An experimental test of the occurrence of competitive interactions among SE Asian seagrasses

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ABSTRACT: The occurrence of competitive interactions among the seagrass species present in a multispecific SE Asian seagrass meadow was tested by the cumulative removal of shoots of an increasing number of seagrass species from the meadow in order of decreasing and increasing resource requirements for plant growth. The removal of shoots of the dominant species *Thalassia hemprichii* had very few effects on shoot size, shoot density and leaf area index of the extant seagrass species. The shoot density of *Enhalus acoroides* decreased when *T. hemprichii* shoots were removed, but that of *Syringodium isoetifolium* increased when the shoots of all the species with higher resource requirements than itself were removed from the experimental plots. The size of *Halophila ovalis* shoots decreased by 30% when both *T. hemprichii* and *E. acoroides* shoots were removed from the plots. The shoot density of *T. hemprichii* increased only when the shoots of all the accompanying species were removed from the plots. The results show that species interactions in this multispecific seagrass meadow are asymmetric. The elucidation of the nature of the interactions among seagrass species provides a key to understanding the maintenance of the high biodiversity and production that characterizes pristine SE Asian coastal ecosystems.

KEY WORDS: Interspecific competition · Tropical seagrasses · SE Asia

INTRODUCTION

Pristine seagrass meadows in SE Asia are typically multispecific, with up to 8 species growing together (Brouns 1987, Nienhuis et al. 1989, Vermaat et al. 1995). As nutrient limitation is widespread in tropical seagrass communities (e.g. Short et al. 1985, Powell et al. 1989, Duarte et al. 1995, Agawin et al. 1996), interspecific competition for nutrients might be common in SE Asian multispecific seagrass meadows. Evidence for the presence of competitive interactions among seagrasses is supported by the observation of species replacement in Caribbean seagrass meadows when nutrient availability is experimentally increased (Williams 1987, Fourqurean et al. 1995) and during recolonization after disturbance (Williams 1990).

Experiments investigating the response of SE Asian seagrass communities to disturbance (sediment burial, cf. Duarte et al. 1997, and siltation, cf. Bach et al. 1998) have shown that the loss of *Thalassia hemprichii*, the dominant species in many of these meadows, results in the opportunistic growth of other species like *Halophila ovalis*, *Halodule uninervis* and *Syringodium isoetifolium*, which suggests that *T. hemprichii* suppresses their growth. These responses might be the result of the alleviation of competitive interactions among *T. hemprichii* and the named species for nutrients, as nutrients are in short supply in these meadows (Agawin et al. 1996). Alternatively, the opportunistic growth of some seagrass species after the loss of the dominant species from the community might be driven by an increase in the availability of light, following the thinning of the leaf canopy. Given the 2-order-of-magnitude difference in

size among SE Asian seagrass species (Vermaat et al. 1995, Terrados et al. 1999a), interspecific competition for light is likely to occur in multispecific seagrass meadows. However, no experimental evidence of competitive interactions among SE Asian seagrasses, nor of the mechanisms underlying these competitive interactions are available yet.

We report here a test of the occurrence of competitive interactions in SE Asian seagrass meadows. The experiments were based on the selective removal of the shoots of some of the species present in a multispecific (7 species) seagrass meadow growing off Silaqui Island (Bolinao, Philippines). The experimental approach adopted is based on the assumption that species with high biomass and production in the meadow have also high absolute requirements of resources for plant growth (nutrients, light), while species with low biomass and production have low absolute resource requirements. The removal of a species with high absolute resource requirements will increase resource availability to the extant species in the experimental plot. The vegetative development of the extant species will then increase if their growth was resource-limited by the resource use of the removed species. We hypothesized that the magnitude of the growth response of the extant species would be positively correlated with the resource requirements of the species removed. We also surmised that a cumulative removal of species in order of decreasing resource requirements would determine an increasing availability of resources and, therefore, large growth responses of the extant species. Additionally, we hypothesized that the removal of species with low biomass and production (low resource requirements) would promote minor growth responses of the extant, more dominant species. We tested the changes in plant size (leaf surface of a shoot), abundance (shoot density) and leaf area index of the extant seagrass species 3 mo after the experimental removal of seagrass shoots.

METHODS

The experiments were performed in a multispecific seagrass meadow growing off Silaqui Island (Bolinao, Pangasinan Province, Philippines; 16° 26.35' N, 119° 55.46' E). The meadow is located in the reef lagoon at an average depth of about 0.8 m (maximum tidal range 0.75 m) and is dominated, both in terms of biomass and production, by *Thalassia hemprichii*, followed by *Enhalus acoroides* and, in order of decreasing biomass and production, *Cymodocea rotundata*, *Syringodium isoetifolium*, *Halodule uninervis*, *Cymodocea serrulata* and *Halophila ovalis* (Vermaat et al. 1995). The annual productivity of this meadow is high (2142 g DW m^{-2} yr^{-1},

Vermaat et al. 1995, cf. Duarte & Chiscano 1999), and seagrass growth is nutrient-limited (Agawin et al. 1996).

We tested the presence of competitive interactions among seagrass species through the complete removal of the shoots (i.e. the leaves and the upper portion of the short shoot rhizome, together with the meristems which produce them) of selected species in the experimental plots. As 7 seagrass species were present in the meadow, a complete factorial design would have required the setting of 351 experimental plots (117 different treatments possible with a minimum of 3 replicates of each). The large number of experimental plots required would extend over a large area introducing additional sources of variability derived from spatial heterogeneity, which could only be accounted for by increasing the number of replicates. We reduced the dimensions of the experiment by performing 2 cumulative removals of seagrass shoots (Table 1).

Expt 1 started by removing the shoots of the species with the highest biomass and production in the meadow, *Thalassia hemprichii* (number of species removed = 1), and continued by removing the shoots of the 2 species with highest biomass and production, *T. hemprichii* and *Enhalus acoroides* (number of species removed = 2), in other replicate plots. We completed the experiment by removing the shoots of an increasing number of species in each treatment (3, 4, 5, and 6 species removed) in additional replicate plots until only the shoots of the species with the lowest biomass and production in the meadow, *Halophila ovalis*, were allowed to grow. In a complementary way, Expt 2 started by removing the shoots of the species with the lowest biomass and production in the meadow, *H. ovalis* (number of species removed = 1), and was completed by removing the shoots of an increasing number of species at each treatment (2, 3, 4, 5, and 6 species removed) until only the shoots of the species with the highest biomass and production, *T. hemprichii*, were left. Both experiments contained control plots where no seagrass shoots were removed.

The experimental plots (0.25 m^2 quadrats) were placed over a visually homogeneous section of the meadow at a distance of at least 1.5 m from each other. The treatments (Table 1) were randomly assigned to the plots and each treatment had 5 replicates (35 plots per experiment). The homogeneity of the species composition in the plots was tested in Expt 2 by comparing (1-way ANOVA) the number of shoots of each seagrass species present in the plots before the removal of shoots among the different treatments. ANOVA results indicate that there were no differences in species composition among the treatments (p > 0.13). Equivalent data for Expt 1 were not obtained, but, as the plots were chosen by the same person and following the same criteria, we con-

Table 1. Treatments applied in the 2 experiments testing the effects of cumulative removal of species, in order of decreasing (Expt 1) or increasing (Expt 2) requirements of resources for plant growth, on a multispecific seagrass meadow off Silaqui Island, Philippines. Net production (g DW m^{-2} yr^{-1}) and the percentage of the total production (in parentheses) of the different species: *Thalassia hemprichii* = 1595 (74.4%), *Enhalus acoroides* = 215.6 (10.0%), *Cymodocea rotundata* = 204.3 (9.5%), *Syringodium isoetifolium* = 57.2 (2.7%), *Halodule uninervis* = 41.8 (1.9%), *Cymodocea serrulata* = 14.9 (0.7%) and *Halophila ovalis* = 13.4 (0.6%) (data from Vermaat et al. 1995)

No. of seagrass species removed	Expt 1: decreasing requirement of nutrients	Expt 2: increasing requirement of nutrients
1	*Thalassia hemprichii*	*Halophila ovalis*
2	*Thalassia hemprichii* *Enhalus acoroides*	*Halophila ovalis* *Cymodocea serrulata*
3	*Thalassia hemprichii* *Enhalus acoroides* *Cymodocea rotundata*	*Halophila ovalis* *Cymodocea serrulata* *Halodule uninervis*
4	*Thalassia hemprichii* *Enhalus acoroides* *Cymodocea rotundata* *Syringodium isoetifolium*	*Halophila ovalis* *Cymodocea serrulata* *Halodule uninervis* *Syringodium isoetifolium*
5	*Thalassia hemprichii* *Enhalus acoroides* *Cymodocea rotundata* *Syringodium isoetifolium* *Halodule uninervis*	*Halophila ovalis* *Cymodocea serrulata* *Halodule uninervis* *Syringodium isoetifolium* *Cymodocea rotundata*
6	*Thalassia hemprichii* *Enhalus acoroides* *Cymodocea rotundata* *Syringodium isoetifolium* *Halodule uninervis* *Cymodocea serrulata*	*Halophila ovalis* *Cymodocea serrulata* *Halodule uninervis* *Syringodium isoetifolium* *Cymodocea rotundata* *Enhalus acoroides*

studied are short (from 2.2 to 35.6 d, cf. Vermaat et al. 1995), and mean annual leaf growth rates are high (from 0.9 to 3.8 cm^2 shoot^{-1} d^{-1}, Agawin et al. unpubl. results), the duration of the experiments (around 3 mo) was long enough to detect changes in shoot size in all the species present (Agawin et al. 1996). Although the production of new shoots proceeds at a slower pace than the production of new leaves or leaf growth (Vermaat et al. 1995), 3 mo should be enough to detect changes in shoot abundance of most of the species (Agawin et al. 1996, Duarte et al. 1997).

We quantified the growth response of each species in terms of changes in shoot size (leaf surface per shoot, cm^2), shoot density (number of shoots m^{-2}) and leaf area index (LAI, m^2 of leaves m^{-2}) because these variables are very sensitive to an increase of resource availability in seagrass meadows (Pérez et al. 1991, Agawin et al. 1996). As there is a 2-order-of-magnitude difference in shoot size among the seagrass species present (Vermaat et al. 1995, Terrados et al. 1999a), the comparisons of species responses based on shoot density only (shoots m^{-2}) might be misleading. To overcome this problem, we combined changes in shoot size and density into an estimate of the LAI per species. In addition, the LAIs of the different species present can be summed up to estimate the community LAI, which allows the examination of the compounded response of the whole seagrass community to the removal of seagrass shoots.

The significance of the growth responses of each seagrass species after the removal of shoots of an increasing number of accompanying species was tested using 1-way ANOVA. Whenever ANOVA analyses indicated a significant response, we used Tukey's HSD multiple comparison test to establish pairwise comparisons and test the significance of differences between treatments (Sokal & Rohlf 1981). We calculated an expected value of the community LAI for each of the treatments based on the mean values of the LAI of each species in the control plots (no seagrass species removed). As an example, the expected community LAI of the treatment in which the shoots of the species *Thalassia hemprichii*, *Enhalus acoroides* and *Cymodocea rotundata* were removed from the plots was estimated as the mean community LAI value in the control plots minus the sum of the mean LAI values of those species removed in the control

sider that plots in this experiment were also likely homogeneous in their species composition. The shoots were removed from the plots by clipping them below the meristem. This manipulation impedes the regrowth and, therefore, the use of resources for plant growth (nutrients, light) by the nominally removed species in the plot without physically disturbing the sediment or the other species present in the plot. The experiments were maintained at monthly intervals by clipping any new shoot observed of the species nominally excluded from each plot. Expt 1 was initiated between 24 and 25 April 1996, and finished between 16 and 17 July 1996, while Expt 2 was initiated between 15 and 16 August 1996, and finished between 4 and 6 November 1996. At the end of the experiments, we collected and counted the shoots of each species present in the plots, and measured the length and width of all the leaves in the shoots to estimate the leaf area per shoot for each species and plot. As the mean annual leaf plastochrone intervals of the seagrass species

plots. The significance of the differences between expected and observed values of community LAI in each experiment was tested using Wilcoxon's signed-ranks test (Sokal & Rohlf 1981).

RESULTS

Removal of shoots of an increasing number of species in order of decreasing requirement of resources for plant growth (Expt 1)

The removal of shoots of the dominant species *Thalassia hemprichii* had very few effects on shoot size, shoot density and LAI of the extant seagrass species (Table 2). Contrary to expectations, the size of *Halophila ovalis* shoots decreased by 30% when both *T. hemprichii* and *Enhalus acoroides* shoots were removed from the plots, and remained low when the shoots of additional species were removed (Fig. 1). The shoot size of *Cymodocea rotundata* increased by a 10% when *T. hemprichii* shoots were removed but decreased <10% when both *T. hemprichii* and *E. acoroides* shoots were removed from the plots. Shoot size of other seagrass species was not affected by any of the shoot-removal treatments. Shoot density of

E. acoroides decreased when *T. hemprichii* shoots were removed, but that of *Syringodium isoetifolium* increased when the shoots of all the species with higher nutrient requirements than itself were removed from the plots (Fig. 2, Table 2). Shoot density of other species was not affected by the shoot removals. As a consequence of the minor changes in shoot size and density observed, the LAI of the species was not significantly affected by any of the treatments (Fig. 3, Table 2). However, a trend of decreasing LAI with the increase in the number of species with shoots removed was suggested by data on *Cymodocea rotundata*, *Halodule uninervis* and *C. serrulata* (Fig. 3).

Community LAI decreased as the number of species with shoots removed from the plots increased (Fig. 4a), which is a direct consequence of the experimental manipulations. However, the observed community LAI values deviated from those expected strictly from the treatments applied. Observed community LAI values were smaller (Wilcoxon's signed rank test, p < 0.05) than those expected from the treatments (data points below the 1:1 line, Fig. 4b). This was particularly evident when only *Thalassia hemprichii* was removed, as indicated by a slope < 1 (*t*-test, p < 0.01) of the regression line between observed and expected community LAI values (Fig. 4b).

Table 2. Effects of removing an increasing number of seagrass species on shoot size, shoot density and leaf area index of the extant species. Differences between means of each treatment were tested using 1-way ANOVA and post hoc Tukey's HSD multiple comparisons test. Values in **bold** indicate significant (p < 0.05) results

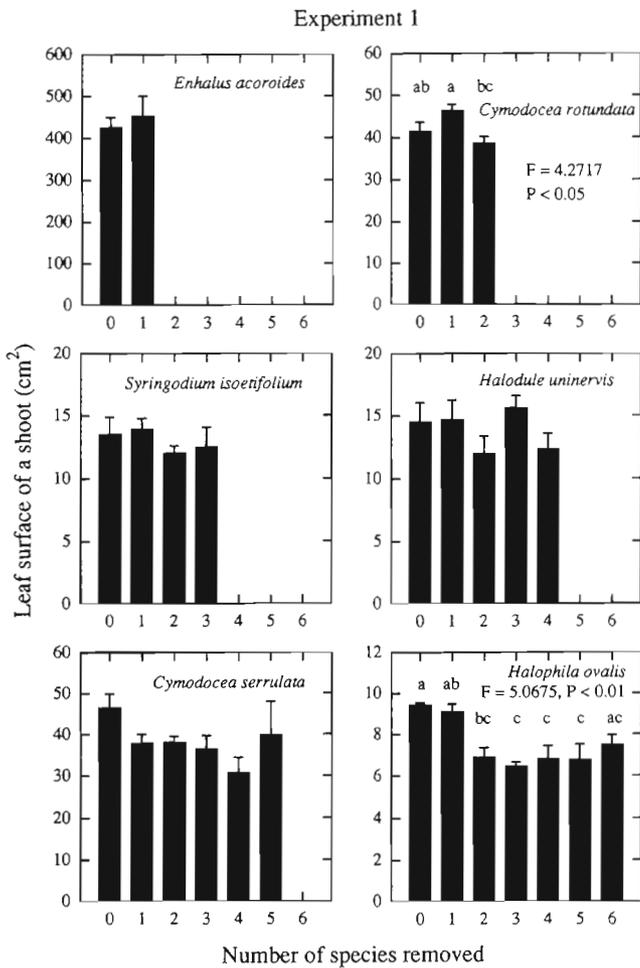|	Shoot size (cm² leaves shoot⁻¹)			Shoot density (shoots m⁻²)			Leaf area index (m² leaves m⁻²)		
	df	F-ratio	p	df	F-ratio	p	df	F-ratio	p
Thalassia hemprichii									
Expt 1	–	–	–	–	–	–	–	–	–
Expt 2	6	0.4709	0.8239	6	**6.4882**	**0.0002**	6	**6.4658**	**0.0002**
Enhalus acoroides									
Expt 1	1	0.2418	0.6361	1	**7.0784**	**0.0288**	1	2.1648	0.1794
Expt 2	5	0.5989	0.7012	5	0.8840	0.5069	5	0.3618	0.8695
Cymodocea rotundata									
Expt 1	2	**4.2717**	**0.0424**	2	3.3667	0.0723	2	2.9091	0.0968
Expt 2	4	1.8969	0.1504	4	0.3512	0.8401	4	0.7665	0.559
Syringodium isoetifolium									
Expt 1	3	0.5836	0.6349	3	**4.0558**	**0.0254**	3	1.1514	0.3607
Expt 2	3	2.6032	0.0878	3	0.0609	0.9796	3	0.2509	0.8595
Halodule uninervis									
Expt 1	4	1.235	0.3292	4	1.1407	0.3660	4	1.3344	0.2935
Expt 2	2	0.3087	0.7405	2	0.1793	0.8380	2	0.0156	0.9845
Cymodocea serrulata									
Expt 1	5	1.3903	0.2647	5	1.1982	0.3398	5	2.1278	0.0983
Expt 2	1	0.0561	0.8195	1	0.2762	0.6134	1	0.1749	0.6883
Halophila ovalis									
Expt 1	6	**5.0675**	**0.0015**	6	1.1445	0.3632	6	1.3939	0.2545
Expt 2	–	–	–	–	–	–	–	–	–

Experiment 1

Experiment 1

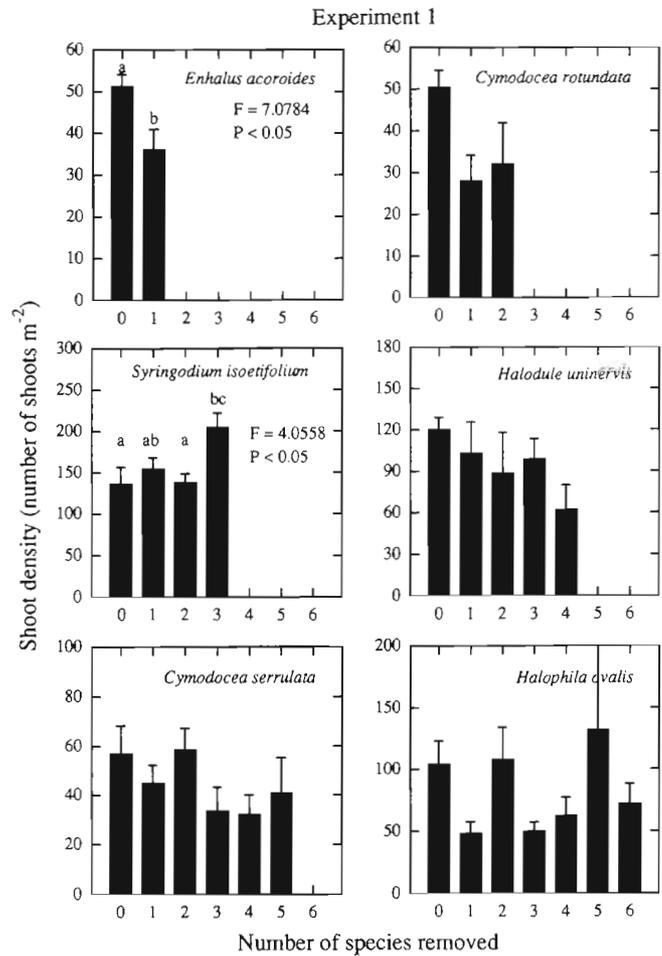Fig. 1. Shoot size (as leaf surface of a shoot, cm^2) of the seagrass species present in the experimental plots 3 mo after the removal of shoots of an increasing number of species in order of decreasing requirement of resources for plant growth (Expt 1). Error bars are +1 SE. Significant differences between individual treatments are indicated by different letters

Fig. 2. Shoot density (number of shoots m^{-2}) of the seagrass species present in the experimental plots 3 mo after the removal of shoots of an increasing number of species in order of decreasing requirement of resources for plant growth (Expt 1). Error bars are +1 SE. Significant differences between individual treatments are indicated by different letters

Removal of shoots of an increasing number of species in order of increasing requirement of resources for plant growth (Expt 2)

The removal of shoots of species with small resource requirements had no effects on the shoot size of the extant species (Fig. 5, Table 2), although non-significant trends of decreasing shoot size with an increasing number of species with shoots removed were suggested by data on *Halodule uninervis*, *Syringodium isoetifolium*, *Cymodocea rotundata* and *Enhalus acoroides*. Only the shoot density (Fig. 6) and LAI (Fig. 7) of *Thalassia hemprichii* increased when the shoots of all the accompanying seagrass species were removed from the plots (Table 2).

Observed community LAI values were similar (Wilcoxon's signed rank test, p > 0.05) to those expect-

ed for the treatments applied when the shoots of seagrass species with small resource requirements were removed first (Fig. 4c,d). However, the observed community LAI value was higher than expected when the shoots of all seagrass species except for *Thalassia hemprichii* were removed, as indicated by a slope < 1 (*t*-test, p < 0.01) of the regression line between observed and expected community LAI values (Fig. 4d).

DISCUSSION

The general lack of response of the extant seagrass species to the cumulative removal of shoots of seagrass species in order of decreasing requirements of resources for plant growth (Expt 1) was unexpected. Pre-
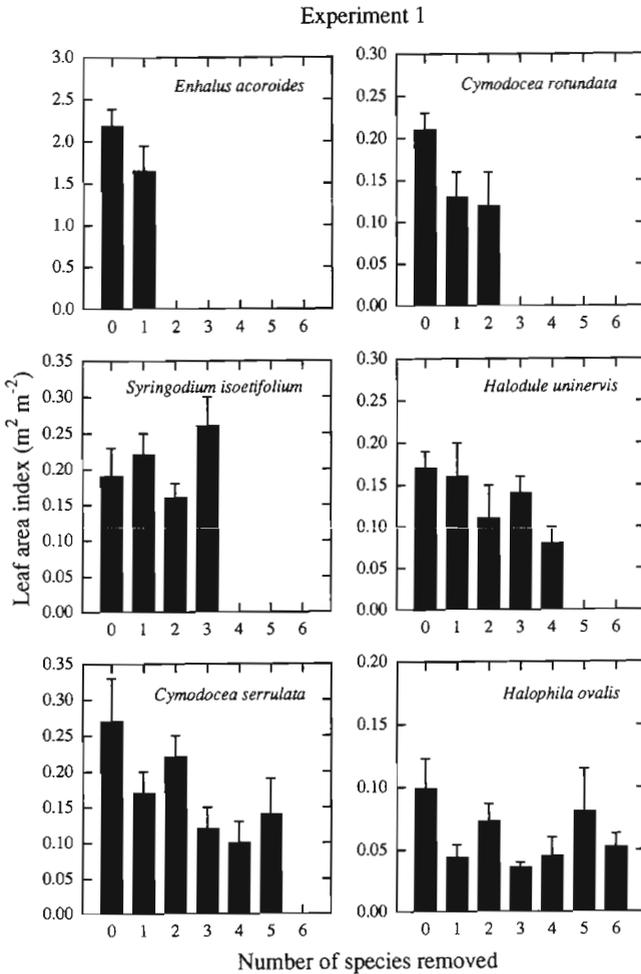
Fig. 3. Leaf area index (m^2 of leaf surface m^{-2}) of the seagrass species present in the experimental plots 3 mo after the removal of shoots of an increasing number of species in order of decreasing requirement of resources for plant growth (Expt 1). Error bars are +1 SE
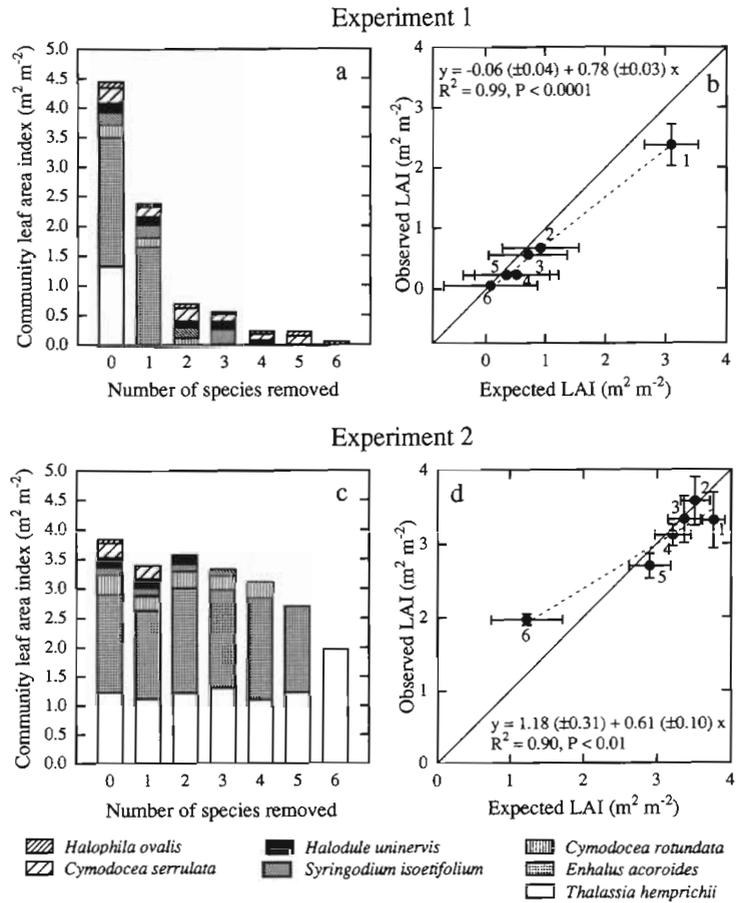

Fig. 4. Community leaf area index (m^2 of leaf surface m^{-2}) 3 mo after the removal of shoots of an increasing number of species in order of (a) decreasing and (c) increasing requirement of resources for plant growth, and in relation to the community leaf area index expected from the experimental manipulations solely (see 'Methods') in (b) Expt 1 and (d) Expt 2. The solid line is the 1:1 line, error bars are ±1 SE, the numbers adjacent to the data points indicate the number of seagrass species removed (see Table 1), and the dashed line and equation represent the fitted linear regression equation. LAI: leaf area index

vious studies (Agawin et al. 1996) have shown that seagrass growth in this multispecific meadow is nutrient-limited, so that the removal of shoots of seagrass species with the highest biomass and production was expected to promote increases in shoot size and density of the extant species. However, only the shoot density of *Syringodium isoetifolium* increased when the shoots of all the species with higher biomass and production (*Thalassia hemprichii* and *Enhalus acoroides*) were removed. In fact, the shoot density of *E. acoroides* decreased after the removal of *T. hemprichii* shoots, and decreasing trends, albeit not statistically significant, in the shoot density of *Cymodocea rotundata*, *Halodule uninervis* and *C. serrulata* were observed. Moreover, the shoot size of the extant seagrass species was not affected, or decreased (*Halophila ovalis*), after removal of shoots of the more dominant species. These

results suggest that competitive interactions among seagrasses might not be very important in this multispecific SE Asian meadow.

As expected, the cumulative removal from the community of shoots of seagrass species in order of increasing requirements of resources for plant growth (Expt 2) had no effects on the vegetative development of the extant species when only the shoots of marginally important species were removed. However, the removal of shoots of species with a cumulative loss of 28% of the above-ground biomass and 22% of the annual above-ground productivity of the meadow (calculated from Vermaat et al. 1995) promoted a significant increase in shoot density of the extant species,
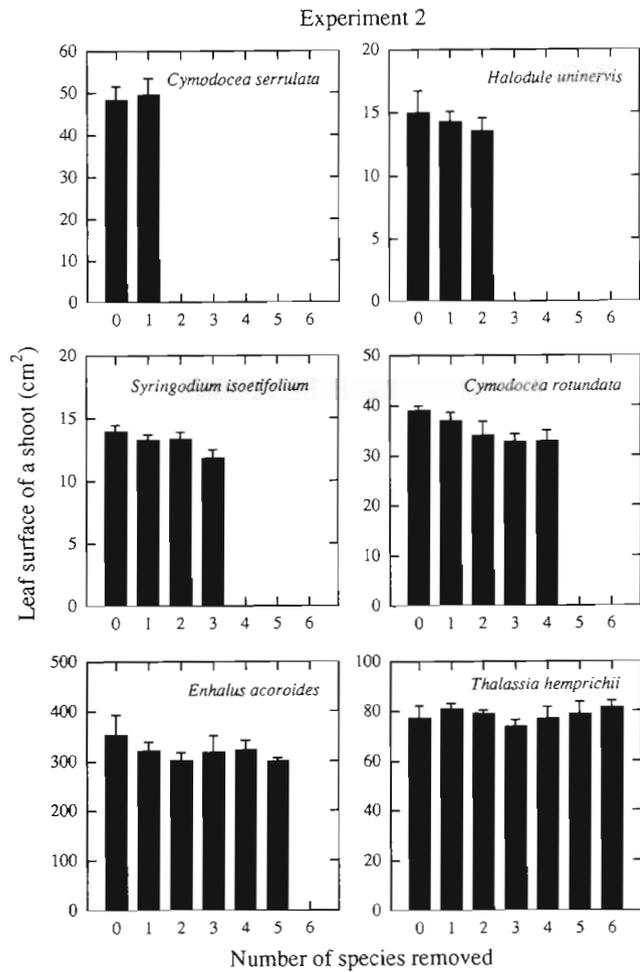
Fig. 5. Shoot size (as leaf surface of a shoot, cm²) of the seagrass species present in the experimental plots 3 mo after the removal of shoots of an increasing number of species in order of increasing requirement of resources for plant growth (Expt 2). Error bars are +1 SE
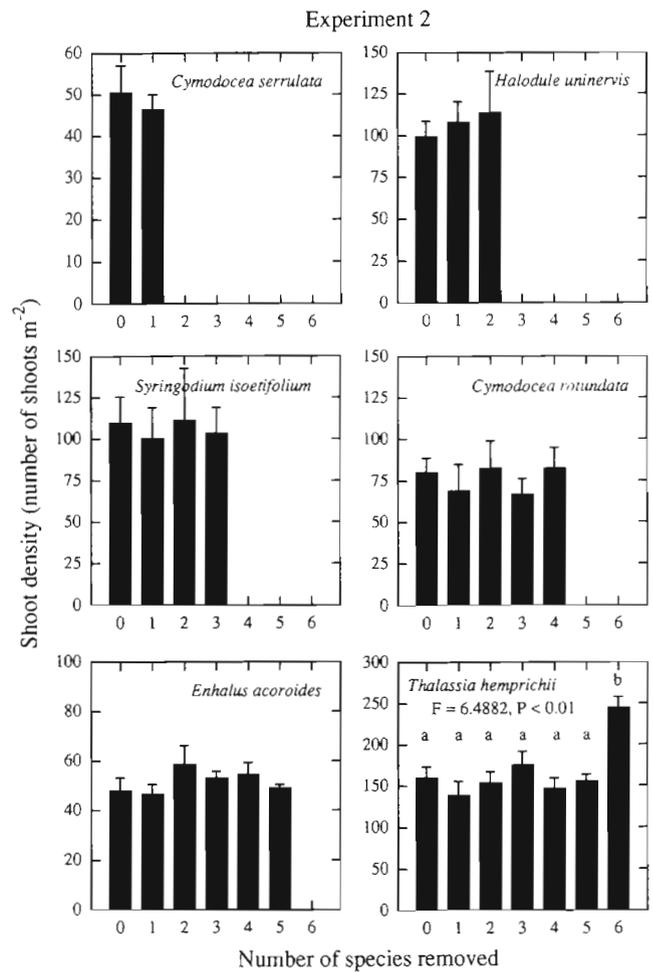

Fig. 6. Shoot density (number of shoots m⁻²) of the seagrass species present in the experimental plots 3 mo after the removal of shoots of an increasing number of species in order of increasing requirement of resources for plant growth (Expt 2). Error bars are +1 SE. Significant differences between individual treatments are indicated by different letters

Thalassia hemprichii. This result suggests that the vegetative development of T. hemprichii is constrained by the presence of other seagrass species and, therefore, that competitive interactions affect the dominant species in this multispecific SE Asian meadow.

The increase in shoot density of Thalassia hemprichii after the removal of all the other species present in the meadow did not suffice to compensate for the leaf biomass removed from the community by the experimental manipulation. Presumably, the duration of the experiment (3 mo) was too short to yield the full response of T. hemprichii to the resources likely made available by the removal of the accompanying species. Shoot density of T. hemprichii should have increased 300% during the experiment to compensate for the leaf loss to the experimental manipulation, and would have re-

quired about 1.5 yr to be realized (based on an annual shoot recruitment rate of 0.77 ln units yr⁻¹, Vermaat et al. 1995). Except for Enhalus acoroides, the annual shoot recruitment rates of the other seagrass species present in the meadow studied are high enough (from 1.08 to 3.10 ln units yr⁻¹, Vermaat et al. 1995) to allow responses in shoot density to the removal of species to be realized within the duration of the experiments. The experimental plots selected in Expt 2 were found to be similar in their species composition, although this was not tested for Expt 1. The results from Expt 1 might be confounded by heterogeneity in species composition among plots, which may explain why the decreasing trends of LAI found in Cymodocea rotundata, Halodule uninervis and C. serrulata in Expt 1 (Fig. 3) were not statistically significant.
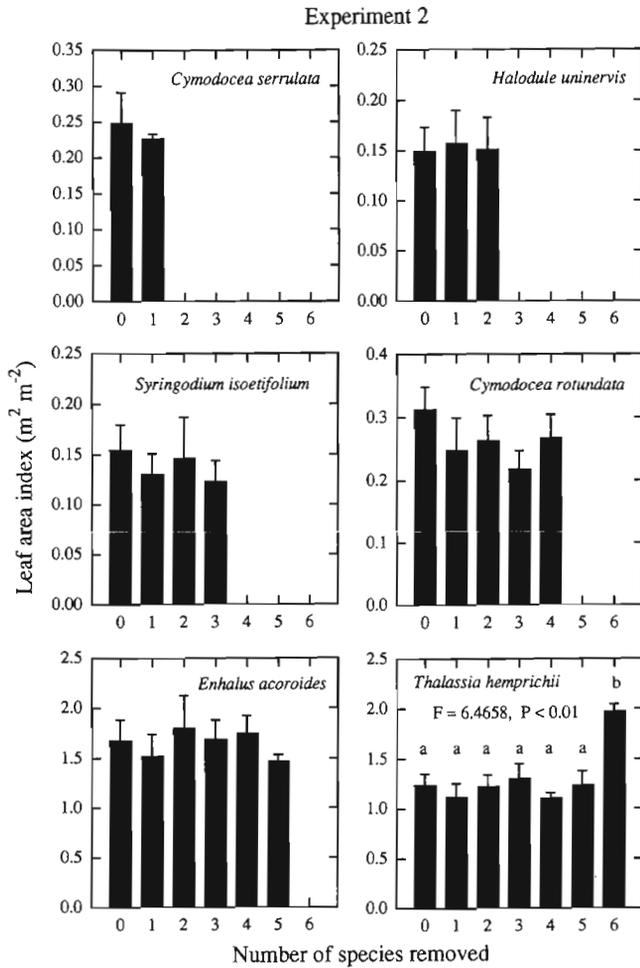
Fig. 7. Leaf area index (m² of leaf surface m⁻²) of the sea-
grass species present in the experimental plots 3 mo after
the removal of shoots of an increasing number of species
in order of increasing requirement of resources for plant
growth (Expt 2). Error bars are +1 SE. Significant differences
between individual treatments are indicated by different
letters

Our results provide evidence of asymmetry in
the interactions among seagrass species in this SE
Asian meadow. The removal of *Thalassia hemprichii*
shoots—the dominant species in terms of biomass,
annual productivity and, likely, requirements of re-
sources for plant growth—did not promote major
changes in the shoot size or density of the extant
species (Expt 1). However, the removal of the shoots of
all these accompanying seagrass species promoted a
significant increase of *T. hemprichii* shoot density
(Expt 2). We suggest that *T. hemprichii* and the accom-
panying species compete for plant growth resources in
the meadow studied, and that the resources required
to support the growth of the accompanying species
prevent *T. hemprichii* from completely matching its
requirements.

Thalassia hemprichii and the accompanying species
might be competing for light. As the size of *Enhalus
acoroides* shoots is larger than that of the other sea-
grass species present in the meadow (Vermaat et al.
1995, Terrados et al. 1999a), *E. acoroides* might de-
crease the availability of light to other seagrass spe-
cies. The upper part of the leaf canopy (from 30 to
100 cm above the sediment surface) is occupied only
by *E. acoroides* leaves, while the leaves of the remain-
ing species occupy the lower part of the canopy (from
the sediment surface to 30 cm above it). The leaves of
Halophila ovalis are restricted to the lower 5 to 10 cm
of the leaf canopy. Measurements of irradiance at the
top of the leaf canopy formed by seagrass species other
than *E. acoroides* in a 7×7 m plot before and after clip-
ping all *E. acoroides* shoots present indicate that the
leaf canopy of *E. acoroides* reduces light availability to
other seagrass species by 5% only (Terrados unpubl.
results). The other seagrass species are more similar in
size and might, therefore, shade each other, but the
lack of a positive response of the extant seagrass spe-
cies to the shoot removals in Expt 1 suggests that light
availability might not be limiting seagrass growth in
our experiments. It is not likely either that the thinning
of the leaf canopy as a consequence of the treatments
would cause photoinhibition of the extant species,
because all of them grow successfully at depths even
shallower than that of the meadow studied.

The observed responses of seagrasses to the treat-
ments could also be considered the result of processes
other than interspecific competition for nutrients. The
death and decomposition of the rhizomes and roots of
the species whose shoots were removed from the plots
could have potentially increased the state of reduction
of the sediment and negatively affected the extant spe-
cies (cf. Goodman et al. 1995, Terrados et al. 1999b).
The decreasing trends of the shoot densities and LAI
values of *Enhalus acoroides, Cymodocea rotundata,
Halodule uninervis* and *C. serrulata* after the treat-
ments of Expt 1 could be associated to increasingly
reduced sediment conditions. However, as these
trends, with the exception of *E. acoroides*, were not
significant (Table 2), and no negative effects could be
detected in Expt 2, we consider that, even if the treat-
ments might have caused an increase in the state of
reduction of the sediment in the plots, the extant sea-
grass species were not likely affected by them. Previ-
ous studies have shown that seagrass growth is nutri-
ent-limited at the meadow studied (Agawin et al.
1996), which suggests that changes in nutrient avail-
ability after the removal of shoots might underlie the
observed plant responses.

The asymmetry of the interactions between *Thalas-
sia hemprichii* and the accompanying seagrass species
could be partly explained by their 2-order-of-magni-

tude difference in size (cf. Vermaat et al. 1995, Duarte et al. 1998, Terrados et al. 1999a). The vertical distributions of root biomass of the different seagrass species show a high degree of overlap in the upper 10 cm of the sediment (Duarte et al. 1998). However, the roots of the largest seagrass species (*Enhalus acoroides, T. hemprichii*) penetrate deeper into the sediment than those of the smallest species (*Halodule uninervis, Halophila ovalis*), and may allow them to exploit nutrient pools unavailable to the small species (Duarte et al. 1998). If part of the nutrient acquisition of *T. hemprichii* and *E. acoroides* is located deeper in the sediment than that of the other species, the removal of *T. hemprichii* and *E. acoroides* from the experimental plots, and the associated reduction of nutrient use by them, might not increase the availability of nutrients for the extant seagrass species or, at least, not as expected from the nutrient requirements of *T. hemprichii* and *E. acoroides*. As a consequence, the extant species would show no or small responses to the removal of *T. hemprichii* and *E. acoroides*. On the other hand, when the cumulative removal of the small seagrass species increased the availability of nutrients in the upper layers of the sediment, *T. hemprichii*, which also has roots in these sediment layers, could exploit the increased nutrient availability to support growth, as the observed increase in shoot density indicates. Our results also suggest that the vegetative development of *Syringodium isoetifolium* is constrained by the nutrient use of other seagrass species, because the cumulative removal of *T. hemprichii, E. acoroides* and *Cymodocea rotundata* promoted a 30% increase of *S. isoetifolium* shoot density (Expt 1).

Knowledge of the interactions between seagrass species is still very limited, and the few studies that have addressed this question indicate that they are mainly negative (Williams 1987, 1990, Nomme & Harrison 1991, Fourqurean et al. 1995). However, positive interactions between plant species are common (Bertness & Callaway 1994), and some examples of facilitation in aquatic plant communities involving the release of oxygen by the roots of the facilitating species are available (Hacker & Bertness 1995, Callaway & King 1996). One of the few significant effects of the different experimental manipulations performed was a decrease of *Enhalus acoroides* shoot density after the removal of *Thalassia hemprichii* (Expt 1). This negative response was unexpected and could indicate that the presence of *T. hemprichii* might facilitate in some way the vegetative development of other seagrass species. The observation of decreasing trends of the shoot densities and LAI values of *Cymodocea rotundata, Halodule uninervis* and *C. serrulata* after the experimental manipulations (Expt 1) would also be consistent with this hypothesis. In addition, the observed value of community LAI after

the removal of only *T. hemprichii* was lower than that expected solely from the experimental manipulation. Although seagrasses have anatomical and physiological adaptations (reviewed in Terrados et al. 1999b) to live in anoxic sediments, some species (e.g. *Thalassia*) are sensitive to an increase in the state of reduction of the sediment (Carlson et al. 1994, Goodman et al. 1995, Terrados et al. 1999b). Seagrasses can release oxygen through the roots to the sediment (Caffrey & Kemp 1991, Pedersen et al. 1998) and, by doing so, reduce the accumulation of toxic compounds in the sediment and facilitate seagrass life. The root system of *T. hemprichii* in the meadow studied is extensive (130 m of roots m^{-2} of sediment, root biomass = 79.3 g DW m^{-2}; Duarte et al. 1998), and gives this species the potential to maintain a suitable sedimentary environment for other seagrasses through the release of oxygen by the roots. Altogether, however, the evidence of a positive interaction between *T. hemprichii* and the other seagrass species provided by our results is weak.

The combination of results of the 2 experiments provides evidence for the occurrence of competitive interactions among seagrass species in this SE Asian multispecific meadow. We suggest that interspecific competition establishes in this seagrass meadow because of the limited availability of nutrients in the environment (Agawin et al. 1996). The interactions between seagrass species are not symmetric, and we suggest that differences in plant size among species (Vermaat et al. 1995, Terrados et al. 1999a) may be partly responsible for that. The roots of large seagrasses penetrate deeper layers of the sediment and can exploit nutrient resources which are not available to the small species (Duarte et al. 1998). The partial vertical segregation of root biomass is likely to also segregate nutrient acquisition by the different seagrass species, and to reduce interspecific competition for nutrients. This hypothesis is consistent with the few significant responses observed after the experimental manipulations. Although elucidation of the nature of species interactions is essential to understand the structure and function of plant communities, data on these interactions in multispecific seagrass meadows, which are common along tropical coasts, are still very limited. Better knowledge of species interactions in seagrass meadows will improve our understanding of how the high biodiversity and production that characterizes pristine SE Asian coastal ecosystems is maintained.

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