Mechanisms producing plant zonation along a water depth gradient: a comparison with the exposure gradient

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A 15-month field experiment was performed in the emergent zone of a freshwater riverine marsh along the Ottawa River, Canada, to determine whether the mechanisms producing plant zonation along the exposure gradient of freshwater shorelines also accounted for the zonal pattern along the water depth gradient. Three species (*Carex crinita, Acorus calamus*, and *Typha angustifolia*) were chosen, having contiguous distributions along a gradient of water depth. Ramets of each were planted within and beyond the field distributions of each, both in the presence and in the absence of the natural vegetation of each site. Although there was strong evidence of growth depression due to the presence of neighbouring plants (interference), there was no evidence of a differential response between species, between sites on the water depth gradient, or a combination of the two. As well, thee was no evidence that the water depth gradient represents a general gradient of decreasing productivity; rather, there was a qualitative change below the low-water level. These results are contrary to previously published results obtained along the exposure gradient of freshwater shorelines, where the effects of plant interference do vary both along the exposure gradient and among species.

Key words: plant zonation, interference, water depth, exposure gradient.

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Cette étude avait pour but de déterminer si les mécanismes qui produisent des zonations de végétation le long d'un gradient d'exposition d'une ligne riveraine d'eau douce peuvent aussi expliquer le patron zonal le long d'un gradient de profondeur de l'eau. A cette fin, les auteurs ont conduit une expérimentation d'une durée de 15 mois dans la zone d'émergence d'un marais d'eau douce riverain le long de la rivière Ottawa, au Canada. Ils ont choisi trois espèces (*Carex crinita, Acorus calamus* et *Typha angustifolia*); il s'agit d'espèces qui ont des distributions contiguës le long d'un gradient de profondeur de l'eau. Des boutures de chacune des espèces ont été plantées à l'intérieur et à l'extérieur de la distribution naturelle de chacune d'elle, aussi bien en présence qu'en absence de la végétation naturelle de chaque site. Bien qu'on observe une forte dépression de la croissance sous l'influence des plantes voisines (interférence) il n'y a pas de preuve qu'il y ait des réactions différentes entre espèces, entre les sites le long du gradient de profondeur ou en combinant les deux. De plus, il n'y pas de preuve que le gradient de profondeur de l'eau constitue un gradient général de productivité décroissante; au contraire il y a un changement qualitatif au dessous du bas niveau de l'eau. Les résultats contredisent ceux qui ont déjà été publiés sur ce sujet, lesquels ont été obtenus le long de gradients d'exposition de lignes riveraines d'eau douce, là où les effets de l'interférence entre les plantes varient à la fois le long du gradient d'exposition et entre les espèces.

Mots clés : zonation végétale, interférence, profondeur de l'eau, gradient d'exposition.

[Traduit par la rédaction]

Introduction

A recurring theme in plant ecology is the pattern of species' distributions along environmental gradients and the mechanisms producing such distributions (Clements 1916; Gleason 1939; Whittaker 1967; Tilman 1982, 1988; Grime 1979; Austin 1990). Shipley and Keddy (1987) described the distributional patterns of emergent macrophytes along a water depth gradient and found that the observed distributional patterns were not consistent with either of the two most influential models in community ecology: the community-unit and individualistic models. They concluded that hypotheses in community ecology must explicitly differentiate between mechanisms and patterns. In this paper we present the results of a 15-month field experiment, conducted along a water depth gradient in the same marsh as described in Shipley and Keddy (1987), that was designed to differentiate between the zonal patterns of wetland species along the gradient of water depth and the mechanisms producing such patterns.

Wilson and Keddy (1986*a*, 1986*b*) proposed an explanation for the zonal paterns found along an exposure gradient in wetlands, based on the work of Grime (1979). The exposure gradient involved correlated changes in productivity and density-independent mortality along the shoreline at a constant water depth, with one extreme consisting of sandy, exposed, wave-swept shores and the other extreme consisting of sheltered bays with organic soil and lacking wave action (Keddy 1982). In Grime's (1979) model, competitive interactions between plants are weak and relatively unimportant in determining local distributions in environments having either high levels of density-independent mortality (disturbance) or low levels of productivity (stress). As either the levels of disturbance or of stress decreases, and therefore as the amount of aboveground biomass increases, the degree of interspecific competition increases in intensity and importance. Furthermore, Grime (1979) assumes a trade-off between the ability to compete with other plant species and the ability to survive and grow in disturbed or stressful environments. Thus, Wilson and Keddy (1986*a*, 1986*b*) suggested that wetland plant species normally occurring at either the stressful or the disturbed ends of the exposure gradient are dominant not because they are the best competitors in such environments, nor because they are physiologically adapted to grow and reproduce best in such environments, but rather because they are the only species who can physiologically tolerate such extreme conditions. On the other hand, wetland plants that normally occur at the least stressful and least disturbed ends of the exposure gradient are dominant in these environments because they are the best competitors. A number of field studies involving terrestrial vegetation (Sharitz and McCormick 1972; Del Morel 1983; Gurevitch 1986; Reader and Best 1989; Reader 1990) have also reported results similar to those obained by Wilson and Keddy (1986*a*, 1986*b*). This explanation for the zonal patterns observed along environmental gradients therefore requires both a monotonic gradient of increasing productivity and biomass (decreasing stress) and a monotonic gradient of increasing intensities of competition.

Few comparable field experiments have been conducted along the water depth gradient (Buttery and Lambert 1965; Grace and Wetzel 1981). In studies of the competitive displacement of *Typha angustifolia* L. by *Typha latifolia* L. along a water depth gradient, Grace and Wetzel (1981) concluded that the pattern displayed by these two species was largely the result of a deep-water refuge for the competitively inferior *T. angustifolia*. This mechanism is similar to the one occurring along the exposure gradient. The purpose of this study was therefore to determine whether the explanation for the zonal patterns of wetland plants along the exposure gradient, described above, also applies to the zonal patterns of wetland plants along the water depth gradient.

Methods

Since the term competition evokes so many different connotations, it is important to define what is meant by this term. Harper (1977, p. 151) differentiates between competition as a mechanistic definition, in which the decrease in fitness (usually growth) of a plant is due to the consumption of a limiting resource by another plant, and competition as a phenomenological definition, termed interference, in which the decrease in the fitness of a plant is due to the presence of another plant without any necessity that the decrease in fitness be due to differential consumption of a limiting resource. In this paper, we will use the term interference to emphasize the phenomenological measure of competition that we and most other workers use. Similarly, the "intensity" of interference refers to the amount of decrease in the growth of a plant due to the presence of other plants.

To determine whether the mechanism producing zonation along the exposure gradient also occurs along the water depth gradient, we conducted the following experiment. Ramets of three species (*Carex crinita* Lam., *Acorus calamus* L., and *T. angustifolia* L.) having contiguous distributions along a gradient of water depth in a freshwater marsh were grown at various positions along this water depth gradient and their growth during the experiment was determined, both in the absence and in the presence of the natural vegetation occurring at that position of the water depth gadient.

Description of the study site

The field site was a freshwater marsh located near Breckenridge, Quebec, Canada, along the Ottawa River (45°48′00″N, 45°57′30″W). The distribution of all emergent macrophytes along the water depth gradient between the average yearly maximum and minimum water levels, and the resulting zonation, can be found in Shipley and Keddy (1987), who also provide details of the sampling procedure. This marsh has a very gently, monotonically sloping shoreline with the emergent plant community extending for over 200 m along the water depth gradient. It is located in a sheltered bay and has fertile organic soil.

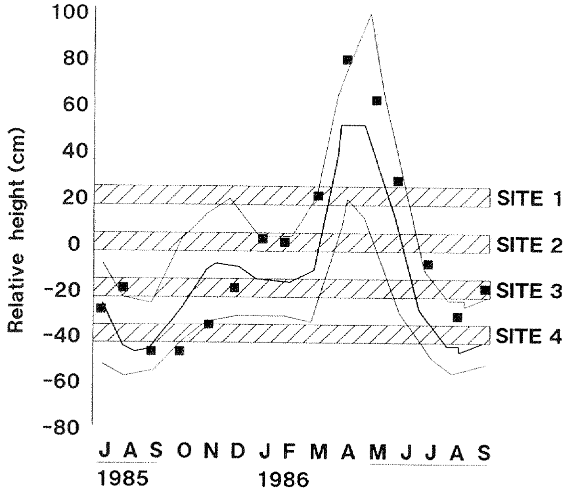

FIG. 1. The thick, solid line shows the average monthly water levels in Breckenridge Bay over the last 20 years. The thin solid lines show 1 SD above and below the monthly averages. The solid squares show the actual mean monthly water levels during the experiment, starting in July 1985 and continuing until September 1986. The four experimental sites are shown relative to the water depth gradient. The months are shown along the bottom and those underlined mark the growing season.

Since field experiments are always open to the criticism of being conducted in unusual environmental conditions, the average monthly water levels in this marsh over the last 20 years as well as one standard deviation are shown (Fig. 1), based on the records at a monitoring station (No. 02KF005) located within the same drainage basin; the standard zero mark is equivalent to a geodetic height of 58.40 m (Water Survey of Canada). Also shown are the water levels during the experiment, from July 1985 to September 1986. As can be seen, water levels during the experiment were typical of the long-term trends.

The boundaries of the species distributions along the water depth gradient were not randomly located but were clustered at two points of the gradient (Shipley and Keddy 1987). The distributions of the first group of species all ended at around the average May 20 water level (approximately 20 cm in Fig. 1). *Carex crinita* was one of the dominant species in this group. A second, smaller, group of species, of which *A. calamus* L. is dominant, had distributions straddling the water depth gradient, with upper limits at around the average June 1 water level and lower limits at around the average June 20 water level. In the third group of species, which began their distribution at around the average July 20 water level, *T. angustifolia* L. was dominant.

Transplant experiment

Four positions were chosen along the water depth gradient and experimental sites were established at each position. The first site was established within the field distribution of *C. crinita*, the second site within that of *A. calamus*, the third within that of *T. angustifolia*, and the fourth site lower on the shore than the lower distributional limits of all three test species. This last site was dominated by *Sparganium eurycarpum* Englm. and was below the average yearly low water level. The substrate at this site was continuously submerged during the experiment. Therefore, each site was in progressively deeper portions of the marsh, had a different species composition, and was inundated for progressively longer periods of the growing season.

Thirty quadrats were established (20 × 40 cm) at each site. Each quadrat was separated from the next 50 cm, was divided into two (20 × 20 cm) subplots, and was surrounded by a plastic barrier sunk 10 cm into the substrate to prevent rhizomes from growing into or out of each subplot. One of the two subplots was randomly chosen and all aboveground biomass was removed (removal treatment). The 30 quadrats in the site were divided into 10 groups of 3 quadrats each. Within each group each of the three test species was randomly assigned to one of the quadrats using a random number table. One ramet of the chosen species was planted in the centre of each subplot in a small hole (5 cm diameter). In the case of subplots containing the natural vegetation of the site, the 5-cm diameter sod containing the vegetation was replaced around the transplanted ramet. There was minimal damage to surrounding vegetation. This was therefore a three-factor experiment: (*i*) species, (*ii*) site, and (*iii*) treatment, i.e., removal of neighbours. Since only aboveground biomass was removed in the treatment subplots, we cannot claim that all potential interference effects were absent, but they were substantially reduced.

Ramets of the three test species were collected from within the same local region of the marsh from July 7 to July 9, 1985. The ramets of each species were chosen to be of approximately the same (within-species) size and the rhizome of each was cut to a standard length. Roots were not immediately washed of soil; instead, the ramets were placed in water for up to 6 days in the shade, after which most soil had fallen off naturally. This was done to reduce damage to the fine roots. Plastic tags were placed around the rhizome of each ramet so that they could be identified at the end of the experiment. Ramets of the appropriate species were then randomly assigned to quadrats.

Ramets were planted during 9–12 July 1985 following a randomized planting schedule to avoid the confounding effects of planting time. During the first 2 weeks following planting, the transplants were shaded and also misted approximately five times daily to prevent transplant shock; only 6 out of 240 plants died during this period (all within a few days of transplanting) and these were replaced. No other plants showed signs of transplant shock. All quadrats were monitored, cleared subplots were weeded of surrounding biomass regularly during the experiment and the condition of the test plants noted, including evidence of herbivory that was due almost exclusively to muskrats. The experiment ran from July 1985 until September 1986, a total of 15 months; the test plants therefore experienced the natural conditions of all four seasons.

Since the plastic barriers prevented rhizomes from leaving the quadrats and the rhizomes of the ramets were tagged, we could harvest both aboveground and belowground biomass. However, some root material was undoubtedly lost. Therefore, our values probably underestimate the final biomass of the test plants.

Statistical analysis

The description of the design of the experiment, given above, shows that there are three sources of random variation arranged in the form of a split-split plot. Analyses of variance, performed using GENSTAT IV (Numerical Algorithms Group 1983) recognized this structure explicitly. No ramets survived in the deepest site (site 4) and so this site was excluded from the analysis. Because some ramets in the other sites did not survive the experiment due to herbivory or physical disturbance, these ramet weights were treated as missing values. As a result there were different numbers of replicates per cell, but since there were no missing cells for any of the factors of interest, the design remained generally balanced. An ANOVA based on the design (see Table 1) was first performed on the observed weights, but since the fitted values plotted against the residuals showed strong evidence of a positive relationshp, a transformation was sought. After some further analyses, it was found that a transformation of ramet weights to their natural logarithms produced homogeneity of variance.

TABLE 1. Summary of the analysis of variance

Source	df	MS	p
Replicates × site			
Site	2	0.87	0.22
Residual	26(1)	0.54	
Replicates × site × species			
Species	2	21.29	<0.001
Species × site	4	4.25	<0.001
Residual	47(7)	0.36	
Replicates × species × observations			
Treatment	1	3.28	0.005
Site × treatment	2	0.50	0.28
Species × treatment	2	0.45	0.32
Site × species × treatment	4	0.64	0.17
Residual	52(29)	0.38	

NOTE: Treatment refers to cleared vs. uncleared subplots, site to the three positions on the water depth gradient, and species to the three test species. Data were transformed to their natural logarithms. Values in parentheses indicate the number of missing values.

Results

There was clear evidence for the presence of depression of growth due to the presence of surrounding vegetation, as shown by the treatment term in the ANOVA ($p = 0.005$, Table 1). On the other hand, there was no evidence that the degree to which growth was reduced due to interference varied significantly along the water depth gradient (site × treatment term, $p = 0.28$). Similarly, there was no evidence that the species differed in the degree of interference that they experienced (species × treatment term, $p = 0.32$), or that the degree of interference experienced by each species changed with position on the water depth gradient (site × species × treatment term, $p = 0.17$). There was no evidence for a decrease in productivity along the water depth gradient (site term, $p = 0.22$). Table 2 summarizes the experimental results. The full data set can be found in appendix 2.1 of Shipley (1987).

Since the rhizomes of the test ramets had been tagged before planting and all quadrats were regularly monitored, we were able to classify all deaths as due to (*i*) herbivory by muskrats, (*ii*) unknown disturbance events during the winter or early spring, most likely caused by wave or ice action, or (*iii*) deaths not due to disturbance (i.e., plant still present and intact, but dead). The relative contributions of these three classes of factors are shown in Fig. 2. Deaths not due to disturbance or herbivory could not be attributed to plant interference since the proportion of deaths in cleared and uncleared plots was approximately equal.

Discussion

Contrary to our initial expectations, there was no evidence for a general decrease in productivity along the water depth gradient from site 1 (high on the shore) to site 3 (low on the shore), as indicated by the nonsignificant effect of site (ANOVA, Table 1). Certainly, ramets of all three species died in the site that was continuously submerged (site 4), but this was a qualitative difference, not an extreme of a monotonic gradient of increasing stress. These results are quite different from the patterns of growth along the exposure gradient reported by Wilson and Keddy (1986*a*, 1986*b*) and Wilson (1986).

Similarly, although there was clear evidence of interference (the treatment term in the ANOVA), there was no evidence for either a systematic increase in the degree of interference along the gradient (the site × treatment term) or for a change in the

TABLE 2. Summary of the experimental results

Species	Site	Cleared	Uncleared
Acorus calamus	1	2.55 ± 0.15(10)	2.01 ± 0.22(9)
	2	2.50 ± 0.15(10)	2.41 ± 0.12(9)
	3	2.05 ± 0.33(4)	0.95 ± 0.40(3)
Carex crinita	1	3.08 ± 0.20(10)	2.44 ± 0.19(10)
	2	2.80 ± 0.15(10)	2.18 ± 0.24(9)
	3	3.15 ± 0.20(3)	2.99 ± 0.25(3)
Typha angustifolia	1	2.90 ± 0.22(10)	3.00 ± 0.17(7)
	2	3.94 ± 0.08(10)	3.32 ± 0.17(10)
	3	3.10 ± 0.34(7)	3.26 ± 0.20(9)

NOTE: The means and their standard errors for each factor combination are listed, with the number of replicates in parentheses. All values are the natural logarithms of dry weight (g).

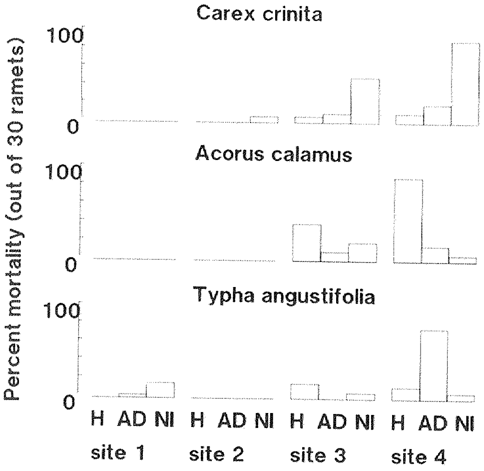

FIG. 2. The percent mortality due to herbivory (H), abiotic disturbance (AD), and death not due to interference, herbivory, or abiotic disturbance (NI) are shown in each block of three histograms. Each block represents one of the four experimental sites. Both cleared and uncleared sites are included.

intensity of interference experienced by each species along the gradient (the site × species × treatment term). These results are also quite different from the patterns of interference that Wilson and Keddy (1986*a*, 1986*b*) found along the exposure gradient. Our results imply that the mechanisms contributing to the zonal patterns along the exposure gradient are not the same as the mechanisms producing zonal patterns along the exposure gradient, as described by Wilson and Keddy (1986*a*, 1986*b*).

Before this conclusion is accepted, however, it is important to consider both the experimental design and the water depth gradient in more detail. In particular, it is possible that the significant effects detected by Wilson and Keddy (1986*a*, 1986*b*) were nonsignificant in our study because of differences in the design of the two sets of experiments. We evaluate this possibility below.

Differences in the results between the two sets of experiments cannot be explained by differences in either the duration of the experiments or in the degrees of replication, since our experiment ran much longer (15 months versus 2 months) with the same levels or replication (10 ramets for each combination of species and site), yet we failed to detect effects that were significant in Wilson and Keddy (1986*a*, 1986*b*). Similarly, our failure to detect the nonsignificant terms in the ANOVA was not due to the confounding effects of sublethal herbivory, since we repeated the ANOVA after removing the few plants that had been partially eaten and obtained the same results as shown in Table 1.

It is unlikely that difference in the sizes of the clearings used can explain the differences in the results either. Wilson and Keddy (1986*b*) used one large clearing at each site, into which all treatment ramets (one per 15-cm diameter pot) were placed. Therefore, each treatment plant was at least 15 cm away from its nearest neighbouring plant. We used paired treatment-control plots to avoid this form of pseudoreplication, with each treatment plant placed at the centre of a 20 × 20 cm clearing. Therefore, each treatment plant in our experiment was at least 10 cm away from is nearest neighbouring plant. The smaller size of the clearings in our study may have reduced our ability to detect significant interactions between interference intensity and gradient position or species differences. Yet we were able to detect highly significant effects of interference (treatment, Table 1) even though both the treatment term and the three interaction terms (site × treatment, species × treatment, site × species × treatment) were tested using the same error term (52 df) and the three interaction terms had larger degrees of freedom (2, 2, and 4 df, respectively) than did the treatment term (1 df). If these nonsignificant interactions exist, their effects must be very small relative to the treatment effect. This is quite different from the results along the exposure gradient (Wilson and Keddy 1986*b*).

Our experiment ran for a longer period of time, with equivalent levels of replication, and was quite able to detect a treatment effect. Therefore, the effect of the slightly smaller clearings used in our experiment is not a likely explanation for the divergent results found between our experiment and that of Wilson and Keddy (1986*b*), although this cannot be completely excluded. In view of the divergent experimental results obained along these two environmental gradients, it is useful to consider the gradients in more detail.

There is a wide range in the amount of aboveground biomass found on the exposure gradient. Moore and Keddy (1989) recorded biomass values from 0.16 to 64 g per 0.04 m^2, a 40 000% increase in biomass over the length of the gradient, although the range of aboveground biomass found in Wilson and Keddy (1986*b*) was not this large. On the water depth gradient the range in the amount of aboveground biomass is much smaller, at least over the depth range included in this experiment. In this study the mean and standard deviation of the dry weights in aboveground biomass in the uncleared subquadrats were 20.14 ± 8.62 (site 1), 15.54 ± 6.88 (site 2), and 24.93 ± 16.43 (site 3) g per 0.04 m^2. Equally important, there were high levels of aboveground biomass at all positions along the water depth gradient in our study.

We re-analyzed the relationship between plant interference (I) and aboveground biomass (B), using only data given in Fig. 1 of Wilson and Keddy (1986*b*), to determine whether these differences in the range of aboveground biomass on the two gradients could help to explain the different results. There was an obvious ($r = 0.887$, $p = 0.003$) nonlinear relation between competitive intensity and aboveground biomass levels. The regression equation is given below; both the slope and the intercept are significant at $p < 0.05$ and values in parentheses are the standard errors of the coefficients:

$$\begin{array}{cccc} \mathrm{I} = & -0.20 & + & 0.13\mathrm{B}^{0.5} \\ & (0.07) & & (0.03) \end{array}$$

When our values were included in the regression along with a categorical variable indicating data set, there were no significant differences between the two data sets ($p = 0.98$) and the original regression equation, based solely on the data of Wilson and Keddy (1986*b*), provided quite good predictions of the measured values of interference found in our study. Furthermore, the regression equation shows that the greatest change in the intensity of interference occurred at the low levels of aboveground biomass found in infertile, exposed sites of Wilson and Keddy (1986*b*) whereas only small changes were found at the sites having biomass levels similar to those found in our study. Our measured values of interference are therefore quite consistent with the previous relationship, and our inability to detect a significant increase in interference along the water depth gradient is also consistent with the data of Wilson and Keddy (1986*b*). This result is further evidence that the different results between the two studies were not a result of differently sized clearings, but rather of differences in the range and amounts of aboveground biomass found along the two environmental gradients.

Since there are clear zonal patterns in the distribution of plant species along the water depth gradient in the apparent absence of differences in the intensity of interference or in a recognizable gradient of productivity, a mechanism other than the one operating along the exposure gradient must produce the zonal patterns. The zonal patterns along the water depth gradient may instead be due to the different physiological responses of each species to this gradient modified by a general level of interference, i.e., each species experiences the stressfulness of each position along the water depth gradient differently. This is the explanation suggested by Hutchinson (1975) for the zonation patterns along the water depth gradient. Of course, this explanation should be treated as a hypothesis yet to be tested, since only a relatively small amount of experimental data exists for emergent macrophyte communities.

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