

Effect of minor water depth treatments on competitive effect and response of eight wetland plants

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Abstract Two facets of plant competition, competitive effect (CE) and competitive response (CR), can be used to explain plant community composition but our understanding of abiotic factors that may differentially affect species' competitive ability is incomplete. We tested whether water-depth affected CE (ability to suppress neighbour) and CR (avoid suppression from neighbour), and if so whether there was consistency in the rank order of both measures of competition under different water depth treatments. CE and CR were measured and compared for eight wetland plant species (*Carex lurida*, *Carex tribuloides*, *Elymus virginicus*, *Juncus tenuis*, *Lythrum salicaria*, *Phalaris arundinacea*, *Rumex orbiculatus* and *Verbesina alternifolia*) at five different water-depth treatments (+2, 0, -2, -4 and -6 cm relative to the substrate). Overall, we found that mean CE was at its lowest value at +2 cm water depth, while mean CR was highest at +2 and -6 cm compared to the other water treatments. There was a significant variation of CE between species, with a defined hierarchical order. Pairwise CE rank order correlations between water depth treatments were significant

but CR correlations were generally not. There was no significant correlation between CE and CR. CE was significantly correlated with biomass of species grown alone but CR was not. These findings indicate that CE may be used as a general measure to predict wetland species performance, and thus community assemblage, across a range of water depths. CR does not seem to demonstrate predictable patterns between species and water depth treatments. Our results suggest that competition intensity may be reduced in a non-resource-stressed flooded environment by a reduction in CE, but the corresponding increase in CR could dampen this effect on overall competitive ability.

Keywords Competitive effect and response · Freshwater wetlands · Non-resource stress · *Phalaris arundinacea* · Phytometer · Water depth

Introduction

In freshwater wetlands, the depth and duration of the water table largely determines wetland type and function (Brinson 1993; Mitsch and Gosselink 2000; Keddy and Fraser 2000; De Steven and Toner 2004). Water-level fluctuation can cause distinct zonation patterns among plants (Keddy and Fraser 2000; van Eck et al. 2004) and determine a specific assemblage of wetland plants (Weiher and Keddy 1995). Biomass accumulation and survivorship of individual wetland

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plants grown at different water depths can vary significantly between species, but when water level is consistently higher than soil level (i.e., flooded) plant growth and survivorship is generally limited (Visser et al. 2000; Kercher and Zedler 2004; van Eck et al. 2004; Fraser and Karnezis 2005). Another important factor contributing to the distribution and composition of freshwater wetland plant communities is competition (Wilson and Keddy 1986; Lenssen et al. 1999; Budelsky and Galatowitsch 2000; Brose and Tielborger 2005). There is limited information on what effect water depth may have on competitive interactions between freshwater wetland plants (Grace and Wetzel 1981; Wetzel and van der Valk 1998; Sher and Marshall 2003; Lenssen and de Kroon 2005). Grace and Wetzel (1981) demonstrated that competition maintained distinct zonation patterns between *Typha latifolia* and *Typha angustifolia* along a water-depth gradient, and Sher and Marshall (2003) found that *Populus deltoides* seedlings had a stronger competitive influence on *Tamarix ramosissima* at relatively lower water levels, suggesting that competitive ability may be dependent on water levels.

Many competition indices have been developed in an attempt to understand and predict plant community patterns (see Weigelt and Jolliffe 2003 for review). Competitive effect (ability to suppress other individuals) has been used to determine patterns in plant communities (Austin et al. 1985; Gaudet and Keddy 1995; Keddy and Shipley 1989; Aarssen and Keogh 2002; Groves et al. 2003; Fraser and Keddy 2005). Competitive effect, though, is only one of the two aspects of competitive ability. The second way competitive ability of an individual can be measured is competitive response: ability to avoid being suppressed (Goldberg and Fleetwood 1987; Goldberg and Landa 1991; Wilson 1994; Keddy et al. 1998). So far, it has proved difficult to identify plant traits that correspond with competitive response (Keddy et al. 1994; Goldberg 1996; Carlyle and Fraser 2006).

A long-running debate in plant ecology concerns whether the intensity of competitive interactions, or the degree to which neighbours reduce plant growth, changes along a gradient of productivity, resource supply or non-resource stress (Grime 1973, 2001; Newman 1973; Tilman 1988; Grace and Tilman 1990; Campbell et al. 1991; Goldberg et al. 1999; Keddy 2001; Callaway et al. 2002; Rajaneimi 2003). In nutrient-poor or otherwise abiotically 'stressed'

habitats, Grime (1973) asserted that the intensity of competition should be weakest; whereas Newman (1973) countered that competition should be intense (particularly belowground) in unproductive environments (Tilman 1988; Grace 1991; Rajaneimi 2003; Craine 2005). Keddy et al. (2000) measured competitive effect (CE) of 26 wetland plants under two different nutrient regimes and found that the CE of plants grown in high-nutrient conditions was greater compared to plants grown in low-nutrient conditions; thus supporting Grime's theory. Cahill et al. (2005) measured CE and CR of 11 genotypes of *Arabidopsis thaliana* at high and low soil nutrient treatments and found that both CE and CR were higher at high rates of fertilization. Nutrient supply rate is one process that can potentially influence competitive outcomes—non-resource factors are also important contributors. Furthermore, CE and CR may act independently (Goldberg and Landa 1991; Keddy et al. 1994; Cahill et al. 2005), such that the traits affecting neighbours may be different from the traits to avoid competition (Carlyle and Fraser 2006).

The purpose of our study was to examine how water depth, in this case a non-resource parameter, interacts with plant competitive ability. We tested competitive effect (CE) and competitive response (CR) of eight wetland species when paired with the phytometer *P. arundinacea* at five different water depths (−6, −4, −2, 0, +2 cm relative to the soil surface). The following hypotheses were tested: (1) Mean CE and CR will be affected by changes in water depth; (2) There will be differences between species in their response to CE and CR with respect to water depth; (3) CE hierarchies will be consistent across the five water level treatments but CR hierarchies will not; (4) There will be no correlation between CE and CR, but CE will be positively correlated with biomass.

Materials and methods

Competitive effect of eight wetland species (Table 1) was measured according to their ability to suppress a phytometer; in this case, *Phalaris arundinacea*. We selected *P. arundinacea* because it has been shown to be a strong competitor at different water levels (Wetzel and van der Valk 1998). Competitive response of the same eight species was measured as

Table 1 Plant species grown in pair-wise combination with the phytometer *Phalaris arundinacea*

Scientific name	Common name	Life form
<i>Carex lurida</i> Wahl.	Shallow Sedge	Sedge
<i>Carex tribuloides</i> Wahl.	Bristlebract Sedge	Sedge
<i>Elymus virginicus</i> L.	Virginia Wildrye	Grass
<i>Juncus tenuis</i> Willd.	Path Rush	Sedge
<i>Lythrum salicaria</i> L.	Purple Loosestrife	Forb
<i>Phalaris arundinacea</i> L.	Canary Reed Grass	Grass
<i>Rumex orbiculatus</i> A. Gray	Great Water Dock	Forb
<i>Verbesina alternifolia</i> L.	Wingstem	Forb

Nomenclature follows Crow and Helquist (2000)

the ability to avoid being suppressed by the phytometer. Six of the species were selected because they are native to Northeast Ohio and are found growing together in freshwater marshes (Crow and Helquist 2000). The other two species, *P. arundinacea* and *Lythrum salicaria*, were selected because they are also commonly found growing in the same freshwater marshes as the six native species but are non-native invasives (Apfelbaum and Sams 1987, Thompson et al. 1987). These eight species were also used in a previous study to measure the effects of minor water depth on biomass accumulation and survivorship (Fraser and Karnezis 2005).

The phytometer approach was used to assess competitive ability of the eight plant species rather than a full pairwise design (Gaudet and Keddy 1988; Weigelt and Jolliffe 2003). While the pairwise design increases the information on competitive interactions, space and time constraints limit the number of species that can be included in a full pairwise design. A common phytometer reduces the number of tests needed for a measure of competitive ability and, because it is a standardized method, allows for future testing on additional species.

Plants were grown in a 475-ml pot filled with a 3:1 mixture of topsoil and sand. Holes were drilled at the base to allow for drainage. The 475-ml pot was placed within a 1050-ml container that had holes for water drainage at the appropriate position relative to the substrate surface of the 475-ml pot. Five different water depth treatments included 6, 4, 2 cm below the surface, at the soil surface, and 2 cm above the soil surface. The 475-ml cup was 14 cm in height; therefore the distances of water level to the bottom of the cup were 8, 10, 12, 14 and 16 cm from lowest to highest water depth. Fraser and Karnezis (2005) found that the percent of plant survivorship of five of

the eight species at water depths greater than 2 cm above the soil surface was zero, and therefore water depth treatments above 2 cm were not included in the experiment reported here. Eight species tested across five water levels, plus five replicates, resulted in a total of 200 pots. In addition, each of the eight species (including the phytometer, *Phalaris arundinacea*) was grown alone (a single individual) at all five water levels, with five replicates each, to be used as a necessary reference for the determination of competitive effect and competitive response.

The seeds were germinated on moist filter paper in petri dishes. Equal sized seedlings that were not more than 2 days old were selected and planted in their respective pots. The timing of germination differed slightly between plant species. The phytometer (*P. arundinacea*) was one of the first plants to germinate, therefore, separate petri dishes of *P. arundinacea* were established for germination every 2 days to ensure that the size and age of *P. arundinacea* seedlings were the same as the species it was paired with. In each pot, three plants of one neighbour species were paired with one *P. arundinacea* plant such that the phytometer was in the centre surrounded by the neighbour species. After a period of 2 weeks in which the plants were allowed to establish, the appropriate water depth treatment was applied. The plants were placed in a temperature, humidity and photo-regulated growth chamber, with an approximate temperature of 22°C, 40–60% humidity, and a 16-h photoperiod using 1,000 watt bulbs averaging a photometer reading of 221.5 $\mu\text{mol}/\text{m}^2/\text{s}$ (± 12.4 SD). A standardized amount of nutrients, 30 ml of a double concentration Rorison's solution (3.36 mg N. 1.86 mg P) (Hendry and Grime 1993), was added to the plants on a weekly basis consistent with an earlier study using the same species and growing conditions (Fraser

and Karnezis 2005) and the pots were watered daily with de-ionized water to maintain appropriate water depths. Holes at the appropriate water depth allowed for overflow so that extra water would flow out.

The pots were arranged in a Latin square design consisting of 25 trays set up in a 5 × 5 layout of rows, alternating among the five water depth treatments. Each tray contained a random arrangement of eight pots with the neighbour species in combination with the phytometer and eight pots with the eight species grown alone.

When the plants started to show signs of senescence, a period of 4 months, all plants were measured for height, harvested, oven-dried, weighed and the above and below-ground biomass determined for each plant. The mean biomass was determined for the phytometer and neighbour species at each water level. Competitive effect and competitive response was determined for each of the different species in each of the different water depth treatments.

Competitive effect was calculated as:

$$CE_n = 1 - P_{\text{mix}}/P_{\text{alone}}$$

and competitive response was calculated as:

$$CR_n = N_{\text{mix}}/N_{\text{alone}}$$

where CE_n is the competitive effect of the neighbour species; P_{mix} is the biomass of the phytometer when grown with the neighbour species in mixture; P_{alone} is the biomass of the phytometer when grown alone; CR_n is the competitive response of the neighbour species; N_{mix} is the mean biomass of the three neighbours when grown with the phytometer species in mixture; N_{alone} is the biomass of the neighbour when grown alone (Goldberg and Fleetwood 1987; Weigelt and Jolliffe 2003).

Our experimental design allows us to measure CE and CR simultaneously (Goldberg and Fleetwood 1987), however the tests are not entirely independent. The values used to calculate CE are not used to calculate CR, and vice versa, but the P_{mix} and N_{mix} are grown together and are therefore dependent measures.

A two-way, fixed-effect analysis of variance was performed to determine significance among water depth treatments and plant species with respect to CE and CR of total biomass. In addition, Tukey HSD was

used for pairwise comparison between treatments. The results were tested for block effect using a general linear model in Systat (1998) by column and row; no significant block effect was detected. A linear regression was applied to CE and water level, while a non-linear regression was applied to CR and water level. Spearman rank correlation coefficients were calculated to determine correlations between rank order among target species and correlation with regards to CE and CR at each water depth. Linear regressions were applied to test the relationship between CE and CR, CE and biomass and CR and biomass. The data were tested for heteroscedasticity and were found to have equal variances. Statistical analyses were done using Systat (1998).

Results

The mean biomass of the phytometer (*Phalaris arundinacea*) grown alone was lowest at the +2 cm water depth and highest at −6 cm (Fig. 1). The other seven species showed variation in biomass between water depth treatments but the lowest biomass was always at the +2 cm water depth (Fig. 1). In general, *P. arundinacea*, *Lythrum salicaria* and *Rumex orbiculatus* had the highest biomass and *Elymus virginicus* and *Verbesina alternifolia* had the lowest biomass.

The mean competitive effect (CE) for the eight species combined was significantly lower in the +2 cm water depth treatment compared to −4 cm water depth (Fig. 2; Table 2). The mean competitive response (CR) was significantly higher at +2 cm and −6 cm water depth compared to the −4 cm level treatment (Fig. 2a; Table 2). A linear regression of the effect of water level on CE and a non-linear regression of water level on CR were statistically significant ($P < 0.05$) but both models explain little of the variation; 0.09 R^2 for CE and a 0.11 R^2 for CR.

The mean CE and CR for each species differed significantly (Table 2); however there was greater variation in CE between species compared to CR. *Lythrum salicaria* had the highest overall mean CE, followed by *R. orbiculatus*. *Verbesina alternifolia* and *Juncus tenuis* had the lowest mean CR values among the eight target species. CR between species was relatively similar except for *R. orbiculatus*, which had a significantly higher CR compared to the other species (Fig. 3).

Fig. 1 Mean biomass of eight wetland species grown alone without neighbours at five different water depth treatments. Error bars represent SE +1

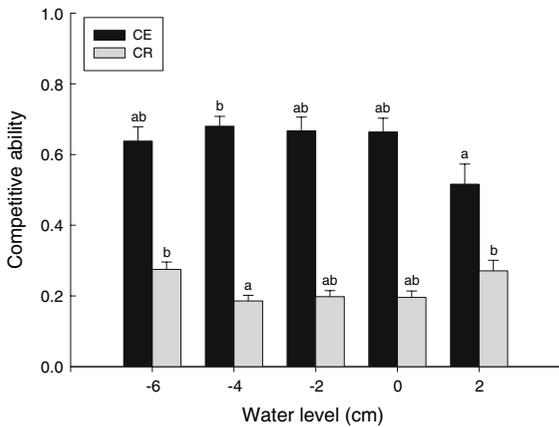
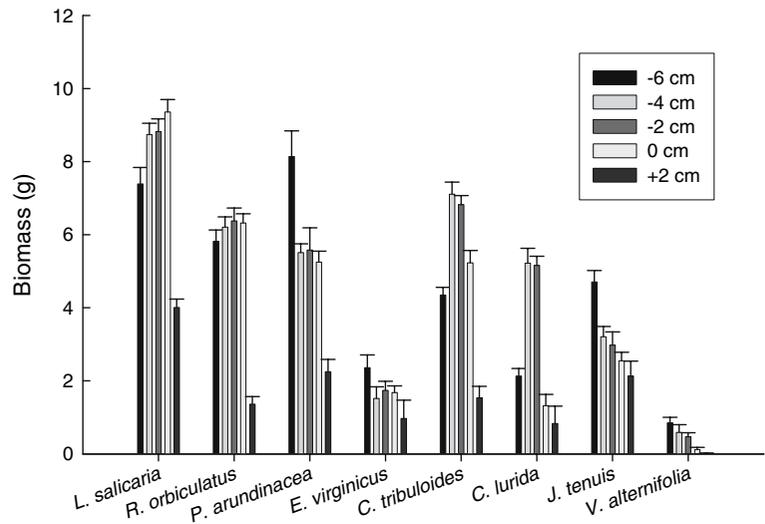


Fig. 2 Mean competitive effect (CE) and response (CR) for eight wetland plants grown at five water depth treatments. Error bars represent SE +1. Bars sharing the same letter are not significantly different using Tukey’s HSD

Although the summary of main effects by water depth and species showed significant patterns, there was also a significant interaction effect between water depth and species (Fig. 3). With respect to each

species, CE differed significantly among water depth treatments for four of the eight species: *Rumex orbiculatus*, *Carex tribuloides*, *Elymus virginicus* and *V. alternifolia* (Fig. 3). In each case, the flooded treatment (+2 cm) significantly reduced CE compared to at least one of the water depth treatments less than 0 cm relative to the soil level. In all cases except for *E. virginicus* there were no significant differences in CE between water depths of –6, –4, –2 and 0 cm. The CE of *E. virginicus* at –6 cm water depth was significantly higher than the CE at –4 and 0, in addition to +2 cm.

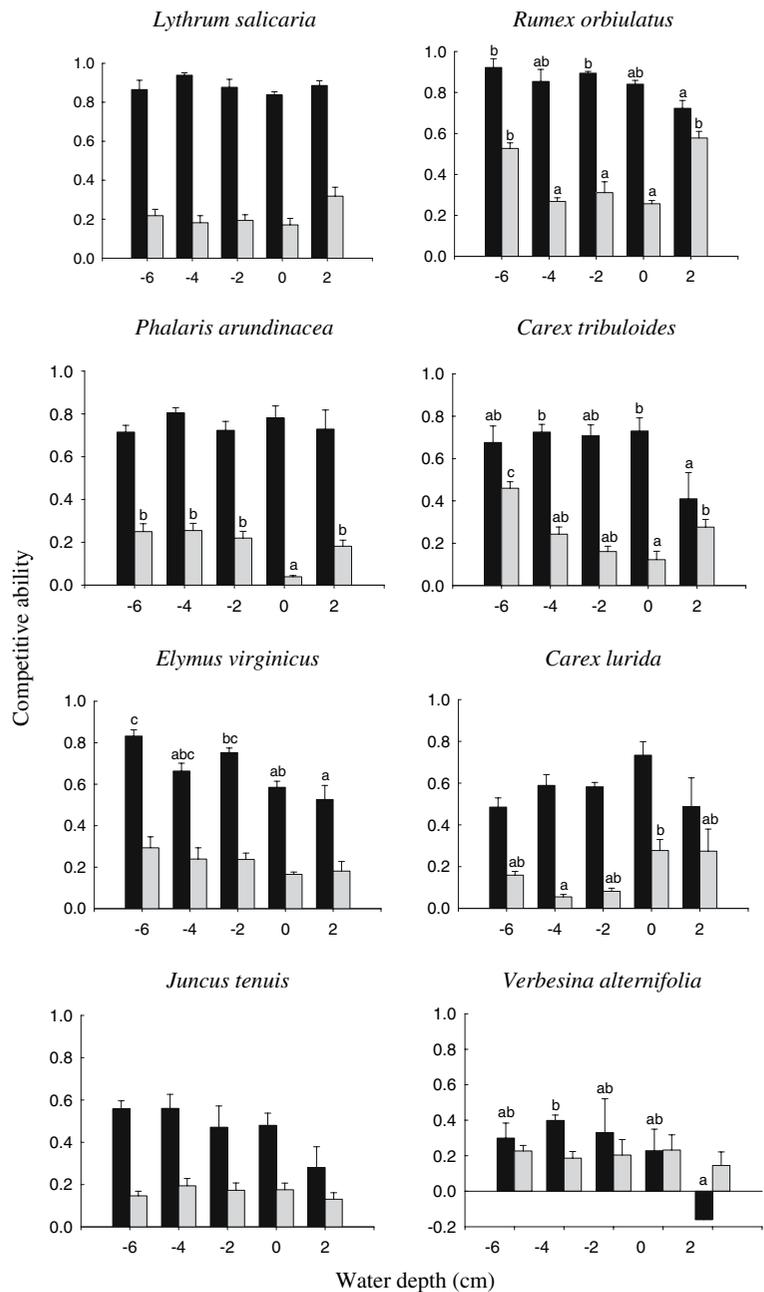
The CR of each species also differed significantly among water depth treatments for four of the eight species, including *R. orbiculatus*, *P. arundinacea*, *C. tribuloides* and *C. lurida* (Fig. 3). CR was generally highest at the extreme ends of the water depth gradient: +2 cm or –6 cm.

The correlation in rank order of CE between water depth treatments was significantly similar for all water depth treatment combinations except for the +2 and –6 cm pair and the 0 and –6 cm pair (Table 3).

Table 2 Results from two 2-way ANOVAs for competitive effect (CE) and competitive response (CR) of total biomass with species and water depth as the independent factors
Error mean square for CE was 0.024 and 0.009 for CR

Source	Degrees freedom	CE		CR	
		F-ratio	P	F-ratio	P
Species	7	7.45	<0.001	8.39	<0.001
Water depth	4	47.81	<0.001	14.11	<0.001
Species × water depth	28	2.32	0.001	4.06	<0.001
Error	160				

Fig. 3 Mean competitive effect (CE) and response (CR) of five water depth treatments by plant species. Error bars represent SE +1. Bars sharing the same letter are not significantly different using Tukey's HSD



Generally, the three species with the highest CE values were *L. salicaria*, *R. orbiculatus* and *P. arundinacea*; while the two with the lowest were *V. alternifolia* and *J. tenuis* (Fig. 3). In contrast, the correlation in rank order of CR between water depth treatments was only significant for three pairs: +2 and -6 cm; -2 and -4 cm; and -2 and -6 cm (Table 3). The only species with any consistent ranking was *R.*

orbiculatus, which had a consistently high CR value across all water depths (Fig. 3).

There was no significant correlation between CE and CR (Fig. 4). A significant positive effect was determined between the biomass of plants grown alone and CE (Fig. 4). However, there was no effect between the biomass of plants grown alone and CR (Fig. 4).

Table 3 Spearman rank correlation coefficient, r_s , for competitive effect and competitive response at each water depth treatment

Competitive effect					
Water level	+2 cm	0 cm	–2 cm	–4 cm	–6 cm
+2 cm	1.000				
0 cm	0.905***	1.000			
–2 cm	0.833***	0.810**	1.000		
–4 cm	0.929***	0.905***	0.929***	1.000	
–6 cm	0.690	0.714	0.905**	0.786*	1.000
Competitive response					
Water level	+2 cm	0 cm	–2 cm	–4 cm	–6 cm
+2 cm	1.000				
0 cm	0.643	1.000			
–2 cm	0.000	–0.381	1.000		
–4 cm	–0.095	–0.476	0.905***	1.000	
–6 cm	0.595*	0.048	0.619*	0.381	1.000

The asterisk indicates levels of significance, where * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Discussion

CE and CR affected by water level

We found that both facets of competitive ability, competitive effect (CE) and competitive response (CR), could be affected by minor changes in water depth, and that there were differences between species in their response to CE and CR, thus, supporting our first two hypotheses. It has been argued that competitive ability can also be analyzed according to its intensity versus its importance: intensity being the direct effect of one individual on another, importance being the proportional effect of one individual on another with respect to other habitat characteristics (Welden and Slauson 1986; Grace 1991; Brooker et al. 2005). According to this criterion, the CE and CR competition indices that we have calculated are a measurement of competition intensity.

Mean CE of the combined species was lowest in the flooded water depth treatment (+2 cm), while mean CR at +2 cm was often the highest. A possible explanation for a reduction of CE in flooded conditions is that this water regime imposed a stressful condition that inhibited plant growth (Lenssen et al. 1999; Sher and Marshall 2003; Miller and Zedler 2003; Kercher and Zedler 2004; Fraser and Karnezis 2005). For example, Fraser and Karnezis (2005) manipulated water levels at

the same 2 cm increments and found that 12 of 14 wetland plants tested had their lowest biomass and survivorship at water depths greater than 0 cm. This same inhibition of plant growth may also indirectly have caused the increase in CR values at +2 cm water depth. That is, with a reduction of biomass in a plant grown at high water level, the suppression of its neighbour may have been comparatively minimal.

Although there was a mean reduction in CE under flooded conditions when species were pooled, at the individual species level the CE between water depths did not differ for all species. CE was reduced in four of the target species tested (*R. orbiculatus*, *C. tribuloides*, *E. virginicus* and *V. alternifolia*), but the CE of the remaining four target species remained statistically unchanged across the five different water depth treatments. Of the four species with a reduction in CE, *R. orbiculatus* and *V. alternifolia* are both relatively large, leafy forbs, while *E. virginicus* is a grass and *C. tribuloides* a sedge. There is no apparent general commonality to suggest why these species would have reduced CE values under flooded conditions except that they all had significantly reduced biomass when grown alone in flooded conditions.

Competitive response was significantly higher in +2 cm and –6 cm water depth treatments, meaning that plants were likely to respond to competition most effectively at the extreme ends of the water

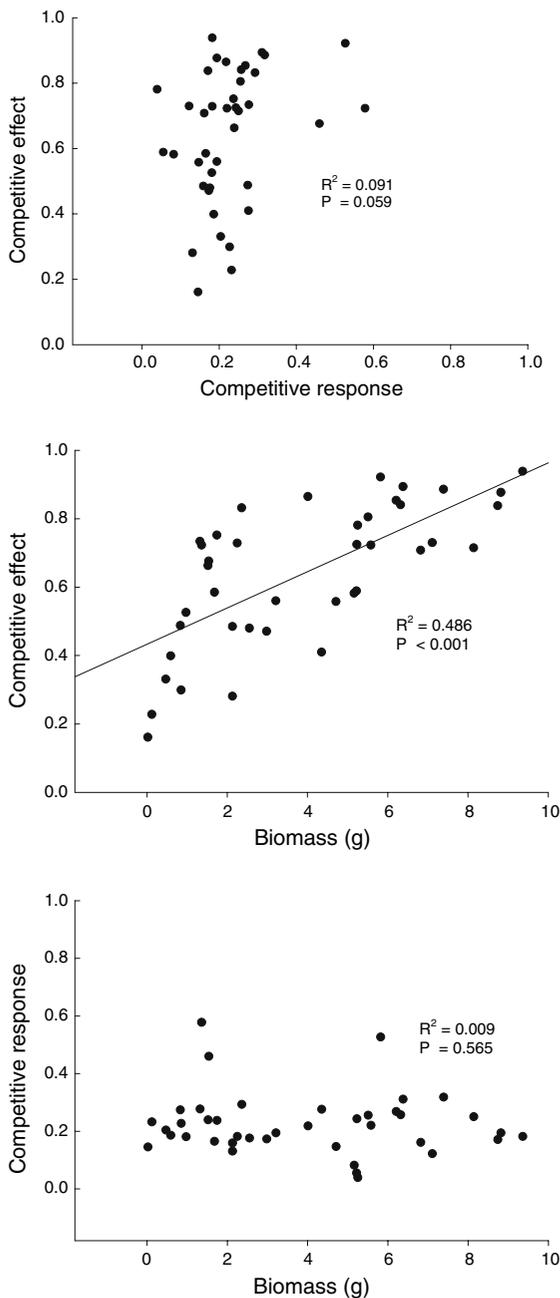


Fig. 4 Linear regression of: (Top) competitive effect (CE) and competitive response (CR); (Middle) CE and biomass of species grown alone; and (Bottom) CR and biomass of species grown alone

depth gradient. At the species level, this pattern was significant for *R. orbiculatus* and *C. tribuloides*. *Phalaris arundinacea* and *C. lurida* also had significant differences in CR between water depth treatments. Competitive ability would therefore

appear to be affected by flooding not only through a reduction in CE but also through an increase in CR. A reduction in CE at +2 cm suggests that the intensity of competition is reduced in flooded, non-resource stressed environments (Lenssen and de Kroon 2005; Pennings et al. 2005), a result that corresponds with the reduction in competition intensity found in comparatively unproductive resource-stressed environments (Austin et al. 1985; Callaway et al. 2002; Fraser and Keddy 2005). However, an increase in CR at the +2 cm flooded treatment potentially offsets this apparent reduction in competition intensity. The reduction in biomass accumulation caused by flooding reduces CE but seems to increase CR. This balance does not appear to be equal (CE = 0.52 and CR = 0.27 at +2 cm, Fig. 2) but the fact that these two aspects of competitive ability can negatively interact potentially reduces or complicates the degree to which competitive ability is affected by environmental conditions (MacDougall and Turkington 2004; Craine 2005). It should be noted that the measurement of CE was of three neighbour individual affects on one target phytometer, while CR was the effect of one target on the mean value of three individuals. This difference may have contributed to a lower CR value compared to the CE measured value.

Consistency of CE and CR hierarchies

Competitive ability hierarchies, which seem to be pervasive in plant communities (Keddy and Shipley 1989; Shipley and Keddy 1994; Keddy et al. 2000; Suding and Goldberg 2001; Emery et al. 2001), were consistent with respect to CE across the five water depth treatments, thus supporting our third hypothesis. The CE hierarchy established in this study changed little at different water depths suggesting that the integrity of these hierarchies was not affected by water level, despite the wide variation between species in their CE values. Similar results have been found with high and low fertility treatments (Keddy et al. 2000; Emery et al. 2001). Such results suggest that a good competitor at one end of an environmental gradient remains a good competitor at the other end, but that the intensity of competitive interactions differs. The intensity of competition is high when environmental conditions are favourable and low

when the environmental conditions limits plant growth (e.g. Grime 1979; Austin et al. 1985; Bertness and Shumway 1993; Fraser and Keddy 2005).

For CR, there was no pattern in rank order correlation between species across water depth treatments. The only consistency between water depth treatments was that *Rumex orbiculatus* had the highest CR value, except at 0 cm where it was ranked second highest. Therefore, *R. orbiculatus* represents a unique species that is consistently high in CE and CR, which may be partially due to its ability to grow fast. Both carex species had high CR values at +2 and 0 cm water depths, but very low CR values at the lower water depths. Obviously, CR can be differentially altered by water depth with species exhibiting varied responses.

CE and CR correlations with plant biomass

Life history traits have been shown to be strongly correlated with competitive ability (Turnbull et al. 2004; Fynn et al. 2005). In particular, CE is correlated with plant biomass (Gaudet and Keddy 1988; Keddy et al. 2002). Large, leafy, fast-growing plants with high biomass generally have the highest CE value. This relationship was supported by our results, thus supporting our fourth hypothesis, but it only explained approximately 50% of the variation. Therefore, properties other than CE must be important in structuring natural communities; for example, different regenerative life-history traits such as dispersal ability and propagule longevity (Grubb 1977; Thompson et al. 1996).

Competitive response was not correlated with biomass. The lack of correlation between CE and CR suggests that CR has a different set of associated plant traits (Keddy et al. 1998; Cahill et al. 2005; Carlyle and Fraser 2006). Carlyle and Fraser (2006) found that seed weight, height and time to reach maximum height were all traits correlated with CR, but that there were different CR plant strategies to avoid competition. For example, seed weight was a plant trait correlated with the ‘escape’ CR strategy, whereas time to reach maximum height was correlated with the ‘persist’ CR strategy (Carlyle and Fraser 2006). Since the species in our experiment are from different CR strategy groups it is not surprising that our general measure of CR across species is not associated with one single plant trait.

Conclusions

The creation of plant zonation patterns in wetlands, both freshwater and marine, is generally caused by a trade-off between competitive ability and stress tolerance (Grace and Wetzel 1981; Pennings and Callaway 1992; Sher and Marshall 2003; Pennings et al. 2005). In this study, flooded water levels (+2 cm) often had a negative impact on CE, but a positive effect on CR. Perhaps the positive response of CR is a reflection of a reduction in competition intensity under stressed environments. Our results suggest that water table levels (a non-resource stress) can affect competitive ability in plants. Despite the opposite reaction between CE and CR at high water levels, relative CE was generally greater than CR values suggesting that overall competitive ability does change along environmental gradients thus supporting Grime’s theory (Grime 1979). More study is needed to define the plant attributes that are associated with CE and CR and to further define competitive abilities in plants according to measures of intensity and importance.

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References

- Aarssen LW, Keogh T (2002) Conundrums of competitive ability in plants: what to measure? *Oikos* 96:531–542
- Apfelbaum SI, Sams CE (1987) Ecology and control of reed canary grass (*Phalaris arundinacea* L.). *Nat Areas J* 7:9–17
- Austin MP, Groves RH, Fresno L et al (1985) Relative growth of six thistles along a nutrient gradient with multispecies competition. *J Ecol* 73:667–684
- Bertness MD, Shumway SW (1993) Competition and facilitation in marsh plants. *Am Nat* 142:718–724
- Brinson MM (1993) Changes in the functioning of wetlands along environmental gradients. *Wetlands* 13:65–74
- Brooker R, Kikvidze Z, Pugnaire FI et al (2005) The importance of importance. *Oikos* 109:73–70
- Brose U, Tielborger K (2005) Subtle differences in environmental stress along a flooding gradient affect the importance of inter-specific competition in an annual plant community. *Vegetatio* 178:51–59
- Budelsky R, Galatowitsch SM (2000) Effects of water regime and competition on the establishment of a native sedge, *Carex lacustris*, in restored wetlands. *J Appl Ecol* 37:971–985

- Cahill JF, Kembel SW, Gustafson DJ (2005) Differential genetic influences on competitive effect and response in *Arabidopsis thaliana*. *J Ecol* 93:958–967
- Callaway RM, Brooker RW, Choler P et al (2002) Positive interactions among alpine plants increase with stress. *Nature* 417:844–848
- Campbell BD, Grime JP, Mackey JML et al (1991) The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. *Func Ecol* 5:241–253
- Carlyle CN, Fraser LH (2006) A test of three juvenile competitive response strategies. *J Veg Sci* 17:11–18
- Craine JM (2005) Reconciling plant strategy theories of Grime and Tilman. *J Ecol* 93:1041–1052
- Crow GE, Helquist CB (2000) Aquatic and wetland plants of northeastern North America. Volume 1. The University of Wisconsin Press, Madison, Wisconsin
- De Steven D, Toner MM (2004) Vegetation of upper coastal plain depression wetlands: environmental templates and wetland dynamics within a landscape framework. *Wetlands* 24:23–42
- Emery NC, Ewanchuk PJ, Bertness MD (2001) Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. *Ecology* 82:2471–2485
- Fraser LH, Karnezis JP (2005) A comparative assessment of seedling survival and biomass accumulation for fourteen wetland plant species grown under minor water-depth differences. *Wetlands* 25:520–530
- Fraser LH, Keddy PA (2005) Can competitive ability predict structure in experimental plant communities. *J Veg Sci* 16:571–578
- Fynn RWS, Morris CD, Kirkman KP (2005) Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. *J Ecol* 93:384–395
- Gaudet CL, Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. *Nature* 334:242–243
- Gaudet CL, Keddy PA (1995) Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology* 75:280–291
- Goldberg DE (1996) Competitive ability: definitions, contingency and correlated traits. *Phil Tran R Soc Lond B* 351:1377–1385
- Goldberg DE, Fleetwood L (1987) Competitive effect and response in four annual plants. *J Ecol* 75:1131–1143
- Goldberg DE, Landa K (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *J Ecol* 79:1013–1030
- Goldberg DE, Rajaniemi T, Gurevitch J et al (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* 80:1118–1131
- Grace JB (1991) A clarification of the debate between Grime and Tilman. *Func Ecol* 5:583–587
- Grace JB, Tilman D (1990) Perspectives on plant competition. Academic Press, New York
- Grace JB, Wetzel RG (1981) Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *Am Nat* 118:463–474
- Grime JP (1973) Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347
- Grime JP (1979) Plant strategies and vegetation processes. John Wiley and Sons, London
- Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties, 2nd edn. John Wiley, Chichester
- Groves RH, Austin MP, Kaye PE (2003) Competition between Australian and introduced grasses along a nutrient gradient. *Aust Ecol* 28:491–498
- Grubb PJ (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol Rev* 52:107–145
- Hendry GAF, Grime JP (1993) Methods in comparative plant ecology. Chapman and Hall, London
- Keddy PA (2001) Competition, 2nd edn. Kluwer, Dordrecht
- Keddy P, Fraser LH (2000) Four general principles for the management and conservation of wetlands in large lakes: the role of water levels, nutrients, competitive hierarchies and centrifugal organization. *Lakes Reserv Res Managt* 5:177–185
- Keddy P, Fraser LH, Wisheu IC (1998) A comparative approach to examine competitive response of 48 wetland plant species. *J Veg Sci* 9:777–786
- Keddy PA, Gaudet C, Fraser LH (2000) Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. *J Ecol* 88:413–423
- Keddy P, Nielsen K, Weiher E et al (2002) Relative competitive performance of 63 species of terrestrial herbaceous plants. *J Veg Sci* 13:5–16
- Keddy PA, Shipley B (1989) Competitive hierarchies in herbaceous plant communities. *Oikos* 54:234–241
- Keddy PA, Twolan-Strutt L, Wisheu IC (1994) Competitive effect and response ranking in 20 wetland plants: are they consistent across three environments? *J Ecol* 82:635–643
- Kercher SM, Zedler JB (2004) Flood tolerance in wetland angiosperms: a comparison of invasive and noninvasive species. *Aqua Bot* 80:89–102
- Lenssen JPM, de Kroon H (2005) Abiotic constraints at the upper boundaries of two *Rumex* species on a freshwater flooding gradient. *J Ecol* 93:138–147
- Lenssen JPM, Menting FBJ, van der Putten WH et al (1999) Effects of sediment type and water level on biomass production of wetland plant species. *Aqua Bot* 64:151–165
- MacDougall A, Turkington R (2004) Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *J Ecol* 92:422–434
- Miller RC, Zedler JB (2003) Responses of native and invasive wetland plants to hydroperiod and water depth. *Plant Ecol* 167:57–69
- Mitsch WJ, Gosselink JG (2000) Wetlands, 3rd edn. John Wiley and Sons, New York
- Newman EI (1973) Competition and diversity in herbaceous vegetation. *Nature* 244:310
- Pennington SC, Callaway RM (1992) Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology* 73:681–690
- Pennington SC, Grant M, Bertness MD (2005) Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. *J Ecol* 93:159–167

- Rajaniemi TK (2003) Explaining productivity–diversity relationships in plants. *Oikos* 101:449–457
- Sher AA, Marshall DL (2003) Seedling competition between native *Populus deltoides* (Salicaceae) and exotic *Tamarix ramosissima* (Tamaricaceae) across water regimes and substrate types. *Am J Bot* 90:413–422
- Shipley B, Keddy PA (1994) Evaluating the evidence for competitive hierarchies in plant communities. *Oikos* 69:340–345
- Suding KN, Goldberg DE (2001) Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. *Ecology* 82:2133–2149
- SYSTAT (1998) SYSTAT® 8.0 Statistics. SPSS Inc., Chicago, IL
- Thompson K, Hillier SH, Grime JP et al (1996) A functional analysis of a limestone grassland community. *J Veg Sci* 7:371–380
- Thompson DQ, Stuckey RL, Thompson EB (1987) Spread and impact and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. *U.S. Fish Wildlife Serv Fish Wildlife Res* 2:1–55
- Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, NJ
- Turnbull LA, Coomes D, Hector A et al (2004) Seed mass and the competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. *J Ecol* 92:97–109
- van Eck WHJM, Van de Steeg HM, Blom CWPM et al (2004) Is tolerance to summer flooding correlated with distribution patterns in river floodplains? A comparative study of 20 terrestrial grassland species. *Oikos* 107:393–405
- Visser EJW, Bogemann GM, Van de Steeg HM et al (2000) Flooding tolerance of *Carex* species in relation to field distribution and aerenchyma formation. *New Phytol* 148:93–103
- Welden CW, Slauson WL (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. *Q Rev Biol* 61:23–44
- Weigelt A, Jolliffe P (2003) Indices of plant competition. *J Ecol* 91:707–720
- Weiher E, Keddy P (1995) The assembly of experimental wetland plant communities. *Oikos* 73:323–335
- Wetzel PR, van der Valk AG (1998) Effects of nutrient and soil moisture on competition between *Carex stricta*, *Phalaris arundinacea*, and *Typha latifolia*. *Plant Ecol* 138:179–190
- Wilson SD (1994) Initial size and the competitive responses of two grasses at two levels of soil nitrogen: a field experiment. *Can J Bot* 72:1349–1354
- Wilson SD, Keddy PA (1986) Species competitive ability and position along a natural stress/disturbance gradient. *Ecology* 67:1236–1242