CHRISTINA E. REYNOLDS

ÉTUDE ÉCOLOGIQUE D'UNE ESPÈCE ENDÉMIQUE DU GOLFE DU SAINT-LAURENT, *ASTER LAURENTIANUS* FERNALD

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RÉSUMÉ

Aster laurentianus Fernald est une espèce se retrouvant principalement en une bande étroite le long des marais salés et des lagunes, particulièrement aux Îles de la Madeleine (Québec). En premier lieu, ce mémoire tente de mettre en relation la distribution spatiale de cette espèce, en milieu naturel, avec trois variables structurantes: la topographie de la rive, la salinité du substrat et l'importance des dépôts de zostère. Les résultats démontrent que le patron de dispersion de *A. laurentianus* varie selon le site. La topographie, la salinité et la présence de zostère ont tous des effets sur la répartition de *A. laurentianus*, mais l'importance relative de ces facteurs semble varier selon les caractéristiques physiques du site considéré.

Nous avons également étudié les effets de stress (salinité élevée et faible lumière) sur la croissance de *A. laurentianus* dans trois expériences en milieu contrôlé. Bien qu'il n'y ait pas d'interaction entre la salinité et l'irradiance, les effets indépendants de ces deux facteurs sont significatifs, de sorte que de faibles irradiances et une salinité élevée limitent la performance de l'espèce. Ces résultats peuvent potentiellement expliquer la répartition de *A. laurentianus* le long des rivages des marais salés et des lagunes.

ABSTRACT

Aster laurentianus Fernald, particularly at Îles de la Madeleine (Québec), occurs in narrow bands along the shores of salt marshes and lagoons. First, a field study examined the spatial relationship between this species and three structuring variables in the natural habitat: topography, substrate salinity and deposition of wrack. Results showed that the distribution pattern of *A. laurentianus* differed from site to site. Topography, salinity and wrack all influenced the distribution pattern of the species; however, the relative importance of each variable changed in relation to the physical characteristics of each site.

Secondly, the effect of stresses (salinity and light) on *A. laurentianus* performance was further investigated with three growth chamber and greenhouse experiments. Despite no interaction between light and salinity, the independent effects of these two factors were significant, such that low light and high salinity reduced plant performance. These results could potentially help explain the distribution of *A. laurentianus* along the shores of salt marshes and lagoons.

AVANT-PROPOS

Tout d'abord, je veux remercier Gilles Houle pour son encadrement tout au long de ce projet, qui a dépassé de beaucoup les responsabilités habituelles d'un directeur de maîtrise. Son ardeur et sa perfection me seront des exemples dans les années à venir! Je tiens aussi à remercier Robert van Hulst qui m'a inspirée, par son grand amour pour ce qu'il fait, à débuter cette maîtrise. J'espère un jour pouvoir amener des élèves à apprécier l'écologie comme vous, Gilles et Robert, l'avez fait pour moi.

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Le mémoire comporte deux chapitres, présentés sous forme d'articles, qui n'ont pas encore été soumis à une revue scientifique. Pour le premier article, l'échantillonnage, l'analyse des données, l'interprétation et la rédaction, ont été réalisés par moi-même. Pour le deuxième chapitre, j'ai incorporé à mon travail les résultats d'une étude sur le taux de croissance relatif et la salinité, effectuée par Christophe Marquis dans le cadre d'un projet d'initiation à la recherche (Université Laval), sous la direction de Gilles Houle. Pour l'expérimentation réalisée par monsieur Marquis, je suis responsable de l'analyse des données, de l'interprétation et de la rédaction de ce deuxième article.

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INTRODUCTION GÉNÉRALE

La diversité spécifique des marais salés est élevée et contribue de façon significative à la diversité régionale des milieux côtiers (Esselink *et al.*, 2000). Pourtant, ces habitats représentent souvent des milieux limitants pour les espèces végétales. Le fait qu'une plante soit restreinte à de tels milieux salins indique soit un besoin en sels relativement élevé, soit une tolérance aux salinités élevées ou encore une incapacité d'être un bon compétiteur dans des environnements plus propices (Ungar, 1991). Même chez les halophytes, la salinité demeure un des facteurs environnementaux qui ont une influence critique sur la germination des graines, l'émergence des plantules, et la croissance et la reproduction des plantes (Katembe *et al.,* 1998).

En plus de l'effet direct de la salinité, les espèces vivant en milieu côtier sont souvent soumises à d'autres facteurs limitatifs tels les stress hydriques, ceux-ci étant amplifiés par le vent et l'exposition à de fortes irradiances. Ces halophytes doivent également s'ajuster à des déficiences en nutriments et aux conditions d'anoxie causées par des inondations fréquentes (Chapman, 1974; Adam, 1990; Ungar, 1991). Ces conditions restreignantes peuvent encourager des interactions positives (i.e. de la facilitation) entre plantes voisines (Bertness et Hacker, 1994). Parfois, l'ombrage apporté par les plantes voisines limite l'évaporation et, par conséquent, l'hypersalinité du substrat (Bertness *et al.*, 1992; Callaway, 1994). De plus, l'oxydation de la rhizosphère des plantes voisines peut contribuer à modérer les conditions anoxiques du substrat (Howes *et al.*, 1981; Shat, 1984; Bertness, 1991). Cependant, même en milieu limitant, la compétition interspécifique pour les ressources telles que la lumière et les nutriments peut être intense. Compétition et facilitation affectent, à leur manière, la distribution des plantes dans ces milieux sévères.

En général, il existe une relation inverse entre l'habileté compétitive et le degré de tolérance à des stress physiques tels que la salinité; ainsi, une espèce ne peut être à la fois la meilleure compétitrice et la plus tolérante aux stress (Grime, 1979). La position qu'une espèce occupe le long d'un gradient opposé de stress et de compétition est donc déterminée par sa tolérance et son habileté compétitive (Whittaker, 1967; Barbour *et al.*, 1980). Dans les marais salés, la salinité est souvent considérée comme le facteur qui détermine la limite inférieure de distribution des espèces, alors que la compétition interspécifique détermine la limite supérieure (Ungar, 1966; Snow et Vince, 1984; Pennings and Callaway, 1992; Mulder *et al.,* 1996). De plus, des perturbations naturelles comme les débris végétaux apportés par les vagues influencent les patrons de répartition des espèces, en fonction de la topographie du substrat (Pennings et Richards, 1998). Selon Brewer *et al.* (1998), ces perturbations interagissent avec les stress abiotiques pour déterminer la distribution des espèces dans ce type d'habitat. Une combinaison de facteurs contrôle donc le patron de répartition des plantes dans ces milieux.

Un exemple d'espèce vivant sous des conditions rigoureuses comme celles-ci est l'aster du Saint-Laurent (*Aster laurentianus* Fernald), une halophyte annuelle endémique de la région du Golfe du Saint-Laurent. Elle occupe des substrats humides à base sablonneuse, régulièrement inondées, telles les plages protégées et les marais salés du Nouveau Brunswick, de l'Île du Prince Edouard et du Québec, et ce, dans environ une quinzaine de localités seulement. Au Québec, la distribution de cette espèce se limite à l'archipel des Îles de la Madeleine où, malgré l'inaccessibilité des sites, elle demeure susceptible aux perturbations anthropiques durant la période de la chasse à la sauvagine (Boudreau et Houle, 1998). En dépit du fait que l'aster du Saint-Laurent appartienne à un genre très répandu et commun, cette espèce se trouve uniquement dans l'est du Canada. En raison de cette répartition restreinte et aussi du faible nombre de sites qu'elle occupe, depuis 1989, l'aster du Saint-Laurent a le statut de plante vulnérable au Canada, attribué par le CSEMDC (Comité sur le Statut des Espèces Menacées de Disparition du Canada: Houle et Haber, 1990). Les populations de *A. laurentianus* des Îles de la Madeleine sont les plus importantes connues dans l'aire de répartition de l'espèce (Labrecque et Gagnon, 1995). Ainsi, le maintien de ces populations est essentiel pour assurer la survie à long terme de cette espèce.

L'établissement des plantules de l'aster du Saint-Laurent s'effectue en juin et leur survie est réduite par une émergence tardive. L'effectif des populations aux Îles de la Madeleine semble subir des fluctuations inter-annuelles importantes: la population de Havre aux Basques a été évaluée à plus d'un million d'individus en 1994 (Gagnon *et al.*, 1995), mais elle aurait diminué considérablement en 1997 (Boudreau et Houle, 1998). En 1999, son effectif était estimé à quelques dizaines de millions d'individus (Houle et Reynolds, 2000). En dépit d'une densité locale souvent élevée (jusqu'à 2000 individus/m^2), l'espèce demeure vulnérable en raison du faible nombre de populations existantes dans l'ensemble de sa répartition. Actuellement, il n'existe aucune mesure de protection pour l'aster du Saint-Laurent. Avant d'élaborer un plan de conservation pour cette espèce aux Îles de la Madeleine, une bonne compréhension des facteurs qui contrôlent son abondance et sa répartition est nécessaire. À présent, nous savons que la salinité agit négativement sur la germination des graines, l'établissement des plantules et la croissance de *A. laurentianus* (Houle *et al.*, *sous presse*). De même, l'espèce est sensible aux stress hydriques qui causent une baisse générale de la performance des individus (Houle et Belleau, 2000). Une expérience d'éradication des espèces végétales partageant l'habitat de l'aster du Saint-Laurent, dans le but d'éliminer la compétition interspécifique, a amélioré la performance des plantes en termes de taux de survie, de biomasse totale et d'effort reproducteur (Boudreau et Houle, 1998).

Le présent projet vise une meilleure connaissance de l'écologie de l'aster du Saint-Laurent à travers deux études. La première tente de mettre en relation la répartition spatiale de *A. laurentianus* sur deux sites aux Îles de la Madeleine avec des variables environnementales identifiées comme étant structurantes dans les marais salés, soit la topographie, la salinité du substrat et l'abondance de débris végétaux de *Zostera marina*. Dans le but de mieux comprendre l'importance relative de la compétition et des stress sur la répartition de l'espèce dans son milieu, une deuxième étude considère l'effet de la lumière, l'effet de la salinité du substrat et l'interaction de ces deux facteurs sur la performance globale de *A. laurentianus*, en milieu contrôlé.

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CHAPTER 1

Topography, salinity and wrack deposition control the distribution of *Aster laurentianus* Fernald in coastal salt marshes

1.1 Résumé

Aster laurentianus Fernald est une halophyte annuelle endémique du Golfe du Saint-Laurent. Cette espèce se retrouve en périphérie des marais salés et des lagunes, sur une bande étroite (ca 50 à 200 cm de largeur). Dans cet habitat, les plantes subissent des perturbations fréquentes sous forme de débris végétaux apportés par les vagues, ainsi que les effets limitatifs de la salinité du substrat. Ces facteurs environnementaux pourraient être en partie responsables de la distribution des espèces en bordure des lagunes. Dans cette étude, nous avons déterminé comment trois variables structurantes, soit la topographie, la salinité et la présence de débris végétaux de *Zostera marina* ou zostère, affectent la densité de *A. laurentianus* sur deux sites aux Îles de la Madeleine, Québec. Des analyses spatiales ont permis de montrer que, sur les deux sites, la salinité, l'abondance de zostère et la densité de *A. laurentianus* sont significativement corrélés à la topographie, et que la présence de zostère affecte la salinité du substrat. Sur le premier site, la densité de *A. laurentianus* varie selon un gradient en fonction de la distance depuis la ligne moyenne des eaux; sur le deuxième site, la densité augmente d'abord, puis diminue avec la distance depuis le rivage. Ceci peut être expliqué par le fait que, sur le premier site, la variable la plus structurante est la présence de zostère comme la salinité n'a pas de relation directe avec la densité. Sur le deuxième site, la présence de zostère étant beaucoup moins importante, la salinité prédomine sur la zostère comme la variable environnementale la plus structurante. Nous proposons donc que la distribution de *A. laurentianus* est limitée par la présence de dépôts de zostère et par la salinité du substrat, mais que l'importance relative de ces deux variables change en fonction des caractéristiques physiques de chaque site.

1.2 Abstract

Aster laurentianus Fernald is an annual halophyte endemic to the Gulf of the St. Lawrence River. It typically occurs in narrow bands (from ca. 50 to 200 cm wide) in salt marshes at the periphery of shallow lagoons. In this habitat, plants are exposed to frequent disturbance in the form of wrack burial as well as to the limiting effects of substrate salinity. Such environmental factors may be responsible for the species distribution. In this study, we determined whether three structuring abiotic variables, topography, salinity and wrack, affect *A. laurentianus* density at two sites at Îles de la Madeleine, Québec. Spatial analyses showed that on both sites, substrate salinity, wrack abundance and density of *A. laurentianus* are significantly correlated to topography, and that wrack abundance affects substrate salinity. On the first site, the distribution pattern of *A. laurentianus* appears to be in the form of a gradient, which varies with distance from the waterline, while on the second site, density increases initially then diminishes with distance from the waterline. This can be explained by the fact that on the first site, the most structuring abiotic variable is wrack deposition, the effect of salinity on density being indirect. On the second site, which is somewhat sheltered, wrack deposition is far less important; therefore, substrate salinity predominates over wrack deposition as the most structuring environmental variable on this site. We propose that *A. laurentianus* distribution is limited both by substrate salinity and wrack deposition, but that the relative importance of these structuring abiotic variables changes with the physical characteristics of each site.

1.3 Introduction

Zonation is a typical feature of plant communities subject to gradients of physical stress and disturbance (Whittaker, 1967; Barbour *et al.*, 1980). Such community patterns are often found in coastal salt marshes (Ungar, 1974; Chapman, 1974; Snow and Vince, 1984; Bertness and Ellison, 1987; Adam, 1990) where substrate salinity, a major limiting factor for plants (Ranwell, 1972; Barbour and DeJong, 1977; Ungar, 1987; Bertness *et al.*, 1992; Sánchez *et al.,* 1998), varies with distance from the waterline. Flooding, as a result of tidal movement, is also considered to be a controlling factor in the establishment and distribution of plant species in these habitats (Waisel, 1972; Chapman, 1974; Adam, 1990; Ungar, 1991; Sánchez *et al.*, 1996). In addition, wrack, or dead plant debris which is deposited by waves along the shoreline, and sometimes rafted to the high marsh during extremely high tides, is generally considered a significant disturbance (Brewer *et al.*, 1998; Pennings and Richards, 1998; Adam, 1990). Distribution and residence time of wrack vary with tidal height, (Valiela and Rietsma, 1995) which in turn is related to the slope of the shore. Together, these factors along with interspecific competition and predation, determine the zonational distribution patterns of plant species in salt marshes (Bertness and Ellison, 1987; Pennings and Callaway, 1992; Mulder *et al.*, 1996). Several characteristic abiotic factors in these habitats such as frequency and duration of tidal inundation, soil salinity and wrack deposition are presumed to correlate with elevation (Vince and Snow, 1984; Sánchez *et al.*, 1996). Since shore elevation integrates these factors, it therefore usually correlates well with species distributions in salt marshes in general (Adams, 1963; Earle and Kershaw, 1989).

In this paper we determine whether there exists a spatial relationship between the abundance of *Aster laurentianus* Fernald, an annual halophyte endemic to the Gulf of the Saint Lawrence River (Houle, 1988) and three major abiotic factors, i.e. shore topography, substrate salinity, and wrack (*Zostera marina*) deposition on the shores of a shallow lagoon located at Îles de la Madeleine (Québec). Our goal was to identify the major environmental factors, among those considered, structuring *A. laurentianus* distribution and abundance.

1.4 Study species

Populations of *A. laurentianus* are found in New Brunswick, Prince Edward Island and Québec. Because of its limited distribution, and the small number of sites which it occupies, *A. laurentianus* is considered a vulnerable species by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC: Houle and Haber, 1990). The most abundant populations are found on the Îles de la Madeleine, Québec (Labrecque and Gagnon, 1995) where the species typically occurs in a narrow band (from ca. 50 to 200 cm wide) along the edges of shallow lagoons and in salt marshes, immediately above the mean summer water level (Houle *et al., in press*).

A. laurentianus is a summer annual: seedlings emerge in June, growth occurs through July and August, and seeds are dispersed in September. As such, this species is exposed to the high tides and storms of late summer and autumn, and to the accumulation of floating plant debris, or wrack, throughout the growing season. Substrate salinities, which attain a maximum during the summer (high evapotranspiration) have been shown to negatively affect *A laurentianus* seed germination and plant growth (Houle *et al.*, *in press*; Reynolds and Houle, unpublished manuscript). Natural gradients of salinity and wrack deposition along marsh shores may thus influence the species distribution.

1.5 Materials and methods

The following sampling was conducted in August and September 1999 at two sites along the edge of the Havre aux Basques lagoon at Îles de la Madeleine (Québec, Canada). The first site was on the eastern side of the lagoon and will be referred to as Havre aux Basques (HAB; Fig. 1). The second site was on the south-western side of the lagoon at a location called Pointe aux Canots (PAC). The first site was exposed to westerly winds and waves, while the second site was located in a north-facing protected bay. Approximately 12 km of shoreline separate these two

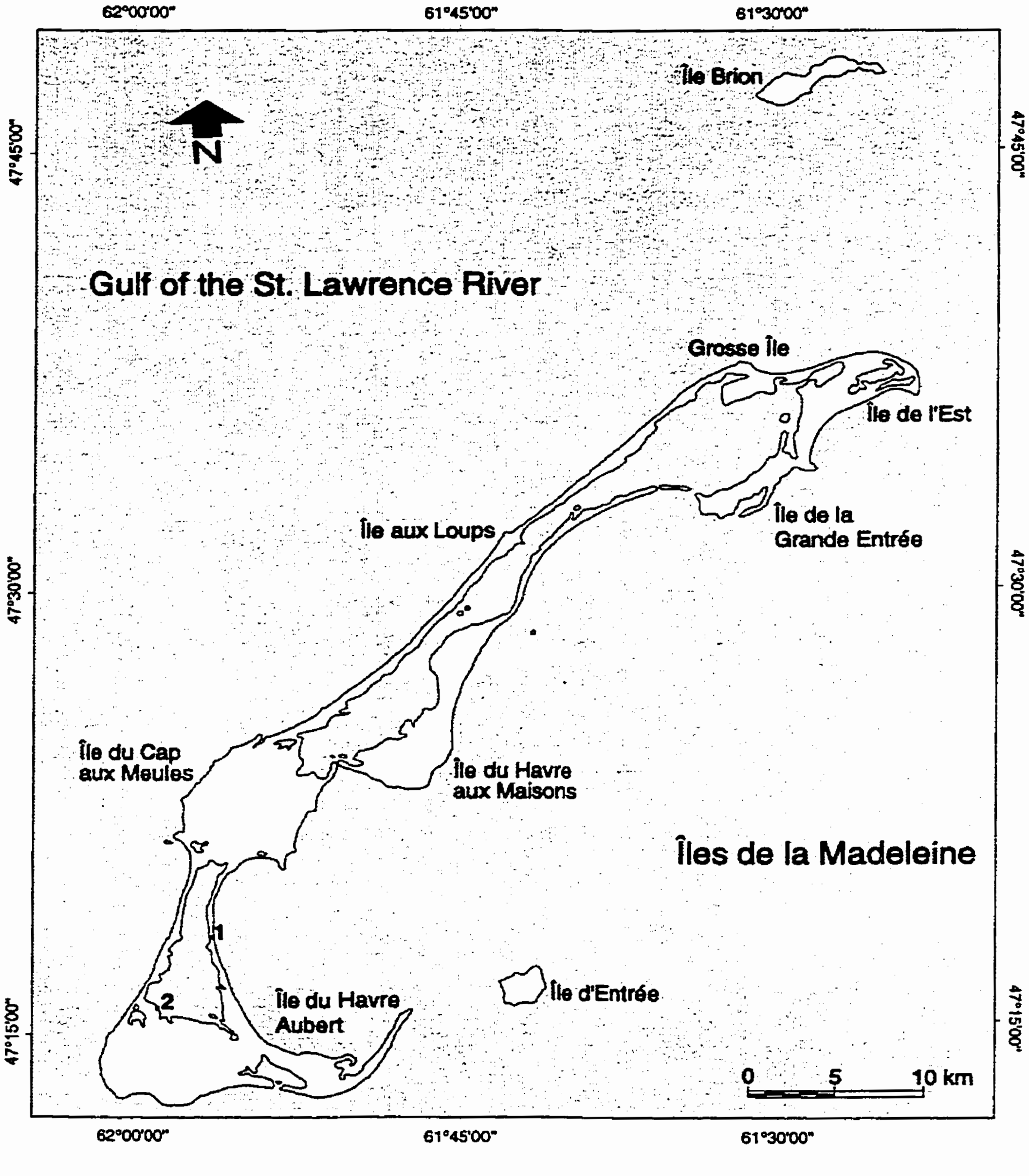


Figure 1. Location of study sites, Îles de la Madeleine, Québec.
1: Havre aux Basques; 2: Pointe aux Canots.

sites, which were chosen based on their accessibility and on the abundance of *A. laurentianus.* At each site, fifteen 3.75-m long transects were set up perpendicularly to the shoreline. The transects were 0.75 m apart and comprised of 15 contiguous quadrats of 25 x 25 cm, for a total of 225 quadrats per site.

Data collected at both sites for each quadrat were the following: number of individuals of *A. laurentianus*, percent cover of wrack (*Zostera marina*), and topography (determined with a level). Two soil samples 12 cm^2 x 8 cm were collected in close proximity to each quadrat to estimate soil salinity and seed bank abundance. A first series of soil samples was dried at 85 °C for 48 hours and then sifted through a 2 mm sieve. Soil salinity was subsequently determined with a Check Mate 90 conductivity meter (Corning Inc., NY) using 10 mL of soil thoroughly mixed with 30 mL of de-ionized water. The other soil sample series was placed in a greenhouse under a 14-h photoperiod with a thermal regime of 19 °C/13 °C (day/night). Samples were watered daily with tap water and germinated seedlings of *A. laurentianus* were counted and removed weekly, for 5 weeks, until no more seedlings emerged.

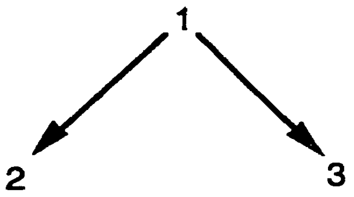
1.6 Statistical analyses

A variable is said to be autocorrelated when it is possible to predict values of the variable, at certain points in space, from known values whose location in space is also known (Cliff and Ord, 1981; Legendre and Fortin, 1989). Autocorrelation may be positive or negative. It is positive when values of the variable, which are spatially close to one another, are similar; it is negative when there is repulsion between closely located values. In this study, we tested for the presence of a spatial structure in the density of *A. laurentianus* and substrate salinity, topography and abundance of wrack using Mantel tests.

The Mantel test calculates a statistic that is similar to a Pearson's *r.* The value of the Mantel statistic can vary from -1 to +1 and is calculated between two distance (or similarity) matrices, such as euclidian distance matrices. However, the interpretation of the sign of the coefficient differs between the Mantel (and partial Mantel) tests and the Pearson's correlation. Indeed a positive Mantel *r* does not necessarily imply a positive correlation between two variables. This is related to the fact that distance (or similarity) matrices are used for the tests, instead of the actual values of the variables.

When a Mantel test is performed between the values of a variable at different sampling locations and the geographical positions of these sampling locations, the statistic then indicates the degree of overall spatial autocorrelation. When the test is performed between the values of two variables measured at the same sampling locations, the statistic represents the intensity of the as in a Pearson's *r*. However, two variables may appear to be correlated simply because they are both linked to a third, common variable, such as location in space. Thus, in the presence of autocorrelation, it is also necessary to remove the effect of this third variable before concluding that the original two variables are indeed correlated, similarly to partial correlations. To calculate correlations between variables in this manner, we used the partial Mantel test, as proposed by Smouse *et al.* (1986). A significant coefficient of correlation (*r*) for the partial Mantel test (with spatial effects considered) indicates that the relationship which exists between the two variables is not related to a common spatial structure (Legendre and Fortin, 1989).

Mantel tests and partial Mantel tests can be used for causal modelling (Legendre and Trousselier, 1988). In this case, a dependent variable (or set of variables) is correlated to "independent" variables and results from those correlations are used to test alternative causal models. For example, a model in which topography (1) influences both *A. laurentianus* density (2) and substrate salinity (3) would be supported by the following results:



Mantel tests

$1 \cdot 2$: $r \neq 0$
$1 \cdot 3$: $r \neq 0$
$2 \cdot 3$: $r \neq 0$ or $r = 0$

Partial Mantel tests

$(1 \cdot 2) \cdot 3$: $r \neq 0$
$(1 \cdot 3) \cdot 2$: $r \neq 0$
$(2 \cdot 3) \cdot 1$: $r = 0$

For both the Mantel tests and partial Mantel tests, the correlations were calculated between the density of *A. laurentianus* and topography, substrate salinity and abundance of deposited wrack. The level of significance for our tests was set at $\alpha = 0.0167$ (Bonferroni correction; i.e. 0.05/3, where 3 represents the number of tests performed for a given data set for a given hypothesis) except for the autocorrelation tests, where $\alpha = 0.05$. All analyses were completed with the *R* software package (Legendre and Vaudor, 1991).

1.7 Results

Interpolated maps of the four variables (topography, salinity, presence of wrack and density of *A. laurentianus*) are represented in Figs. 2 and 3, based on data taken on the 225 quadrats per site.

These show evident differences in the spatial structure of the two sites. For HAB, *A. laurentianus* density (mean ± 1 SE) was 0.738 ± 0.127 individuals / 625 cm^2, salinity was 389.885 ± 13.299 mg L^{-1} and wrack was 46.338 ± 2.863 % cover. For PAC, *A. laurentianus* density (mean ± 1 SE) was 29.376 ± 2.659 individuals / 625 cm^2, salinity was 462.122 ± 26.553 mg L^{-1} and wrack was 4.244 ± 0.883 % cover.

For HAB, the statistical analyses show that topography, salinity and wrack, but not *A. laurentianus* density, are spatially autocorrelated (Table 1). The Mantel tests show that topography is significantly correlated with salinity, wrack and density (positive r). Presence of wrack is correlated with salinity and density (positive r), while salinity is not significantly correlated with density. Partial Mantel tests, which test for correlation without the effect of space, confirm these relationships (Table 1).

For PAC, all variables (i.e. density of *A. laurentianus*, topography, salinity and wrack) are spatially autocorrelated (Table 2). Mantel tests show that topography is correlated with salinity and wrack (positive r), and with density (negative r). Substrate salinity is correlated with topography, density and wrack (positive r), while wrack is not significantly correlated with density. Partial Mantel tests indicate that these correlations do not change greatly when the effect of space is removed, except for salinity and density, for which r then becomes negative (Table 2).

A. laurentianus seed bank is spatially autocorrelated for PAC ($r = 0.10225$; $P = 0.000$) but not for HAB ($r = -0.03943$; $P = 0.073$). No correlation exists between seed bank abundance and *A. laurentianus* density for either site ($P > 0.05$). Mantel

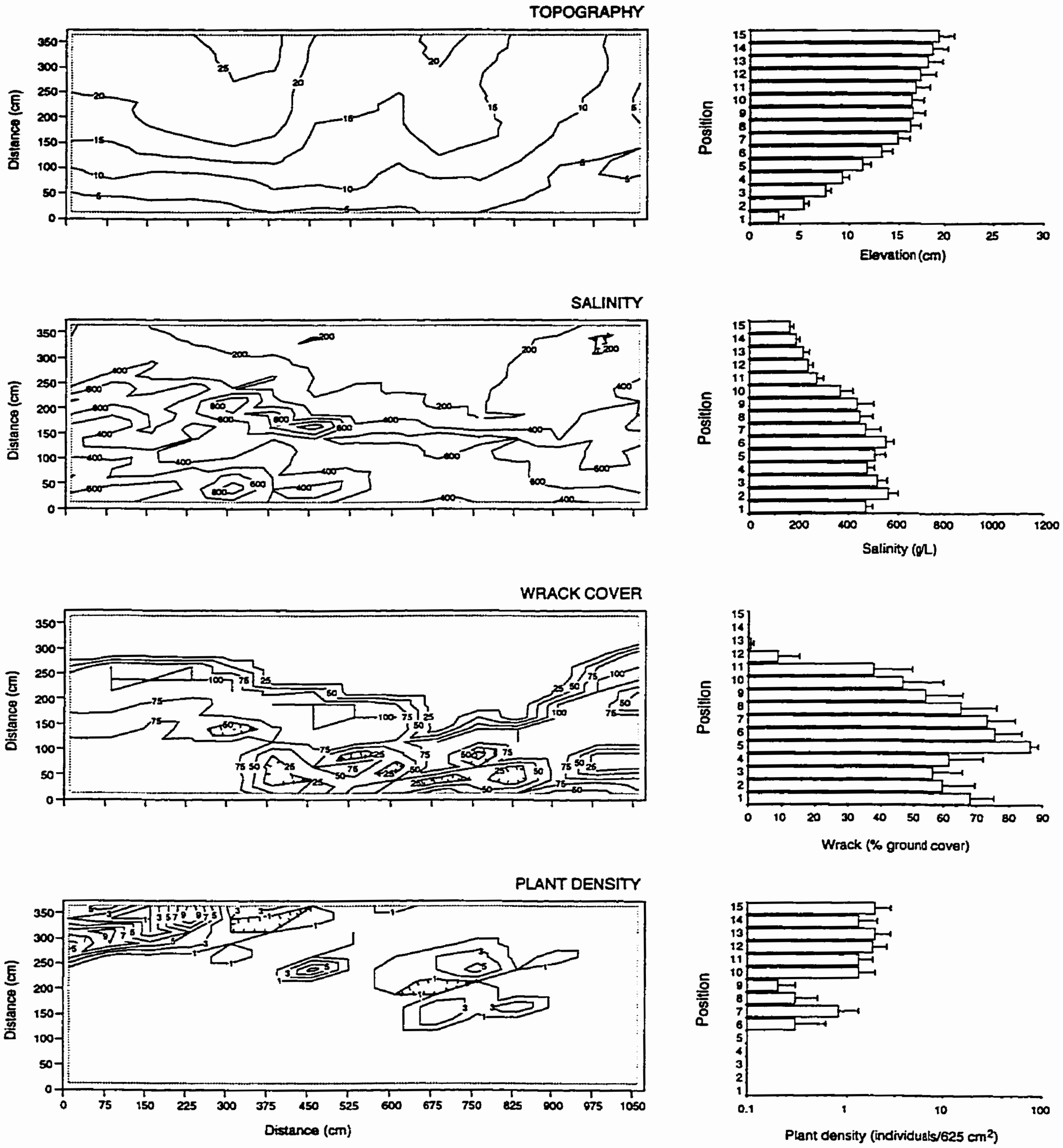


Figure 2. Topography (cm), salinity (mg/L), presence of wrack (% cover) and density of *A. laurentianus* (# individuals/625 cm^2), for site 1, i.e. HAB (Havre aux Basques). Distance 0 on y-axis indicates the mean water line.

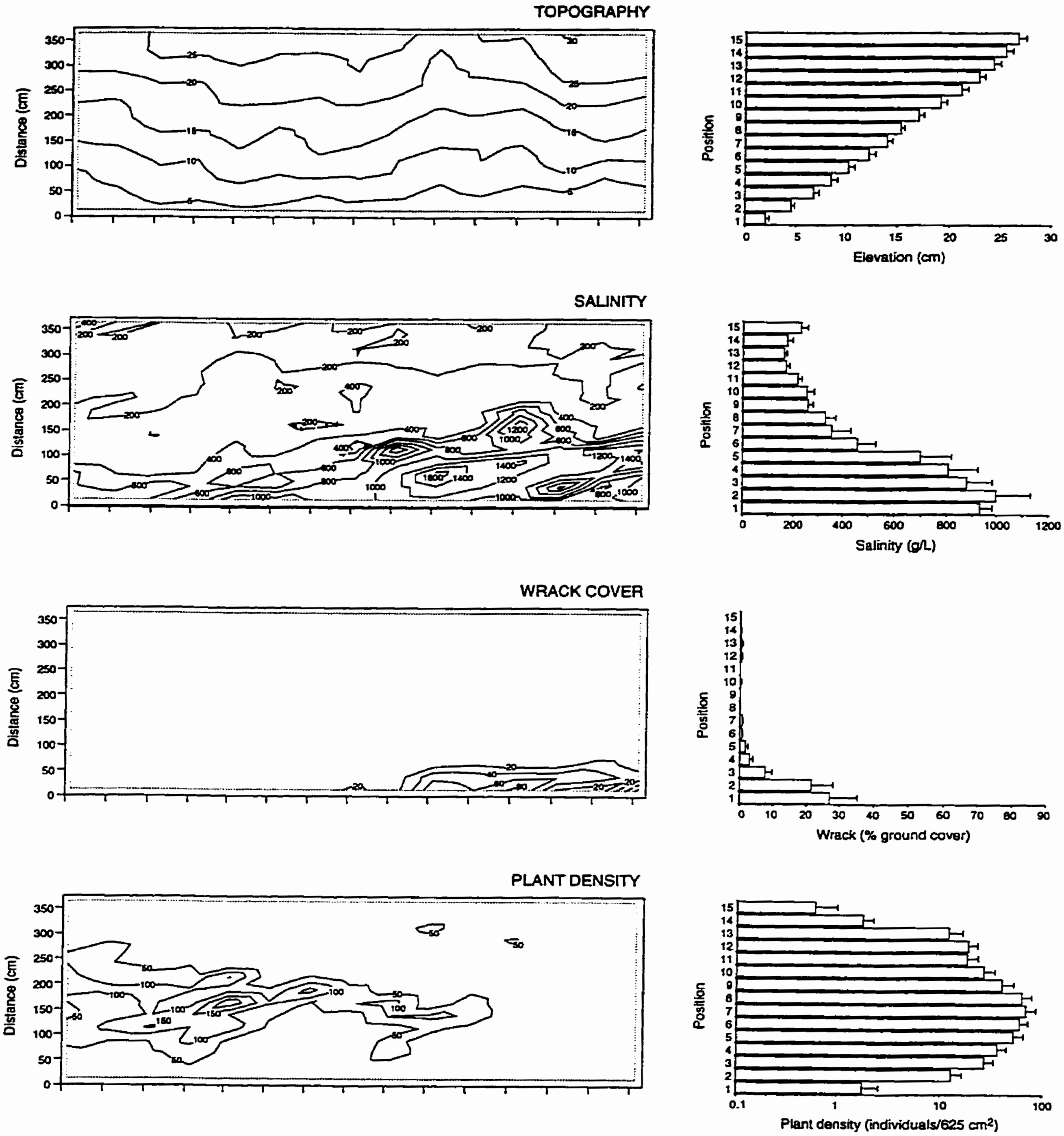


Figure 3. Topography (cm), salinity (mg/L), presence of wrack (% cover) and density of *A. laurentianus* (# individuals/625 cm^2), for site 2, i.e. PAC (Pointe aux Canots). Distance 0 on y-axis indicates the mean water line.

Table 1. Mantel tests (above the diagonal) and partial Mantel tests (below the diagonal) between different environmental variables (topography, substrate salinity and wrack abundance) and the density of *A. laurentianus*, for site 1, i.e. Havre aux Basques. On the diagonal, results of Mantel spatial autocorrelation. Values in bold are significant at $P < 0.0167$; for autocorrelation, $P < 0.05$; $n = 225$.

	Density		**Topography**		**Salinity**		**Wrack**	
	r	***P***	***r***	***P***	***r***	***P***	***r***	***P***
Density	0.0421	0.0716	0.0982	**0.0009**	-0.0224	0.3461	0.0532	**0.0000**
Topography	0.0897	**0.0025**	0.2986	**0.0000**	0.1268	**0.0000**	0.0915	**0.0000**
Salinity	-0.0252	0.3279	0.1401	**0.0000**	0.0649	**0.0107**	0.2168	**0.0000**
Wrack	0.0504	**0.0000**	0.0739	**0.0000**	0.2138	**0.0000**	0.0707	**0.0000**

Table 2. Mantel tests (above the diagonal) and partial Mantel tests (below the diagonal) between different environmental variables (topography, substrate salinity and wrack abundance) and the density of *A. laurentianus*, for site 2, i.e. Pointe aux Canots. On the diagonal, results of Mantel spatial autocorrelation. Values in bold are significant at $P < 0.0167$; for autocorrelation, $P < 0.05$; $n = 225$.

	Density		**Topography**		**Salinity**		**Wrack**	
	r	***P***	***r***	***P***	***r***	***P***	***r***	***P***
Density	0.0835	**0.0005**	-0.0786	**0.0024**	0.0975	**0.0108**	-0.0756	0.0733
Topography	-0.0891	**0.0007**	0.1158	**0.0000**	0.4089	**0.0000**	0.2933	**0.0000**
Salinity	-0.1067	**0.0065**	0.4202	**0.0000**	0.1004	**0.0000**	0.4283	**0.0000**
Wrack	-0.0808	0.0616	0.2891	**0.0000**	0.4253	**0.0000**	0.0576	**0.0264**

test statistics are, for HAB: $r = 0.0275$; $P = 0.305$; for site 2: $r = -0.0066$; $P = 0.442$. The partial Mantel test statistics are, for HAB: $r = 0.0292$; $P = 0.294$; for PAC: $r = -0.0153$, $P = 0.368$. For HAB, seed density is 0.782 ± 0.087 seeds / sample, while for PAC, seed density is 1.342 ± 0.142 seeds / sample (mean ± 1 SE).

1.8 Discussion

For the Havre aux Basques site (HAB), topography, salinity and wrack are all spatially autocorrelated, indicating that these variables follow a certain predictable pattern in space: values which are close to one another tend to be similar. The interpolated maps of these variables confirm the patterns, which appear to be gradients. *A. laurentianus* density is not spatially autocorrelated, however, suggesting that the variable is randomly dispersed in space (no specific structure).

Studies have shown that frequency and duration of tidal inundation, soil waterlogging and salinity are all negatively correlated with topography (Adams, 1963; Earle and Kershaw, 1989). Our results are consistent with these findings and show a significant correlation between topography, salinity and wrack, even when spatial autocorrelation is accounted for. Wrack may reinforce gradients of flooding and salinity caused by differences in elevation and terrestrial runoff (Pennings and Richards, 1998) and determine plant species distribution (Brewer *et al.*,1998). At HAB, high densities of *A. laurentianus* were associated with high values of topography and low values of wrack accumulation. Topography, by its influence on wrack, may thus control *A. laurentianus* density. Topography and wrack also influence salinity which, however, does not have any direct effect *on A. laurentianus* density for this site.

For the Pointe aux Canots site (PAC), results are somewhat different. *A. laurentianus* density, topography, salinity and wrack are all spatially autocorrelated. All patterns are gradients, except for *A. laurentianus* density which forms a “wave” (high values in the middle portion of the shore). Topography is correlated with wrack, salinity and *A. laurentianus* density. In addition, Mantel's *r* is negative between *A. laurentianus* density and topography, with or without the effect of space accounted for. Unlike a Pearson's *r*, a negative Mantel's *r* does not indicate a negative relationship between two variables. Instead, a negative Mantel's *r* indicates that small differences between two points for one variable are associated with large differences between two points for the second variable. This occurs, for example, when one variable is distributed along a gradient, while the second forms a wave pattern. Therefore, large differences in topography are associated with small differences in *A. laurentianus* density at PAC. For example, there are large differences in topography between the waterline and the landward part of the quadrats, but only small differences in density of *A. laurentianus* (very low near the waterline and at the landward part of the quadrat). This relationship is similar to that between *A. laurentianus* density and salinity, as Mantel's *r* becomes negative for the correlation between the two variables when the effect of space is removed. For this site, the most important structuring abiotic variable for *A. laurentianus* density is also topography, by its influence on salinity, not on wrack, however. Indeed, *A. laurentianus* density is not directly associated with wrack, although all three abiotic variables are associated with one another. Wrack deposition may appear to affect *A. laurentianus* density indirectly, through its positive correlation with salinity.

In salt marsh communities, salinity, along with flooding and tidal action, is considered to be one of the controlling factors in the establishment and distribution of plant species (Adams, 1963; Ranwell, 1972; Chapman, 1974; Adam, 1990; Ungar, 1991; Sanchez *et al.*, 1996). It has also been suggested that salinity determines the lower limits of halophyte distribution in saline habitats, while the upper limits of distribution are determined mostly by competition (Snow and Vince, 1984; Pennings and Callaway, 1992; Mulder *et al.*, 1996).

The differences observed in the relationship among the variables analyzed for the two sites can largely be related to their position along the edge of the Havre aux Basques lagoon. HAB is located on the exposed eastern side of the lagoon, while

PAC is located in a protected bay on the south-western side of the same lagoon (Fig 1). As such, HAB is more likely to suffer from the disturbance of wave and tidal action, and prevailing westerly winds. In fact, a storm in August 1999 caused several days of flooding on HAB, while the effect was barely noticeable on PAC (personal observations). Such natural disturbances increase wrack deposition along the shoreline. For instance, at HAB, wrack deposition during the summer was significant, in some cases reaching thicknesses of 25 cm in the lower marsh zone (unpublished data). Mean values show that the percent cover of wrack on this site was 46 %, while for PAC it was approximately 10 times smaller. For HAB, patches of wrack were thick enough to kill underlying vegetation, displacing *A. laurentianus* plants to the higher marsh zones where wrack deposition was less abundant. At PAC, salinity was slightly higher than at HAB (462 mg L^{-1} versus 390 mg L^{-1}). The density of *A. laurentianus* was not significantly associated with wrack, but with salinity.

For certain species, phenological adaptations to salinity and other limiting salt marsh conditions include germination during periods of reduced salinity and the production of soil seed banks (Hopkins and Parker, 1984; Bakker *et al.*, 1985; Ungar, 1987; Ungar and Woodell, 1993). We wished to investigate seed bank abundance in relation to density of mature *A. laurentianus* plants. A positive relationship between seed bank and density would indicate that seeds tend to accumulate in portions of the habitat occupied by mature plants. A negative relationship would indicate that germinated seeds reduce the seed bank in areas where plant density is high. Our analyses showed that autocorrelation was present at PAC but not at HAB. However, Mantel and partial Mantel tests calculated between the seed bank and *A. laurentianus* density for both sites were not significant, suggesting that seed dispersal for this species is likely the result of a complex series of processes. Houle *et al.* (*in press*) showed that despite germination being decreased and sometimes inhibited by salinity for *A. laurentianus*, seed viability was not affected. Therefore, the seed bank of *A. laurentianus* most likely represents several years of seed accumulation which would obscure the spatial relationship between soil seed density and emerging plant density, in any given year.

1.9 Conclusion

Variables other than the ones analyzed in this study, such as water logging and nutrient availability, may influence the density of *A. laurentianus* in the field. However, Houle and Belleau (1999) showed that water logging had no significant effect on *A. laurentianus* growth and biomass allocation. Therefore, we feel that the abiotic variables considered, i.e. topography, substrate salinity and deposited wrack, are those most likely to be responsible for the structure of the *A. laurentianus* populations on the two study sites, especially. Both salinity and wrack accumulation are directly associated with topography, since both tend to be higher close to the shoreline and lower in the high marsh. Topography can be useful in helping to predict the intensity of physical factors such as salinity and wrack accumulation on the field. Based on the data obtained, it can be said that limiting factors often vary depending on site characteristics. As was observed for HAB, physical factors such as wrack accumulation can sometimes interfere with existing natural gradients such as those of salinity to influence plant distribution. Plant distribution in salt marshes is therefore controlled by a variety of interacting factors, some of which may be more important than others based on intrinsic site characteristics.

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CHAPTER 2

The effect of light and salinity on the performance of *Aster laurentianus* Fernald

2.1 Résumé

Le long des marais salés et des lagunes des Îles de la Madeleine, Québec, les populations de *Aster laurentianus* Fernald semblent fluctuer de façon significative d'année en année. En général, cette espèce est restreinte à une bande étroite, à quelques centimètres au-dessus du niveau moyen de la ligne des basses eaux. Des études précédentes sur cette halophyte annuelle, endémique de l'estuaire du Saint-Laurent, ont démontré que la salinité élevée du substrat et la compétition interspécifique pour la lumière sont des facteurs qui limitent l'établissement et la distribution de cette espèce. Dans cette étude, nous avons déterminé les effets indépendants de l'irradiance et de la salinité sur la croissance, ainsi que l'effet combiné de ces deux facteurs sur la performance de *A. laurentianus*, en milieu contrôlé. Les résultats démontrent que la croissance de cette espèce est réduite à de fortes salinités et à de faibles irradiances, et que l'effet de ces deux facteurs est additif. Comme la salinité et la lumière sont négativement corrélées en milieu naturel, nous proposons qu'il existe un compromis entre la tolérance de *A. laurentianus* à de fortes salinités et de faibles irradiances qui contrôle la distribution de cette espèce le long des marais salés et des lagunes.

2.2 Abstract

Along the edges of salt marshes and lagoons at Îles de la Madeleine, Québec, *Aster laurentianus* Fernald populations seem to fluctuate significantly from year to year. In general, this species is restricted to a narrow band a few centimeters above the average waterline. Previous studies of this small annual halophyte, endemic to the St. Lawrence Estuary, have shown that high substrate salinity and interspecific competition for light may be the most significant limiting factors for this species success and distribution. In this study, we determined experimentally the effects of photosynthetic photon flux density (PPFD) and salinity on *A. laurentianus* performance. Results showed that plant growth and performance were limited by low PPFD and high salinity, and that the effects of these two factors were additive. Since PPFD and salinity were negatively correlated in the field, we propose that a trade-off between tolerance to low PPFD and tolerance to high salinity restricts *A. laurentianus* distribution to narrow bands along the edges of salt marshes and lagoons.

2.3 Introduction

Plants of coastal habitats often cope with the major limiting effect of high substrate salinity (Ranwell, 1972; Ungar, 1987; Bertness *et al.,* 1992; Sánchez *et al.,* 1998). These salt-tolerant plants are called halophytes and may face additional stresses related to their habitat such as flooding, water-logging or drought, low nutrient availability and, in many cases, high radiation levels (Ranwell, 1972; Ungar, 1991; Pennings and Callaway, 1992; Levine *et al.,* 1998). In coastal salt marshes, plants must also survive wrack deposition and tidal and wave abrasion (Chapman, 1974), as well as interspecific competition and other limiting factors faced by plants in general. Together these factors along with interspecific competition and predation determine the zonational distribution pattern of species in salt marshes (Ungar, 1979, Bertness and Ellison, 1987; Ungar, 1991; Pennings and Callaway, 1992; Mulder *et al.*, 1996).

According to Bertness and Ellison (1987), plant zonation in coastal habitats is primarily driven by competitve processes, where poorer competitors are displaced to areas with greater disturbance or stress, providing a refuge from superior competitors. Competition for light appears to be a significant factor in determining which species survive in a particular salt marsh zone (Ungar, 1998). Competitive ability for light is often associated with a high relative growth rate, enabling the best competitor to shade its neighbours and therefore monopolize the available resources. Effects of low light availability on growth can include a relative increase in biomass allocation to leaves and an increase in leaf surface per unit leaf mass (Poorter and Remkes, 1990; Lambers and Poorter, 1992; Chazdon and Kaufmann, 1993; Garnier and Vacaeyzeele, 1994). Experiments have also shown that low light availability decreases net carbon assimilation rate and Rubisco activity (Björkman, 1968), leading to decreased relative growth rate (RGR; Mooney *et al.,* 1978).

Salinity, a significant limiting factor in salt marshes, affects seed germination and seedling development (Katembe *et al.,* 1998). In mature plants, substrate salinity may restrict water and nutrient uptake by the roots, as a result of lower substrate water potential; high salinity may also cause ionic imbalance and toxicity in plants (Larcher, 1995; Lambers *et al.*, 1998). It has been suggested that, in general, there exists an inverse relationship between the tolerance level of a plant for a physical stress, such as salinity, and its competitive ability. Thus, no species can be both the most successful competitor and the most stress-tolerant in a given habitat (Grime, 1979). As such, salinity is said to be the determining factor controlling the lower limits of halophyte distribution in salt marshes, while competition may play a key role in determining the upper limits of a species distribution along the salinity gradient (Ungar, 1966; Snow and Vince, 1984; Pennings and Callaway, 1992; Mulder *et al.*, 1996).

Aster laurentianus Fernald is an annual halophyte, endemic to the Gulf of the Saint-Lawrence River (Houle, 1988). This species occurs typically in salt marshes and on sheltered beaches in New Brunswick, Prince Edward Island and Québec, the most important populations being on the Îles de la Madeleine, Québec (Labrecque and Gagnon, 1995). As a result of its limited distribution and also because of the small number of sites it occupies, *A. laurentianus* has been attributed the status of vulnerable species by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC: Houle and Haber, 1990). Seedlings of *A. laurentianus* emerge in June, at a time when the herbaceous canopy is developing in the marshes; since canopy development is heterogeneous, seedlings are exposed to variable radiation levels. Preliminary studies have suggested that interspecific competition for light and high substrate salinity are the most significant limiting factors in the life-cycle of *A. laurentianus* (Morel, 1998; Boudreau and Houle, 1998; Houle *et al., in press*). Therefore, the objectives of this study were to determine (1) the independent effects of photosynthetic photon flux density (PPFD) and salinity on *A. laurentianus* growth, and (2) the combined effect of PPFD and salinity on plant performance, through a series of greenhouse and growth chamber experiments.

2.4 Study species

The life cycle of *A. laurentianus* begins with seed germination in June. Growth occurs through July and August. Plants occur typically in narrow bands (ca. 50 - 200 cm) along the edges of sheltered beaches and salt marshes, immediately above the mean summer water level. At high densities, simple stems (10-15 cm high) are produced, although at lower densities stems may be taller (40 cm) and quite ramified (Boudreau and Houle 1998). Flowering begins in mid-August. The fruit is an achene which bears a pappus. In September most seeds are wind-disseminated, although some may survive water-dissemination since buoyancy in water is possible.

2.5 Materials and methods

In the following three experiments, we used achenes of *A. laurentianus* collected in September of 1997 along the Havre aux Basques lagoon, Îles de la Madeleine (Québec, Canada).

2.5.1 Relative growth rate, photosynthetic photon flux density (PPFD) and salinity

For the two experiments on relative growth rates, achenes of *A. laurentianus* were placed in Petri dishes on one layer of filter paper wetted with distilled water. Dishes were placed in a germination cabinet under a 14 h photoperiod with a thermal regime of 25°C/15°C (day/night). After two weeks, seedlings of similar size (cotyledon stage) were transplanted into 500-cm^3 pots filled with sand.

2.5.1.1 Relative growth rate and PPFD

The aim of this first experiment was to determine the relative growth rate (RGR) of *A. laurentianus* under three levels of photosynthetic photon flux density (PPFD): control, shade treatment 1 and shade treatment 2. To create the three levels of PPFD, shade cages were designed to shelter eight pots each. Wooden frames were covered with either one (shade 1) or two (shade 2) layers of black fiberglass netting, or one layer of transparent plastic (control) into which holes had been pierced to allow for air circulation. For each PPFD level, there were three cages sheltering eight randomly chosen pots of one seedling each. Shade cages were placed in a growth chamber in three blocks, each consisting of the three PPFD treatments. Conditions in the growth chamber were identical to those of the germination cabinet (see above).

Throughout the experiment the plants were soaked until saturation once a week with a complete nutrient solution of 1.12 g L^{-1} of a 20-20-20 fertilizer (N-P-K); the rest of the week they were watered with distilled water in the same manner.

PPFD (μmol m^{-2} s^{-1}) and temperature (°C) measurements were obtained for each cage at the start of the experiment. One seedling per cage was collected at this point and, afterwards, harvesting occurred weekly for a period of six weeks. For each sampling date, one individual per cage was collected and its biomass divided into roots, stems and leaves. Fresh leaf area for each individual was determined with a leaf area meter (CI-202, CID Inc., Vancouver, WA, USA) and each biomass component was dried at 75°C for 24 hours and weighed. The following variables were calculated over the 42 d period according to Hunt (1990):

$$\text{relative growth rate, RGR} = \frac{\log_e (W_2 - W_1)}{t_2 - t_1},$$

where W_n represents plant biomass at time t_n; leaf area ratio, LAR, which represents the ratio of leaf surface to total plant biomass; specific leaf area, SLA, which represents the ratio of leaf surface to leaf mass;
leaf mass ratio, LR, which represents the ratio of leaf mass to total plant biomass; and

$$\text{unit leaf rate, ULR} = \frac{(W_2 - W_1)}{t_2 - t_1} \times \frac{\log_e (LA_2/LA_1)}{LA_2 - LA_1}$$

where LA_n represents leaf area at time t_n. For SLA and LR, values were calculated only for the 7-42 d period, because initial leaf mass was too small to be measured accurately (i.e. ≤ 0.0001 g).

The relationship between all variables is: $RGR = ULR \times LAR = ULR \times SLA \times LR$

After appropriate transformation, the growth variables were analyzed in randomized complete block design analyses of variance (ANOVAs) .

2.5.1.2 RGR and salinity

The aim of this second experiment was to determine the influence of salinity on the RGR of *A. laurentianus*. After transplantation, the seedlings were placed in a greenhouse under conditions similar to those in experiment 1. PPFD, at midday, reached 525 µmol $m^{-2}s^{-1}$ on cloudless days. Seedlings were randomly assigned to five salinity treatments, namely 0 (control), 2.5, 5, 7.5 and 10 g L^{-1} sea salt within each of five blocks. For each level of salinity, there were thus five replicates.

Throughout the experiment, plants were watered as follows: once weekly with a complete nutrient solution (2 g L^{-1} of a 20-20-20 fertilizer, N-P-K), three times weekly with their respective saline solutions and three times weekly with distilled water, on alternate days. Except for one weekly watering from above with distilled water, the rest of the week the plants were watered from underneath; in all cases plants were watered until saturation.

One plant per block was harvested at the start of the experiment and then harvesting occurred once a week for six weeks. As in the previous experiment, fresh leaf area was determined and plant biomass was divided into roots, stems and leaves, dried at 75°C for 24 hours and weighed. RGR, LAR , SLA, LR and ULR were calculated as above. All variables were calculated for the entire period.

Growth variables were analyzed as above in a randomized complete block design ANOVAs.

2.5.2 The combined effect of salinity and PPFD

The aim of this third experiment was to evaluate the combined effect of photosynthetic photon flux density (PPFD) and salinity on the growth of *A. laurentianus*. Achenes were planted directly into 500-cm^3 pots filled with sand. The pots were placed in a greenhouse under a 14-h photoperiod with temperatures varying from approximately 15°C to 30°C. On occasion, temperatures at midday reached close to 40°C. The pots were randomly assigned to a combination of salinity and PPFD treatments. The salinity treatments were: 0 (control), 5 and 10 g/L sea salt, and those of PPFD were: control, shade treatment 1 and shade treatment 2, giving nine combinations of salinity and PPFD treatments. The three levels of PPFD were achieved using the same shade cages as in the first experiment (see above). Cages were grouped in blocks of three PPFD treatments (control, shade 1 and shade 2) and each shade cage sheltered three pots representing the three levels of salinity. There were ten blocks, in all.

Plants were watered once weekly from underneath until saturation with a complete nutrient solution (2 g L^{-1} of a 20-20-20 fertilizer, N-P-K), then alternately with 27 mL of distilled water (dispensed from above) and respective saline solutions (from underneath) for the rest of the week. The volume (27 mL) was determined based on the average daily rainfall on the field.

PPFD (μmol m^{-2} s^{-1}) measurements were obtained for each cage at the start of the experiment under uniform atmospheric conditions. Harvesting occurred after six weeks of growth, while the individuals were still in their vegetative phase. Fresh leaf area for each individual was determined with a leaf area meter as above and biomass was divided into roots, stems and leaves (dried at 75°C for 24 hours and weighed). A soil sample was taken from each of the pots and salinity was measured with a Check mate 90 conducting meter (Corning Inc. Scientific Products Division, Corning, NY). The following variables were calculated: LR and SLA as above; root ratio, RR, which represents the ratio of root mass to total plant biomass; and stem ratio, SR, which represents the ratio of stem mass to total plant biomass.

The growth variables were analyzed in randomized complete block design ANOVAs. Multiple comparison tests (LSD) were used to identify differences among treatment means when the ANOVAs indicated significant differences.

2.6 Results

2.6.1 RGR and PPFD

Values of photosynthetic photon flux densities (PPFDs) were 295 ± 4, 151 ± 10, and 76 ± 1 μmol m^{-2} s^{-1} for the control, treatment shade 1, and treatment shade 2, respectively (mean ± 1 SE; means are significantly different from one another at $P = 0.0001$). Initial seedling biomass and leaf area did not differ significantly among PPFD treatments ($P = 0.4134$ and $P = 0.6447$, respectively). Initial biomass varied from 0.0015 ± 0.0006 to 0.0017 ± 0.0003 g, while leaf area varied from 0.14 ± 0.03 to 0.18 ± 0.03 cm^2 (mean ± 1 SE; Fig. 1). There were significant differences in final seedling biomass among PPFD treatments ($P = 0.0280$). Control seedlings had approximately 2.7 times and 7.8 times more biomass than treatment shade 1 and treatment shade 2, respectively (Fig. 1). Final leaf area did not differ significantly among PPFD treatments ($P = 0.2128$), although control seedlings had approximately 3.2 times and 5.6 times more leaf area than treatment shade 1 and treatment shade 2, respectively.

RGR values differed significantly among PPFD treatments ($P = 0.0293$). They were approximately 2.8 times higher for the control than for treatment shade 2 (Table 1). The RGR value of treatment shade 1 was intermediate between that of the control and the treatment shade 2. ULR differed significantly among treatments ($P = 0.0328$), with higher values for the control than for treatment shade 2 (Table 1). However, there were no significant differences in LAR, SLA, and LR between PPFD treatments (Table 1; $P = 0.3336$, $P = 0.4133$, and $P = 0.1412$, respectively).

2.6.2 RGR and salinity

Initial biomass and leaf area did not differ significantly among salinity treatments ($P = 0.4715$ and $P = 0.1663$, respectively, Fig. 2). Initial biomass was 0.0009 ± 0.0001 g for the control and ranged from 0.0010 ± 0.0002 to 0.0012 ± 0.0001 g for the experimental treatments, while initial leaf area was 0.18 ± 0.02 cm^2 for the control and ranged from 0.14 ± 0.01 to 0.15 ± 0.01 cm^2 for the experimental treatments (mean ± 1 SE; $n = 5$). Total final biomass and leaf area showed significant differences among treatments ($P = 0.0017$ and $P = 0.0060$, respectively). Control seedlings had approximately 4.1 and 10.9 times more biomass, and approximately 5.0 and 13.8 times more leaf area than treatments 2.5 g L^{-1} and 10 g L^{-1}, respectively. Values for treatments 5 g L^{-1} and 7.5 g L^{-1} were intermediate between those of treatments 2.5 g L^{-1} and 10 g L^{-1}.

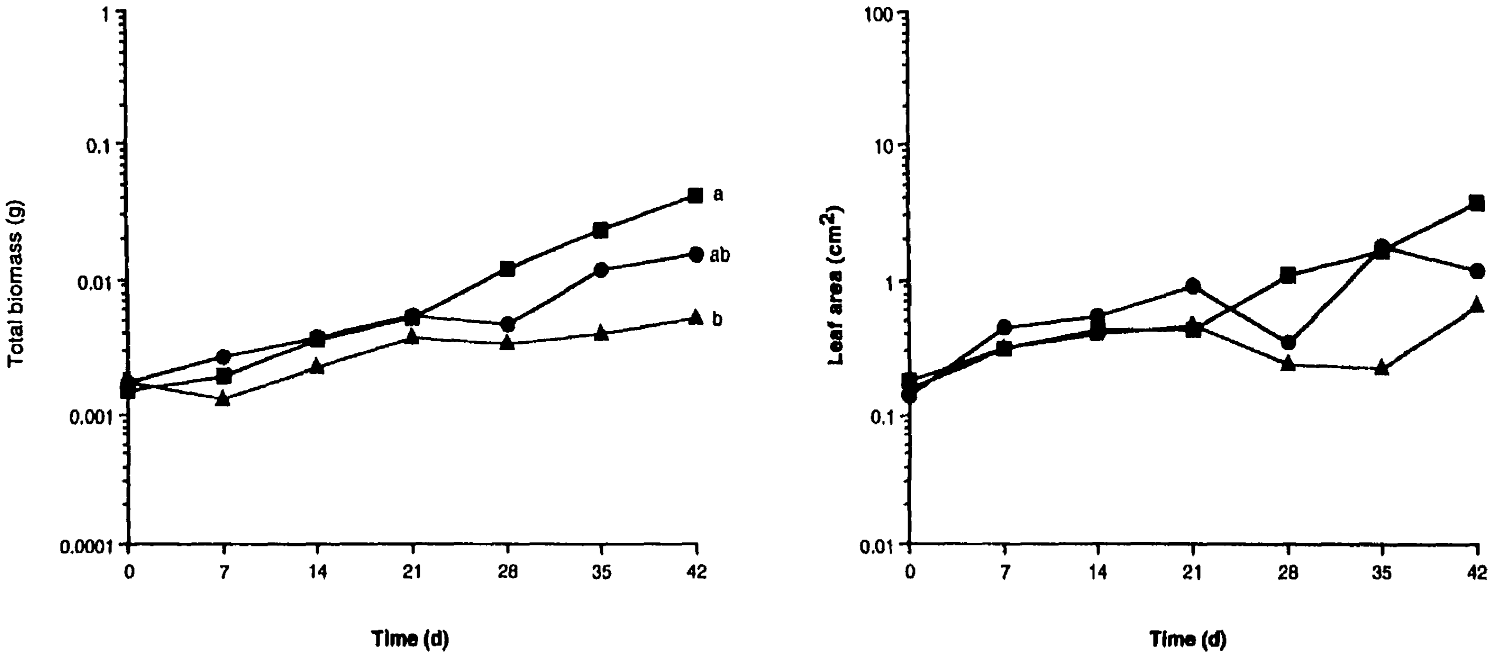

Figure 1. Total biomass and leaf area of *Aster laurentianus* plants according to photosynthetic photon flux density (PPFD) treatments during a 42 d growth period. Squares: control; circles: shade 1; triangles: shade 2. Values are means of three replicates. [a, b] Different letters indicate significant differences between PPFD levels for final biomass ($P \leq 0.05$, protected LSD tests). There were no significant differences among PPFD treatments for final leaf area ($P > 0.05$, randomized complete block design ANOVAs).

Table 1. Relative growth rate (RGR), unit leaf rate (ULR), leaf area ratio (LAR), specific leaf area (SLA) and leaf mass ratio (LR) of *Aster laurentianus* plants exposed to different photosynthetic photon flux densities (PPFDs). Mean ± 1 SE (*n* = 3).

	PPFD levels[1]		
Variables	**Control**	**Shade 1**	**Shade 2**
RGR (g g^{-1} d^{-1})	0.0766±0.0094a	0.0471±0.0083ab	0.0279±0.0039b
ULR (g cm^{-2} d^{-1})	0.0009±0.0001a	0.0006± 0.0001ab	0.0003± 0.0000b
LAR (cm^2 g^{-1})	109.2±14.4	79.2±8.7	105.7±19.9
SLA (cm^2 g^{-1})	227.9±67.3	246.0±8.7	318.2±23.5
LR	0.698±0.039	0.596±0.048	0.561±0.047

[a,b] Different letters indicate significant differences between PPFD levels for RGR and ULR ($P \leq 0.05$; randomized complete block design analysis of variance followed by LSD tests). There are no significant differences among PPFD levels for LAR, SLA and LR ($P > 0.05$).

[1] For exact PPFD values, see the beginning of the Results section.

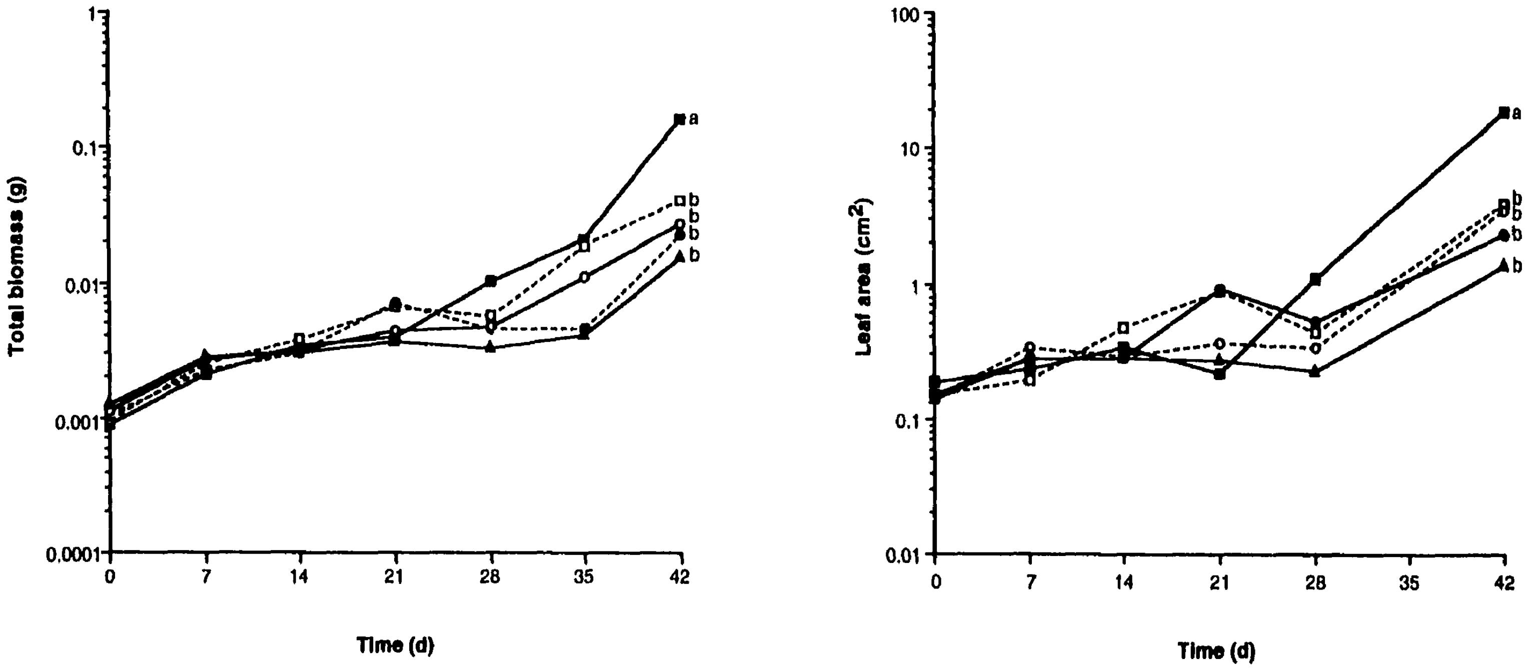

Figure 2. Total biomass and leaf area of *Aster laurentianus* plants according to salinity levels during a 42-d growth period. Black squares: control, 0 g sea salt L^{-1}; open squares: 2.5 g sea salt L^{-1}; black circles: 5.0 g sea salt L^{-1}; open circles: 7.5 g sea salt L^{-1}; triangles: 10 g sea salt L^{-1}. Values are means of five replicates.

$^{a, b}$ Different letters indicate significant differences among salinity treatments

RGR values differed significantly among salinity treatments ($P = 0.0005$; Table 2). Protected LSD tests showed that although RGR decreased as salinity increased from 0 to 10 g L^{-1}, only the RGR value for the control was significantly different from the other treatments: they were approximately 1.5 and 2.2 times higher for the control than for treatments 2.5 g L^{-1} and 10 g L^{-1}, respectively (Table 2), with values for 5 g L^{-1} and 7.5 g L^{-1} intermediate. LAR differed significantly among treatments ($P = 0.0405$), such that values for the control were significantly different from those for 7.5 g L^{-1} and 10 g L^{-1}, while values for 2.5 g L^{-1} and 5.0 g L^{-1} were intermediate. LAR for the control was approximately 1.7 times higher than for 10 g L^{-1}. Although ULR was only marginally significant ($P = 0.0786$), values for the control were approximately 1.7 times higher than for 10 g L^{-1}. SLA and LR did not differ significantly among treatments ($P = 0.9114$ and $P = 0.1192$ respectively).

2.6.3 The combined effect of salinity and PPFD on plant performance

Average values of PPFD, under uniform atmospheric conditions, were 348 ± 30 (control), 188 ± 16 (treatment shade 1) and 109 ± 6 (treatment shade 2) $\mu mol m^{-2} s^{-1}$ (all significantly different from one another at $P \leq 0.05$, protected LSD test). Average calculated values of soil salinity measured for salinity treatments 0, 5 and 10 g L^{-1} respectively, were: 0.1850 ± 0.0249, 1.530 ± 0.1584 and 2.1071± 0.2156 g L^{-1} for control PPFD; 0.2615 ± 0.0302, 1.2530 ± 0.0998 and 1.7300 ± 0.2778 g L^{-1} for PPFD treatment 1; and 0.1752 ± 0.0144, 1.5449 ± 0.2355 and 2.3414 ± 0.1688 g L^{-1} for PPFD treatment 2 (mean ± 1 SE, $n = 10$; significant salinity effect at $P = 0.0001$, but no PPFD effect at $P = 0.7844$).

The interaction between PPFD and salinity was not significant for total biomass ($P = 0.8733$) nor for total leaf area ($P = 0.8293$). However, there was a significant effect of PPFD on total plant biomass but not on leaf area ($P = 0.0001$ and $P = 0.1333$, respectively) and a significant effect of salinity on total plant biomass and leaf area ($P = 0.0001$).

Table 2. Relative growth rate (RGR), unit leaf rate (ULR), leaf area ratio (LAR), specific leaf area (SLA), and leaf mass ratio (LR) of *Aster laurentianus* plants exposed to different salinity levels. Mean ± 1 SE (*n* = 5).

	Salinity levels (g L^{-1})				
Variables	0	2.5	5	7.5	10
RGR (g g^{-1} d^{-1})	0.1176± 0.0098a	0.0771± 0.0118b	0.0720± 0.0058b	0.0667± 0.0113b	0.0545± 0.0077b
ULR (g cm^{-2} d^{-1})	0.0010±0.0001	0.0007±0.0001	0.0007±0.0000	0.0007±0.0001	0.0006±0.0000
LAR (cm^2 g^{-1})	166.2±12.7a	129.9±12.5ab	124.1±13.6ab	112.9±21.2b	97.4±9.9b
SLA (cm^2 g^{-1})	275.3±19.9	350.4±107.9	247.4±22.7	338.9±146.1	282.8±96.4
LR	0.629±0.019	0.540±0.056	0.572±0.034	0.510±0.027	0.486±0.045

[a,b] Different letters indicate significant differences between salinity levels for RGR and LAR ($P \leq 0.05$; randomized complete block design analysis of variance followed by LSD tests).
There are no significant differences among salinity levels for ULR, SLA and RR ($P > 0.05$).

There were no interactions between PPFD and salinity treatments on SLA ($P = 0.0582$), RR ($P = 0.8033$), SR ($P = 0.2130$) and LR ($P = 0.7799$; Fig. 3; Table 3). However, taken independently, PPFD had a significant effect on both SLA ($P = 0.0001$) and SR ($P = 0.0091$), but none on LR ($P = 0.7602$) or RR ($P = 0.3607$). For SLA, values were lower in the control than in the treatment shade 1 and treatment shade 2. In addition, control and treatment shade 1 plants had a lower SR than treatment shade 2 plants. Salinity had a significant independent effect on SLA ($P = 0.0001$), RR ($P = 0.0001$), SR ($P = 0.0056$) and LR ($P = 0.0001$). Salinity affected SLA such that all treatments were significantly different from one another. For RR, SR and LR, the 10 g L^{-1} treatment was significantly different from the control and the 5 g L^{-1} treatment.

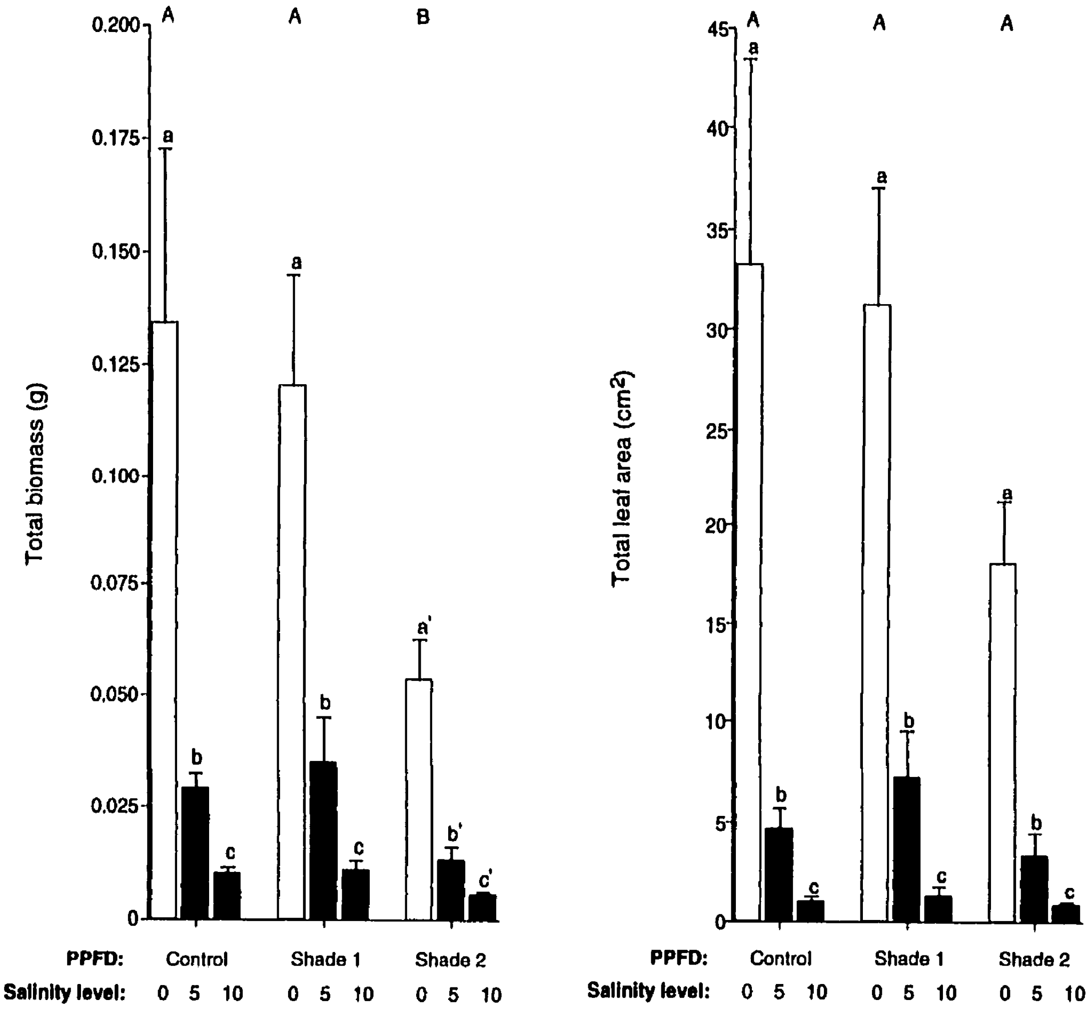

Figure 3. Total biomass and leaf area of *Aster laurentianus* plants according to different combinations of salinity and photosynthetic photon flux density treatments. For exact PPFD values, see Results section. For salinity, open bars = 0 g sea salt L^{-1}; grey bars = 5 g sea salt L^{-1}; black bars = 10 g sea salt L^{-1}. Values are means ± 1 SE, *n* = 10. Different letters indicate significant differences between levels for each factor: upper case letters for differences in PPFD levels; lower case letters for differences in salinity levels ($P \leq 0.05$; randomized complete block design analysis of variance followed by LSD tests).

Table 3. Specific leaf area (SLA), root mass ratio (RR), stem mass ratio (SR) and leaf mass ratio (LR) of *A. laurentianus* plants exposed to different combinations of salinity and photosynthetic photon flux density (PPFD) treatments. Mean ± 1 SE (n = 10).

Salinity level: 0 g L^{-1}	PPFD		
	0	1	2
SLA (cm^{2}g^{-1})	440.0±16.6Aa	486.4±10.0Ba'	582.5±14.5Ba'
RR	0.362±0.021Aa	0.330±0.014Aa	0.298±0.015Aa
SR	0.098±0.011Aa	0.125±0.011Aa	0.134±0.011Ba'
LR	0.540±0.016Aa	0.545±0.015Aa	0.568±0.013Aa
Salinity level: 5 g L^{-1}	**PPFD**		
	0	1	2
SLA (cm^{2}g^{-1})	316.9±22.6Ab	360.3±20.3Bb'	375.0±43.1Bb'
RR	0.330±0.045Aa	0.367±0.042Aa	0.357±0.065Aa
SR	0.111±0.008Aa	0.112±0.008Aa	0.144±0.025Ba'
LR	0.560±0.038Aa	0.521±0.038Aa	0.499±0.049Aa
Salinity level: 10 g L^{-1}	**PPFD**		
	0	1	2
SLA (cm^{2}g^{-1})	210.5±20.0Ac	272.3±23.6Bc	305.7±27.7Bc'
RR	0.507±0.084Ab	0.579±0.093Ab	0.480±0.063Ab
SR	0.099±0.013Ab	0.074±0.016Ab	0.115±0.014Bb'
LR	0.394±0.076Ab	0.347±0.084Ab	0.405±0.057Ab

[A, B, a, b] Different letters indicate differences between salinity levels (lower case letters) or between PPFD levels (upper case letters; P ≤ 0.05, randomized complete block design analysis of variance followed by LSD tests).

' Primes indicate differences between salinity levels for different PPFD levels which differ significantly from other PPFD levels.

For exact PPFD levels, see the Results section.

2.7 Discussion

2.7.1 RGR and PPFD

Shade treatments reduced final seedling biomass of *A. laurentianus*. This response occurred in conjunction with significant decreases in RGR and ULR. In general, differences in LAR tend to be offset by differences in ULR (Young, 1975; Sims *et al.,* 1994; Hunt and Cornelissen, 1997) so that little or no effect of PPFD is felt on RGR. In our case, LAR showed no effect of increased shade, although a higher LAR is a common response to a lower PPFD, as a result of a higher SLA (Nobel *et al.*, 1975; Pons, 1977; Björkman, 1981; Sims *et al.,* 1994). Here, SLA increased only slightly with decreased PPFD, while LR decreased little; this compensation may explain why LAR showed no effect of increased shade (since $LAR = LR \cdot SLA$). The RGR response we observed was therefore primarily a result of ULR, and not LAR or its components.

Mean RGR values for herbaceous dicots were found to be approximately 0.173 d^{-1} (from 0.073 to 0.268 d^{-1}; McKenna and Shipley, 1999) and 0.194 d^{-1}(from 0.101 to 0.307 d^{-1}; Hunt and Cornelissen, 1997). RGRs calculated in this experiment are in the low range of these values (Table 1), indicating that *A. laurentianus* is a relatively slow-growing species.

Although growth is possible under low light conditions, light appears to remain a limiting factor in the growth and development of *A. laurentianus.* The highest experimental light level we used (control) was the most optimal for growth. Our results suggest that *A. laurentianus* seeds which germinate in areas where the established canopy excludes a significant amount of light (such as shade treatment 2) may place the seedlings at a competitive disadvantage by reducing their RGR. Indeed, observations in the field suggest that plants that are found in less shaded and dense environments produce far greater stem ramifications and longer stems (up to 40 cm compared to 10-15 cm when crowded; Boudreau and Houle, 1998).

These individuals also produce a greater number of flowers and, therefore, of seeds (personal observation). In short, seedlings grow best at higher than at lower PPFDs.

2.7.2 RGR and salinity

Salinity significantly decreased total biomass and leaf area of *A. laurentianus*. These results are similar to those reported for other salt marsh species (Wang *et al.,* 1997; Lissner and Schierup, 1997; Bernstein *et al.,* 1995; Ewing, 1981; Shininger, 1979). High salinity affects growth by reducing the soil water potential (Pennings and Callaway, 1992) which reduces water uptake and therefore nutrient absorption by the plant. This water stress may lead to decreased transpiration, lower stomatal conductance and decreased C-fixation. Increased osmoregulation requires greater energy, and consequently an allocation of the end-products of photosynthesis to osmoregulation as opposed to growth (Lissner and Schierup, 1997). Houle *et al.* (in press) showed that salinity does not affect the instantaneous photosynthetic rate of *A. laurentianus* and suggested that the lower biomass of salt-stressed plants is not associated with decreased net carbon assimilation rate but that respiration, particularly root and maintenance respiration, is significantly higher in salt-stressed plants. Respiration represents another process which requires an allocation of the end-products of photosynthesis, therefore decreasing potential seedling growth.

Salinity significantly decreased RGR and LAR, but only moderately decreased ULR. Our results for RGR are supported by those of Schwartz and Gale (1984) and Wang *et al.* (1997) which suggest that RGR decreases significantly with increasing salinity. The effect of salinity on SLA was not significant, which indicates that decreased LAR with increased salinity is mostly associated with decreased LR. This may be related to leaf shedding, a phenomenon which reduces water stress, and was observed for plants under high salinity treatments in this experiment. Therefore, growth is reduced by salinity, but plants can still persist. This indicates that except for the possible effects of flooding and water-logging, *A. laurentianus* can tolerate the salinity conditions in its natural habitat. As shown by Houle *et al.* (*in press*), seed germination seems to be the stage most sensitive to salinity for this species, not growth.

2.7.3 Combined effect of PPFD and salinity

Contrary to our original hypothesis, there were no significant interactions between PPFD and salinity on any of the variables analyzed. As for the independent effect of decreased PPFD, it significantly decreased total biomass and increased SLA and SR. The independent effect of increased salinity significantly decreased all variables (total biomass, total leaf area, SLA, SR and LR) except for RR, which increased significantly. These results compare with those obtained for the previous two experiments.

Despite a lack of interaction between the two variables, light likely serves to reinforce existing salinity gradients through increased evapotranspiration of the substrate complex. Spatial analysis shows that in the field, there exists a positive relationship between PPFD and salinity; that is, where there is the highest level of radiation, there is also the greatest substrate salinity (unpublished data). Indeed, plants observed in open and exposed areas in the field were generally located much farther from the water's edge than those found under the herbaceous canopy (personal observations). Therefore, *A. laurentianus* may actually benefit from interspecific competition for light as the presence of a herbaceous canopy reduces evapotranspiration from the substrate and may help the plant avoid hypersaline conditions.

2.8 Conclusion

When no other factors are limiting, PPFD is an important limiting factor in the growth of *A. laurentianus*. However, the natural habitat of this species is also characterized by high substrate salinity and threats of water-level fluctuations and sometimes water-logging (Houle *et al., in press*). Under these circumstances, and as our results indicate, salinity may be equally limiting. As was suggested above, a herbaceous canopy may serve to reduce the hypersaline conditions often found in summer when these plants emerge. *A. laurentianus* life-cycle as a summer annual may thus be related to the development of a herbaceous canopy along the shoreline and the resulting reduction in substrate salinity (Houle *et al.*, *in press*). However, this herbaceous canopy also reduces PPFD availability. Thus, the trade-off between *A. laurentianus* tolerance to low PPFD and to high substrate salinity appears to be responsible for this species distribution in narrow bands along the edges of salt marshes and sheltered beaches.

2.9 Literature cited

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CONCLUSION GÉNÉRALE

La zonation d'espèces végétales est une caractéristique typique des milieux sujets à des stress physiques et aux perturbations fréquentes. Le long des rivages côtiers, un stress physique reconnu comme étant important est la salinité du substrat. Ce facteur limitant est souvent amplifié par des perturbations naturelles tel l'effet des vagues et des débris végétaux sur le rivage. De plus, en agissant comme un stress physique par sa réduction de la productivité des plantes, la compétition interspécifique pour les ressources peut aussi limiter la distribution des espèces.

Dans les milieux côtiers, il a été suggéré que la salinité détermine la limite inférieure de distribution des espèces végétales, tandis que la limite supérieure des espèces est déterminée par la compétition interspécifique pour les ressources telles que la lumière, les nutriments et l'eau. Pour les plantes endémiques et rares de ces milieux, une connaissance des facteurs biotiques et abiotiques qui limitent l'abondance et la performance des populations végétales est essentielle pour développer des stratégies de gestion et de conservation de ces espèces.

Aster laurentianus Fernald est une espèce endémique et rare du golfe du Saint-Laurent, ses populations principales se retrouvant aux îles de la Madeleine, Québec. Il a été démontré, par une première étude, que l'importance relative des variables physiques et structurantes de son milieu change selon les caractéristiques physiques du site donné. Cette importance relative est souvent déterminée par l'exposition aux vagues et au vent des rivages des lagunes et des marais salés où l'espèce se trouve. Une perturbation est définie comme étant tout facteur qui détruit la biomasse. Ainsi, même si la salinité demeure un facteur qui limite la répartition de *A. laurentianus* le long des marais salés, certaines perturbations environnementales comme l'importance des dépôts de plantes mortes (zostère) peuvent renforcer et parfois prédominer sur les gradients de stress existants.

Cette première étude a donc considéré l'effet de la topographie, la salinité et les dépôts de zostère sur la distribution de *A. laurentianus* sur deux sites différents en milieu naturel. Il a été démontré, pour chaque site, que la topographie a un effet structurant sur la salinité du substrat, les dépôts de zostère et la densité de *A. laurentianus*. Sur un premier site très exposé aux vagues et au vent, la densité de l'espèce est influencée par la présence de zostère; ici, la salinité n'agit pas de façon directe sur cette variable. Sur un deuxième site protégé, la salinité, non pas la zostère, détermine la répartition de l'espèce. Il apparaît alors que la salinité et les dépôts de zostère ont tous deux un effet structurant sur la densité de *A. laurentianus*, selon les particularités du site étudié.

Dans les marais salés, il a été démontré que la salinité et la compétition pour la lumière sont deux facteurs abiotiques limitants pour la croissance et la performance des espèces végétales. Cette observation a été vérifée, pour *A. laurentianus*, par une seconde étude en milieu contrôlé. Cette étude a démontré qu'un taux de salinité élevé ainsi qu'un taux de lumière faible affectent négativement la performance de *A. laurentianus*. Par contre, la salinité et la lumière sont positivement corrélées en milieu naturel, de sorte que les conditions idéales pour la croissance et la performance de *A. laurentianus* sont rarement atteintes en milieu naturel. Selon l'énoncé de Grime (1979), une espèce végétale ne peut être à la fois la meilleure compétitrice (pour la lumière) et la plus tolérante aux stress (salinité). Ainsi, *A. laurentianus* doit maximiser sa tolérance aux salinités élevées et à la lumière faible pour se maintenir dans son milieu. Cette compensation serait donc potentiellement responsable de la distribution de cette espèce le long des rivages des lagunes et des marais salés, aux Îles de la Madeleine.

A. laurentianus est une espèce dont les populations semblent fluctuer de façon importante d'année en année. À partir des études présentées, nous avons une meilleure compréhension des facteurs qui limitent la répartition et l'abondance de cette espèce aux Îles de la Madeleine, et des facteurs qui affectent sa croissance et sa performance en milieu contrôlé. Ces données sont importantes non seulement sa performance en milieu contrôlé. Ces données sont importantes non seulement pour la compréhension des facteurs limitatifs pour les plantes en milieu salin en général, mais surtout pour aider à comprendre davantage la dynamique des populations de cette espèce si peu connue.

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