities. The overall objective of this study was to determine to what extent relative growth rate, photosynthetic rate, light use efficiency, allocation of biomass, and bicarbonate use efficiency during establishment could explain the rank assigned to 5 species in the WRAM: *Hydrilla verticillata* (Linn.f.) Royle, *Ceratophyllum demersum* L., *Egeria densa* Planchon, *Lagarosiphon major* (Ridley) Moss, and *Elodea canadensis* Michaux. Overall, our results indicate that the parameters measured for 5 invasive species do not support the rank assigned to these same species in the WRAM. Our study investigated only the growth performance of shoots during establishment and thus only a small part of a plant's life cycle. Although a high rate of establishment might result in a high local abundance, as well as a high regional distribution, our study illustrates that this is a single component to determining overall invasive status of the plants. Consequently, this indicates that other parts of the life cycle and ecology also contribute to high rate of invasion by the highly ranked species *H. verticillata* and *C. demersum*.

Key words: *Ceratophyllum demersum*, *Elodea canadensis*, *Egeria densa*, *Hydrilla verticillata*, *Lagarosiphon major*, relative growth rate, photosynthetic rate.

INTRODUCTION

Freshwater ecosystems have numerous invasive plant species, of which some have a huge impact on the ecosystems they invade (Barrat-Segretain 2005). This has been illustrated in New Zealand since the middle of the 19th century, where human colonization has resulted in extensive introductions of plants from Europe (Champion and Clayton 2000). This has led to New Zealand having one of the highest percentages of introduced flora in the world, where estimates are around 50%. More than 50 invasive aquatic plant species are now naturalized, and 75% of these have been imported as ornamental plants for aquariums and garden ponds (Williamson 1996, Champion 1998). The invasion of aquatic species to the freshwater systems of New Zealand has led to an inevitable loss of native biodiversity (Champion and Clayton 2000).

Ceratophyllum demersum L. and 4 species from the family Hydrocharitaceae—*Elodea canadensis* Michaux, *Egeria densa* Planchon, *Hydrilla verticillata* (Linn.f.) Royle, and *Lagarosiphon major* (Ridley) Moss—which are introduced and invasive obligate submerged aquatic species, have the potential to cause widespread problems throughout New Zealand (Howard-Williams 1993, Hofstra et al. 2010). *Ceratophyllum demersum*, *Egeria densa*, and *L. major* constitute the greatest impact on the native vegetation primarily due to their tall, surface-reaching growth form (Clayton and Champion 2006). The indigenous submerged aquatic flora has no canopy-forming species and is generally of low stature, which has made them particularly prone to invasion displacement as they are quickly overgrown and light-excluded (Champion and Clayton 2000). In addition to an advantageous growth form, these 5 species tolerate a wide range of light intensities, which enables them to inhabit a diverse trophic range of water bodies and proliferate throughout the littoral zone (Howard-Williams 1993, Champion and Clayton 2000).

To improve management of invasive aquatic plants, a Weed Risk Assessment Model (WRAM) on aquatic plant species in New Zealand was introduced in 2000 (Champion and Clayton 2000, 2001). The model evaluates different attributes such as habitat versatility, competitive ability, reproductive output, dispersal mechanisms, range of potential impacts, potential distribution, and resistance to management activities. Data and experience from other countries also were included in order to predict the potential spread of already established invasive species with limited distribution so far. The individual scores of all attributes were summed and constituted the final impact rank. The 5 species included in this study are among the 6 highest ranked submerged plant species in the WRAM (Champion and Clayton 2000).

The overall objective of this study was to determine to what extent (1) relative growth rate, (2) photosynthetic rate, (3) light use efficiency, (4) allocation of biomass, and (5) bicarbonate use efficiency during establishment can explain the rank assigned to 5 species in the WRAM, which is: 1, *Hydrilla verticillata*; 2, *Ceratophyllum demersum*; 3, *Egeria densa*; 4, *Lagarosiphon major*; and 6, *Elodea canadensis* (Champion and Clayton 2000, 2001). We hypothesized that plants with the highest invasive impact score also had the highest growth and photosynthetic rates, and a high allocation to green biomass distributed on numerous branches. Moreover, we

*First and second authors: Department of Bioscience, Aarhus University, DK-8000 Aarhus C, Denmark. Third author: National Institute of Water and Atmospheric Research, PO Box 11115, Hamilton, New Zealand. Corresponding author's E-mail: tenna.riis@biology.au.dk.
Received for publication February 25, 2012 and in revised form November 16, 2012.

expected that plants with high impact scores also had high light and bicarbonate use efficiencies. These traits would be an advantage to plants in their ability to colonize habitats and compete with other species with similar growth form. The parameters were measured at 2 light intensities to simulate and evaluate the impact of the different species at shallow and deeper waters in natural lakes.

METHODS

Experimental setup

The experiment was conducted in 2 outdoor, temperature-controlled tanks (width: 1.2 m, length: 2.4 m, depth 0.525 m; for further information see Burnett et al. 2007) at National Institute of Water and Atmospheric Research (NIWA) research facility, Hamilton, New Zealand. The tanks were shaded with mesh nets, allowing penetration of 50 and 25% of ambient light, respectively. The maximal irradiation varied between 300 and 500 µmol photons m^{-2} s^{-1} in the 50% tank, and between 150 and 250 µmol photons m^{-2} s^{-1} in the 25% tank. Shoots in the 50% tank were expected to be light saturated, but limited in the 25% tank. The overall amount of light during the growth period varied in accordance to ambient light conditions and hours of daylight. The tanks were filled with tap water, and water level was controlled automatically and fixed to 40 cm during the experiment. Concentration of nitrogen and phosphorus in the water was 11.5 µg NH_4-N L^{-1} and 5 µg PO_4^{3-}-P L^{-1}. Alkalinity was 0.6 mEq L^{-1} and pH was 7.48 (Riis et al. 2010). These conditions constituted no nutrient limitation to the plants during growth (Hofstra et al. 1999). In order to simulate natural temperature fluctuations during the day, temperature in the tank was controlled automatically and had a 24-h fluctuation between 22 and 27 C.

Plant material of *Elodea canadensis* and *L. major* was collected in the Waikato river system, New Zealand, in March 2009. The samples were stored at 5 C prior to the experiment. Shoots of *H. verticillata*, *C. demersum*, and *Egeria densa* were collected from culture tanks at NIWA research facility, Hamilton, New Zealand. For each of the 5 species, 30 shoots with a length of 20 cm were selected. In order to obtain minimal deviance in biomass among replicates, morphologically similar shoots without branches were selected. Side buds shorter than 1 cm were ignored. The shoots were planted in plastic pots (diameter: 10 cm, height: 8 cm) containing garden topsoil collected at the facility. A layer of fine sand was added to minimize disturbance of sediment during planting and growth in the tank. The bottom of the shoots was embedded into the sediment to avoid detachment. Fifteen shoot replicates of each species were placed in each of the 2 tanks. To avoid potential differences in incoming irradiation, the pots were placed in diagonal lines with equal numbers of species in each column and row (column space: 10 cm, row space: 20 cm).

Plant parameters

Plant parameters were measured before and after the growth period that varied from 14 to 20 d among individuals. To avoid damage on the replicates used in the growth experiment, a number ($n = 20$) of separate replicates were used to measure preexperiment parameters.

Relative growth rate (RGR) and photosynthetic rates (PS) were measured at ambient conditions after the growth period. RGR of the plants was based on total green biomass and calculated by:

$$\mathrm{RGR}\,(\mathrm{d}^{-1}) = \ln(\mathrm{DW}_{\mathrm{final}}) - \ln(\mathrm{DW}_{\mathrm{ini}})/\mathrm{time(d)} \qquad [1]$$

where DW_{final} is the dry weight (g) at the end of the experiment; DW_{ini} (g) is the mean dry weight estimated by the initial shoots; and time is the number of growing days. Rate of photosynthesis was measured on 5 apical shoots of 4 cm. The shoots were selected randomly from different individuals and transferred to airtight glass bottles filled with tank water adjusted to 80% oxygen saturation. The bottles were incubated in the tank for approximately 30 min. Outdoor irradiation was measured as a proxy for light intensity in the tank (> 800 µmol photons m^{-2} s^{-1} ambient light) during incubation. After incubation, the bottles were brought to the laboratory and oxygen concentration was measured with a fiber optic oxygen sensor[1]. The shoots were oven-dried for 24 h, and dry weight (DW) was measured. Photosynthetic rates were calculated using:

$$\begin{aligned}&\text{Rate of photosynthesis } (\mu\text{mol g}^{-1}\text{DW h}^{-1})\\ &\quad = (\mathrm{O2}_{\mathrm{end}}[\mu\text{mol L}^{-1}] - \mathrm{O2}_{\mathrm{blind}}[\mu\text{mol L}^{-1}]) \qquad [2]\\ &\qquad /\text{Bottle Volume (ml)}/\mathrm{DW}_{\mathrm{shoot}}/\Delta t(\text{min}) \times 60/1,000\end{aligned}$$

where $O2_{end}$ is the amount of oxygen in the bottle at the end of the incubation, and $O2_{blind}$ is the amount of oxygen in the bottle at the beginning of the experiment. This was estimated by the use of blind-sample bottles, in which no shoot fragments were present during incubation. Δt is the incubation time. DW_{shoot} is the dry weight of the shoot.

Biomass allocation was characterized as total stem length increase and number of branches. In addition, derived morphology parameters branching degree and lateral spread were calculated according to Hérault et al. (2008). Branching degree describes the number of branches per stem length, and a high value designates a high number of branches per stem length. Lateral spread describes the degree of lateral growth by comparing the total length of the plant to the total length of all side shoots. As with branching degree, a high value is equal to a high degree of lateral to horizontal spread. In general, high values in branching degree and lateral spread are considered competitive compared to low values. Dry weights of plant material were obtained after drying at 80 C for 24 h.

In order to estimate initial dry weight (DW_{ini}) of the shoots, an additional 20 initial-shoots of *Elodea canadensis*, *Egeria densa*, and *L. major* were selected, dried, and weighed prior to the experiment. Due to the highly branched growth form of *H. verticillata* and *C. demersum*, it was not possible to ignore branching in these 2 species and selection was done by morphological similarity and, therefore, *H. verticillata* was excluded from branching degree analysis and *C. demersum* was excluded from branching degree and lateral spread analysis. The fresh weight (FW) of each shoot was weighed prior to planting in order to estimate the DW_{ini} by FW/DW relations.

Light use efficiency (α), maximum photosynthesis (P_{max}), and dark respiration (R_{dark}) were measured on 3 shoots of each species grown at 50% light intensity. Photosynthesis, as a function of light intensity, was calculated by measuring rates of photosynthesis as oxygen exchange at different light intensities. Shoots were incubated in a 145-ml closed Perspex chambers in N- and P-free medium with an alkalinity of 0.85 mEq L^{-1} (Smart and Barko 1985). The medium was mixed continuously with a magnetic stirrer. The chamber was placed in a water bath at a constant temperature (19 C). Oxygen was measured by a fiber optic oxygen sensor[1] calibrated to 0 and 100% O_2. To obtain respiration rates and light response curve, 1 shoot was placed inside the chamber in darkness. Measurements were performed at light intensities of 25, 38, 64, 105, 170, 280, 400, 910, and 1200 μmol photons m^{-2} s^{-1}. Oxygen development was logged every 10 s, and intervals lasted for 15 min. A light response curve (O_2 production as a function of light intensity) was made for each shoot tested. Light use efficiency (α) was estimated by linear regression on the initial slope of the curve. All shoots used in this part of the experiment were dried at 80 C for 24 h, and the dry weight was determined. All results are expressed on a dry mass basis.

Concentration of chlorophyll *a* in the plants used for the light–response curves was determined by selecting 3 shoot fragments of each plant from both tanks. Samples were freeze-dried in the laboratory; chlorophyll was extracted with ethanol, and the absorbance of the extract at 470.0, 648.6, and 664.2 nm was measured on a spectrophotometer (Lichtenthaler 1987).

Inorganic carbon use efficiency of the plants was determined by pH-drift experiment as described in Allen and Spence (1981) and Maberly and Spence (1983). Apical shoots of 5 cm were incubated in glass bottles with a standard Barko solution (Smart and Barko 1985) with an alkalinity of 0.85 mEq L^{-1} and an O_2 concentration of 80%. Glass bottles were placed in a water bath at 20 C with an irradiance of 250 μmol photons m^{-2} s^{-1} and stirred for 16 h, with pH measured subsequently.

Data analysis

Differences in response parameters between species were tested using 1-way ANOVA ($P < 0.05$) within each of the 2 light intensities separately. Differences between species were performed with an ANOVA Tukey test. Data were transformed to approach normal distribution of data when necessary.

RESULTS AND DISCUSSION

Growth rate (Figure 1) varied between the 5 species at both 25% light intensity (ANOVA; $F_{4,70} = 78.55$, $P < 0.001$) and at 50% light intensity (ANOVA; $F_{4,68} = 63.09$, $P < 0.001$). At 50% light *Elodea canadensis* had the highest growth rate and at 25% light *Egeria densa* had the highest growth rate (Figure 1).

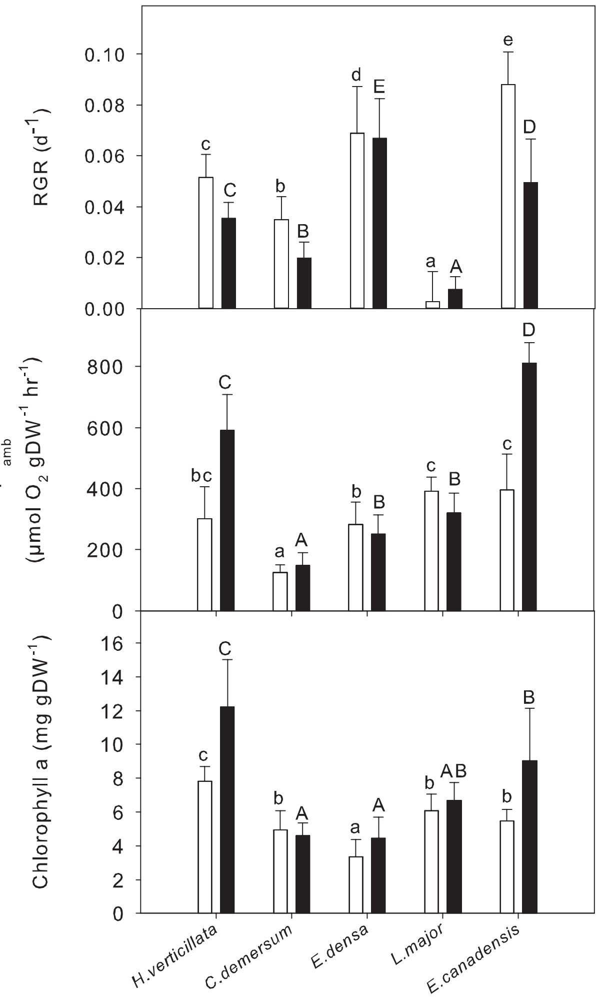

Figure 1. Relative growth rates and ambient photosynthetic rates of *Elodea canadensis*, *Egeria densa*, *Hydrilla verticillata*, *Ceratophyllum demersum*, and *Lagarosiphon major* grown at 50% (white) and 25% (black) ambient light intensity. Plants were grown 2 to 3 wk in outdoor tanks prior to measurements (see Methods for further description). Letters indicate significant differences between species in 50% (lowercase letters) and 25% (capital letters). Chlorophyll *a* content in the plants are shown in the lower panel. For all panels mean values (± SD, $n = 9$–15) are shown.

Rate of photosynthesis (P_{amb}) also differed between the species within both 50% light (ANOVA; $F_{4,20} = 9.21$, $P < 0.001$) and 25% light (ANOVA; $F_{4,19} = 63.31$, $P < 0.001$). In 50% light the highest photosynthetic rate was attained by *Elodea canadensis* and *L. major*, whereas *C. demersum* had the lowest rate (Figure 1). In 25% light, the highest photosynthetic rate was attained by *Elodea canadensis* and *H. verticillata*, whereas *C. demersum* also had the lowest rate (Figure 1).

The highest increase in stem length was seen in *Elodea canadensis* and *C. demersum* at high light intensity ($F_{3,14} = 17.55$, $P < 0.001$) and *Elodea canadensis*, *C. demersum*, and *Egeria densa* at low light intensity ($F_{3,14} = 8.82$, $P < 0.001$), as only *L. major* had a significantly lower stem length than the other species (Figure 2).

Elodea canadensis had the highest number of branches at high light conditions ($F_{3,14} = 16.42$, $P < 0.001$), while *Elodea canadensis* and *H. verticillata* had the highest number of branches at low light intensity ($F_{3,14} = 40.34$, $P < 0.001$).

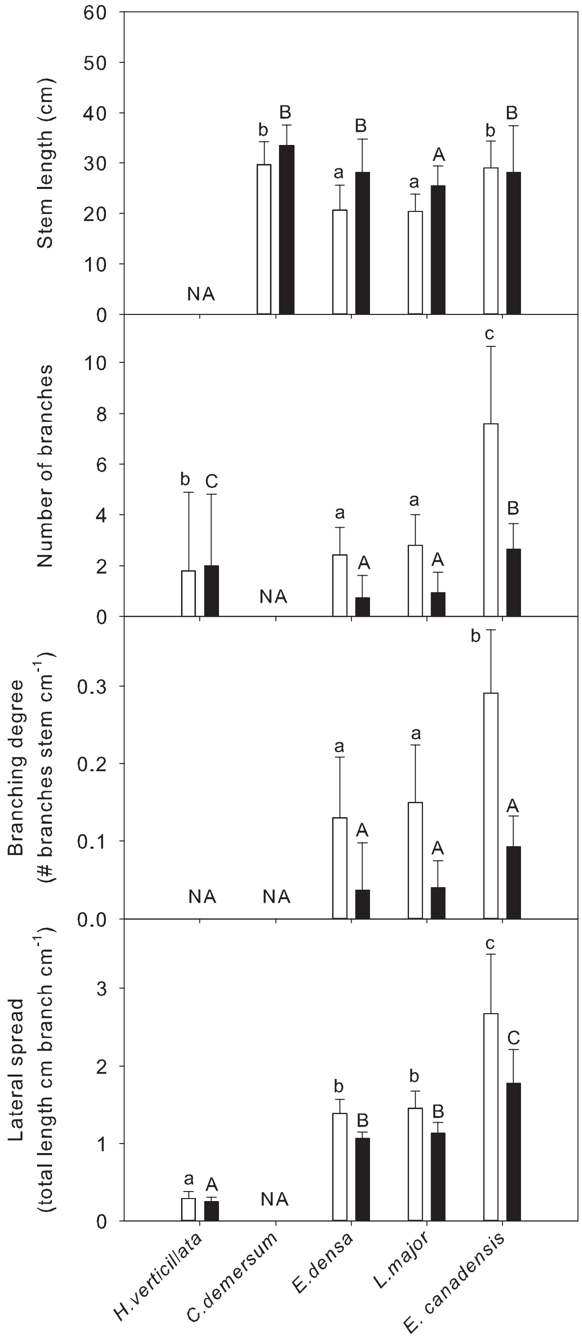

Figure 2. Morphological parameters of *Elodea canadensis*, *Egeria densa*, *Hydrilla verticillata*, *Ceratophyllum demersum*, and *Lagarosiphon major* grown at 50% (white) and 25% (black) ambient light intensity. Plants were grown 2 to 3 wk in outdoor tanks prior to measurements (see Methods for further description). Letters indicate significant differences between species in 50% (lowercase letters) and 25% (capital letters). For all panels mean values (± SD, $n = 9$–15) are shown. NA = not applicable.

Egeria densa and *L. major* had the lowest number of branches at both light intensities. *Elodea canadensis* also had the highest branching degree at high light intensity. Lateral spread differed between all 4 species at both high ($F_{3,14} = 227.6$, $P < 0.001$) and low ($F_{3,14} = 361.1$, $P < 0.001$) light intensity. At both light intensities, *Elodea canadensis* had the highest lateral spread, while *H. verticillata* had the lowest.

Light use efficiency was highest in *Elodea canadensis*, *H. verticillata*, and *C. demersum* ($F_{4,4} = 3.99$, $P < 0.05$; Table 1). Maximum rate of photosynthesis was highest in *L. major* ($F_{4,4} = 4.50$, $P < 0.05$) but did not vary between the remaining 4 species. The respiration rate ranged from 22 to 149 μmol O_2 g DW^{-1} h^{-1} and was highest for *Elodea canadensis*.

All 5 species were able to push the pH value above 10, indicating that all species were efficient in utilizing bicarbonate as the inorganic carbon source. *Hydrilla verticillata* and *Elodea canadensis* had the highest pH and *C. demersum* the lowest at the end of the drift experiment (Table 2).

Beforehand, we expected that plants with highest invasive impact score in the WRAM (see ranking in Table 1) would have high growth and photosynthetic rate, high allocation to green biomass distributed on numerous branches, and high light and bicarbonate use efficiencies. Relative growth rates and rates of photosynthesis of the 5 species did not correspond to ranks assigned to the species in WRAM. With the exception of *L. major*, the growth rates ranged between 0.003 and 0.088 d^{-1} (50% light) and 0.007 and 0.067 d^{-1} (25% light) and were within the range of freshwater angiosperms proposed by Nielsen et al. (1996). The growth rates for *L. major* were much lower than the relative growth rates found by James et al. (2006) in a field study. Overall, *Elodea canadensis* had the highest relative growth rate (0.088 d^{-1}) in shoots incubated at 50% light intensity, which is similar to the rate of 0.086 d^{-1} obtained in aquarium studies by Nielsen and Sand-Jensen (1991). In the plants incubated at 25% light intensity *Egeria densa* had the highest growth rate (0.067 d^{-1}), but this did not differ significantly from the rate of *Egeria densa* in 50% light intensity (0.069 d^{-1}). These results indicate that *Elodea canadensis* is faster at establishing in waters with high light conditions, whereas *Egeria densa* is better at establishing in deeper waters with lower light intensities. This result is supported by Champion and Clayton (2000), who found that *Egeria densa* is able to grow deeper than *Elodea canadensis* and *L. major*, which ultimately has led to the displacement of these 2 species in several water bodies of New Zealand.

There was no direct correspondence between growth rate and photosynthetic rate. This is not surprising because photosynthesis is only one of several factors controlling growth in plants (Körner 1991). The photosynthetic rate was not necessarily expected to be expressed in the relative growth rate of the plant as respiration rates can be highly variable between species. For example, the relatively high ambient photosynthesis rate of *L. major* in high light did not result in a correspondingly high growth rate, which is most likely due to high respiration rates in this plant. The higher ambient photosynthetic rate in *Elodea canadensis* and *H. verticillata* in low light conditions is assumed to be a result of the higher chlorophyll *a* content in those plants.

There was no correlation between the morphological traits of the plants and the rank of the 5 species. In the WRAM, *H. verticillata* and *C. demersum* are ranked as the most aggressive invasive species and therefore we would expect these 2 species to be the best performers in a growth experiment, as expressed by the longest stem length, the highest number of branches, the highest branching degree,

TABLE 1. LIGHT USE EFFICIENCY (MEAN ± SD, $n = 5$), AND MAXIMAL RATE OF PHOTOSYNTHESIS IN SHOOT FRAGMENTS OF *ELODEA CANADENSIS*, *EGERIA DENSA*, *H. VERTICILLATA*, *C. DEMERSUM*, AND *L. MAJOR* GROWN AT 50% AMBIENT LIGHT INTENSITY. LETTERS INDICATE SIGNIFICANT DIFFERENCES BETWEEN SPECIES (ANOVA; $P < 0.05$). THE RANKING OF THE SPECIES IN WEED RISK ASSESSMENT MODEL (WRAM) (CHAMPION AND CLAYTON 2000, 2001) IS ALSO GIVEN. DW = DRY WEIGHT.

	WRAM ranking	Light use efficiency µmol O_2 g DW^{-1} h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$	Maximum photosynthesis µmol O_2 g DW^{-1} h^{-1}	Dark respiration µmol O_2 g DW^{-1} h^{-1}
Hydrilla verticillata	1	9.88 ± 1.03^{b}	$1{,}026 \pm 192.1^{a}$	110.9 ± 19.8^{a}
Ceratophyllum demersum	2	12.14 ± 4.08^{b}	$1{,}250 \pm 222.2^{ab}$	82.6 ± 30.8^{a}
Egeria densa	3	4.95 ± 1.14^{a}	966.6 ± 10.0^{a}	21.7 ± 14.4^{ab}
Lagarosiphon major	4	8.56 ± 2.03^{ab}	$1{,}563 \pm 163.7^{b}$	149.2 ± 132.3^{a}
Elodea canadensis	6	10.05 ± 1.03^{b}	$1{,}092.5 \pm 277.8^{a}$	142.6 ± 107.1^{b}

and the highest lateral spread. All 5 species in this study had very similar total stem length. In traits related to the different aspects of the plants' ability to occupy and expand their distribution in the initial phase, *Elodea canadensis* was the most favorable in this study. This could be of competitive significance during establishment where space is limited and competition is high, as plants occupying most space in the initial phase are also most likely to have a higher chance of being dominant later in the growth season. This result is supported by a similar experiment showing that growth morphology of *Elodea canadensis* compared to *Egeria densa* and *L. major* was the most competitive in terms of beneficial morphological traits during establishment (Riis et al. 2012).

The ability of these 5 species to efficiently utilize available light and bicarbonate did not correspond to the rank assigned in the WRAM either. Although light use efficiency was higher for *H. verticillata* and *C. demersum*, it was not significantly different from *Elodea canadensis*, which was the lowest ranked species in WRAM. Cavalli et al. (2012) showed that *C. demersum* is able to sustain an equally high level of bicarbonate use efficiency across a range of alkalinities in the growth medium; whereas, bicarbonate use efficiency of *L. major* and *Egeria densa* was highest for plants incubated at low alkalinity. Hence, even though we do find correspondence in bicarbonate use efficiency and WRAM rank of species, the ability of *C. demersum* to sustain high bicarbonate use efficiency in a broad range of growth conditions could potentially support the establishment of this species in a broader range of habitat types.

Overall, our results indicate that the parameters measured for 5 invasive species do not support the rank assigned to these same species in WRAM. For example, the growth of whole plant beds and their ability to out-shade the other species by concentrating their biomass in the upper part of the water column in the established phase of their life cycle can be particularly important in determining the extent of invasion (Howard-Williams et al. 1987). On the other hand, species ranking in WRAM is based on a wide spectrum of plant traits, including tolerance to environmental variables (e.g., water temperature, trophic status), reproduction strategy and propagule dispersal mechanisms, alterations to invaded habitats, and resistance to management. Our study investigated only the growth of shoots during establishment and thus only a small part of a plant's life cycle. Although a high rate of establishment might result in a high local abundance, as well as a high regional distribution, our study illustrates that this is a single component to determining overall invasive status of the plants. Consequently, this indicates that other parts of the life cycle and ecology also contribute to the extent of invasion by the highly ranked species *H. verticillata* and *C. demersum*.

TABLE 2. FINAL pH (MEAN ± SD, $n = 5$) MEASURED AFTER pH DRIFT EXPERIMENT. APICAL SHOOTS OF 5 CM WERE INCUBATED IN GLASS BOTTLES WITH A STANDARD BARKO SOLUTION WITH AN ALKALINITY OF 0.85 MEQ L^{-1} AND AN O_2 CONCENTRATION OF 80%. GLASS BOTTLES WERE PLACED IN A WATER BATH AT 20 C WITH AN IRRADIANCE OF 250 µMOL PHOTONS M^{-2} S^{-1} AND STIRRED FOR 16 H.

Species	End pH
Hydrilla verticillata	10.50 ± 0.04^{b}
Elodea canadensis	10.47 ± 0.14^{b}
Egeria densa	10.35 ± 0.09^{ab}
Lagarosiphon major	10.31 ± 0.06^{ab}
Ceratophyllum demersum	10.00 ± 0.23^{a}

SOURCES OF MATERIALS

[1]Oxy-4 Micro; PreSens Precision Sensing GmbH, Regensburg, Germany.

ACKNOWLEDGEMENT

We thank The Danish Natural Science Research Council for financial support.

LITERATURE CITED

Allen ED, Spence DHN. 1981. The differential ability of aquatic plants to utilize the inorganic carbon supply in fresh water. New Phytol. 89:269–283.

Barrat-Segretain MH. 2005. Competition between invasive and indigenous species: Impact of spatial pattern and developmental stage. Plant Ecol. 180:153–160.

Burnett DA, Champion PD, Clayton JS, Ogden J. 2007. A system for investigation of the temperature responses of emergent aquatic plants. Aquat. Bot. 86:187–190.

Cavalli G, Riis T, Baattrup-Pedersen A. 2012. Bicarbonate use in three invasive aquatic plants. Aquat. Bot. 98:57–60.

Champion PD. 1998. Freshwater Aquatic Weeds in New Zealand. National Institute of Water and Atmospheric Research Consultancy Report to Department of Conservation, Hamilton, New Zealand. 78 pp.

Champion PD, Clayton JS. 2000. Border Control for Potential Aquatic Weeds. Stage 1: Weed Risk Model. Science for Conservation 141. Department of Conservation, Wellington, New Zealand. 48 pp.

Champion PD, Clayton JS. 2001. A weed risk assessment model for aquatic weeds in New Zealand, pp. 194–202. In: R. H. Groves, F. D. Panetta, and J. G. Virtue (*eds.*). Weed Risk Assessment. CSIRO Publications, Melbourne. 244 pp.

Clayton JS, Champion P. 2006. Risk assessment for submerged weeds in New Zealand hydroelectrical lakes. Hydrobiologia 570:183–188.

Hérault B, Bornet A, Trémolières M. 2008. Redundancy and niche differentiation among the European invasive *Elodea* species. Biol. Invasions 10:1099–1107.
Hofstra DE, Champion P, Clayton, JS. 2010. Predicting invasive success of *Hydrilla verticillata* (L.f.) Royle in flowing water. Hydrobiologia 656:213–219.
Hofstra DE, Clayton J, Green JD, Auger M. 1999. Competitive performance of *Hydrilla verticillata* in New Zealand. Aquat. Bot. 63:305–324.
Howard-Williams C. 1993. Processes of aquatic weed invasions: The New Zealand example [plenary address]. J. Aquat. Plant Manage. 31:17–21.
Howard-Williams C, Clayton JS, Coffey BT, Johnstone IM. 1987. Macrophyte invasions. In: A. B. Viner (*ed.*). Inland Waters of New Zealand. DSIR Bull. 241, Wellington, New Zealand. 494 pp.
James CS, Eaton JW, Hardwick K. 2006. Responses of three invasive aquatic macrophytes to nutrient enrichment do not explain their observed field displacements. Aquat. Bot. 84:347–353.
Körner CH. 1991. Some often overlooked plant characteristics as determinants of plant growth: A reconsideration. Funct. Ecol. 5:162–173.
Lichtenthaler HK. 1987. Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. Methods Enzymol. 148:331–382.
Maberly SC, Spence DHN. 1983. Photosynthetic inorganic carbon use by fresh water plants. J. Ecol. 71:705–724.
Nielsen SL, Enríquez S, Duarte CM, Sand-Jensen K. 1996. Scaling maximum growth rates across photosynthetic organisms. Funct. Ecol. 10:167–175.
Nielsen SL, Sand-Jensen K. 1991. Variation in growth rates of submerged rooted macrophytes. Aquat. Bot. 39:109–120.
Riis T, Lambertini C, Olesen B, Clayton J, Brix H, Sorrell BK. 2010. Invasion strategies in clonal aquatic plants: Are phenotypic differences caused by phenotypic plasticity or local adaptation? Ann. Bot. 106:813–822.
Riis T, Olesen B, Clayton JS, Lambertini C, Brix H, Sorrell BK. 2012. Growth and morphology in relation to temperature and light availability during the establishment of three invasive aquatic plant species. Aquat. Bot. 102:56–64.
Smart RM, Barko JW. 1985. Laboratory culture of submerged freshwater macrophytes on natural sediments. Aquat. Bot. 21:251–263.
Williamson M. 1996. Invasions. Ecography 22:5–12.