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Production ecology of *Posidonia oceanica* (L.) Delile meadows in Nueva Tabarca Marine Reserve: Growth, biomass and nutrient stocks along a bathymetric gradient

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SUMMARY

The effects of the interaction between depth and nutrients on the primary production of the seagrass *Posidonia oceanica* in a meadow off Nueva Tabarca island (E Spain) were investigated by assessing C, N and P concentration in the plant, the resource allocation of the different nutrients and the response of the plant to nutrient additions along a bathymetric gradient (1-24 m).

The results point to a nutrient limitation in the shallow zone (1- 5 m). The N and P concentrations were low (0.7-1.8 %N; 0.05-0.1%P relative to dry weight) and the N/P atomic ratio high (30-40). Clear tissue enrichment was found after both N and P addition, with lowering of the N/P ratio (to values of 25 by atoms). However, such a possible limitation was not supported by an increment in leaf growth after nutrient addition, although some of the growth features were modified (e.g., relative growth contribution of different leaves to total shoot growth). In a plant with a complex growth mechanism such as *Posidonia oceanica,* a short-term nutrient addition (1 month) do not suffice to induce a significant growth response. Thus, we conclude that *P. oceanica* growth off Nueva Tabarca island is probably nutrient limited in shallow areas (1-5 m) in early summer, and that this limitation is due to different concurrent factors: general oligotrophy of the area, massive leaf litter export and leaf losses due to both hydrodynamism and grazing.

KEYWORDS: Production, *Posidonia oceanica,* nutrients, nitrogen, phosphorus, resource allocation, detritus.

RESUMEN

Ecología de la producción de la fanerógama marina *Posidonia oceanica* (L.) Delile en la reserva submarina de la isla de Nueva Tabarca: crecimiento, biomasa y nutrientes a lo largo de un transecto batimétrico. En este trabajo se ha analizado el efecto de la interacción entre la profundidad y los nutrientes sobre la producción primaria de *Posidonia oceanica* en una pradera de la isla de Nueva Tabarca (este de la península Ibérica, España) mediante el estudio de la concentración de C, N y P en los tejidos vegetales, la variación en la asignación de recursos y la respuesta de la planta frente a adiciones de nutrientes a lo largo de un gradiente batimétrico (1-24 m).

Los resultados obtenidos indican una limitación por nutrientes en la zona somera (1-5 m). Las concentraciones de N y P en los tejidos son bajas (0,7-1,8 % N; 0,05-0,1 % P respecto a peso seco), el cociente atómico N:P es elevado (30-40), y las hojas de las plantas muestran un enriquecimiento tisular en nutrientes después de la fertilización tanto con N como con P, con una disminución asociada del cociente N:P (hasta valores de 25). Pero esta limitación no fue corroborada por un incremento neto del crecimiento foliar después de la adición de nutrientes, a pesar de que algunas características del crecimiento resultaron modificados (por ejemplo, la contribución relativa de las distintas hojas al crecimiento del haz). La duración de la fertilización (un mes) no fue suficiente para eliminar o mitigar la limitación por nutrientes en una planta con un mecanismo de crecimiento complejo como el que presenta *Posidonia oceanica*. Concluimos que el crecimiento de *P. oceanica* en los fondos someros (1-5 m) de la isla de Nueva Tabarca está limitado por nutrientes a principios de verano y que esta limitación es debida a varios factores coincidentes: oligotrofia general del área, exportación masiva de hojarasca y pérdidas de material foliar por hidrodinamismo y acción de los herbívoros.

PALABRAS CLAVE: Producción, *Posidonia oceanica,* nutrientes, nitrógeno, fósforo, asignación de recursos, detritos.

INTRODUCTION

The Mediterranean seagrass *Posidonia oceanica* occurs along a wide bathymetric range (0-25 m; down to 45 m in very clear waters: Ros et al., 1985), and this implies a great heterogeneity of growth conditions. Plant response to depth has been studied from different aspects: annual growth (Ott, 1980; Bay, 1984; Romero, 1989a; Buia et al., 1992), phenology (Giraud, 1979; Caye, 1982; Romero, 1989b; Sánchez-Lizaso, 1993), biomass and storage products (Pirc, 1985, 1989), and morphology (Mariani-Colombo et al., 1983), among others. Light reduction with depth causes a decrease in seagrass production, which can be of up to one order of magnitude (Duarte, 1989), and thus in nutrient demand; since nutrient availability (both in the sediment and the water column) in general increases with depth, nutritional conditions should strongly change along a bathymetric gradient. To our knowledge, the assessment of such changes and their implications for plant growth and production have not been already attempted for this species.

Here we examine the interaction between nutrients and depth on the production of *Posidonia oceanica* by two complementary approaches: (i) the measurement of carbon, nitrogen and phosphorus concentrations in the different plant organs and their detritus, as well as the estimation of stocks of the corresponding elements along a depth gradient, and (ii) the evaluation of the extent of nutrient limitation at different depths.

METHODS

Study site

The study was carried out between June and July 1991 in a *Posidonia oceanica* meadow in the Nueva Tabarca Island marine reserve (Alicante, East Spain) extending from near the surface to ca. 24 m depth (Fig. 1; see Ramos, 1985, for detailed site description).

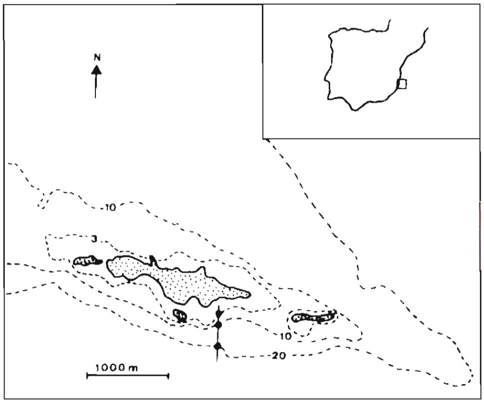


FIGURE 1. Study site, with the transect where the samples were taken. *Localización del área de estudio, con el transecto en el que se tomaron las muestras.*

Shoot density and leaf nutrient content along a bathymetric gradient.

Samples were taken at 1, 3, 5, 10, 15, 20, and 24 m depth. At each depth, a 40 x 40 cm quadrat was placed on the seagrass bed, the number of shoots recorded and three of them (chosen at random) were collected for element analysis. This procedure was performed in triplicate at each depth. Leaf material was then sorted into three categories: young leaves (less than 15 cm), intermediate leaves, and old leaves (following Giraud, 1979). Each fraction was dried at 70°C and weighed. Subsamples of each were analysed for C, N and P content (see below). Old leaves included epiphytes, while in intermediate and young leaves only the portions uncovered by epiphytes were used.

Belowground parts (roots and rhizomes) and detritus stocks

Samples were taken at 5 and 20 m. Leaf litter was sampled using a suction device inside a 35 x 35 cm quadrat, in triplicate. Sediment was washed off through a 1mm mesh and the non-leaf detritus was discarded. Two fractions, fine litter (<0.8 cm) and coarse litter (>0.8 cm) were separated. More details on the method can be found elsewhere (Romero et al., 1992).

Belowground parts were sampled with a diver-operated corer, 15 cm in diameter and 20 cm high. Samples were washed thoroughly and sorted into the following parts: living rhizomes, dead rhizomes, living roots, dead roots, and fine undifferentiated fraction (particle size between 0.1 and 0.8 cm). Each fraction was dried as above and weighed. Subsamples were kept for element analysis.

Experimental nutrient addition

In situ nutrient additions were performed at 3, 10, and 20 m depth. Twelve plots (0.05 m^2) were marked at each depth, and the following treatments were randomly assigned to subsets of 3 plots: P addition (K_2HPO_4 - 8 g P m^2), N addition (NH_4NO_3 - 15 g N m^{-2}), N + P addition (15 g N m^{-2}, 8 g P m^{-2}), no addition (control). Nutrients were added in the form of slow-release fertilizer introduced in the sediment. Ten shoots per plot were marked (Zieman, 1974; Romero, 1989a) and recovered one month later to estimate leaf growth, biomass and other phenological features as described elsewhere (Romero, 1985). Details on leaf apex were recorded for all leaves within a shoot. Four categories were distinguished, according to Boudouresque & Meinesz (1982): intact, broken, eaten by fishes and eaten by sea-urchins. After epiphyte removal, C, N, and P concentration of plant tissue were analyzed.

Element analysis

C and N were analyzed with a Carlo-Erba NA1500 autoanalyzer at the Serveis Científico-Tècnics, Universitat de Barcelona. Phosphorus content was determined by ICP (Induced Coupled Plasma) after wet digestion in a microwave oven (Mateo & Sabaté, 1993).

Statistical procedures

Differences in biomass/necromass stocks were tested using two-way ANOVA. The dependent variable was the dry weight and independent variables were depth (5 and 20 m) and status (living or dead). Differences in nutrient concentration of biomass/necromass were tested using a three-way MANOVA, where the dependent variables were C, N and P concentrations and independent variables were depth (5 and 20 m), status (as above) and plant part (leaves, rhizomes and roots). Differences in resource allocation pattern and contribution of the different leaves to the overall shoot production were analyzed following Abrahamson & Caswell (1982). Changes in nutrient content in leaves along the depth transect were analyzed using one-way MANCOVA, using the C, N and P concentration as dependent variables, leaf age (young, intermediate, old) as independent variable and depth as covariate. Statistical significance of the results of fertilization experiment was tested using three-way MANOVA, using nitrogen addition (yes or no), phosphorus addition (yes or no) and depth (3, 10 and 20 m) as independent variables, growth response or element concentration as dependent variables, and variance between replicate plots and within plots as error terms. Differences in the causes of breakage of leaf apex (hydrodynamisn or herbivory) at different depths were tested using one-way MANCOVA.

Other statistical methods included

regression analysis and Tukey post-hoc tests. Departures from the null hypothesis were considered significant at 5 % probability level.

RESULTS

Biomass, necromass and nutrient concentrations at 5 and 20 m

Biomass, necromass and tissue nutrient concentration are shown in Table I. Total organic standing stocks (living+dead) were higher at 5 m than at 20 m. Biomass was higher than necromass at 5 m, and the reverse occurred at 20 m. Nitrogen and phosphorus concentrations in living parts were always higher than in dead parts. Leaves showed higher N and P concentrations than roots and rhizomes (up to three times in some cases). Carbon content in the plant was higher at the shallow station than at the deep one.

Mineral resource allocation (percentage of the element considered in a plant part relative to the total pool; Harper, 1977) is summarized in figure 2. Differences in allocation patterns for, on the one hand, carbon, and, on the other hand, nitrogen and phosphorus, are quite evident. While the first is basically accumulated in belowground parts (roots and rhizomes), the others, especially phosphorus, are allocated to the leaves.

TABLE I. Biomass or necromass (as dry weight per square meter) and nutrient (carbon, nitrogen and phosphorus) concentrations (as % of dry weight) values of the different compartments studied at the two stations (5 and 20 m). For each value the mean standard error are given (SEM, with n=3). *Valores de biomasa o necromasa (en peso seco por metro cuadrado) y concentraciones (en % de peso seco) de nutrientes (carbono, nitrógeno y fósforo) de los distintos compartimientos estudiados en las dos estaciones (5 y 20 m). Para cada valor se da el error típico de la media (SEM, con n=3).*

			g DW m^{-2}	**C**	**N**	**P**
	LIVING	**LEAVES**	1637.33±372	28.97±1.56	1.35±0.18	0.107±0.010
		RHIZOMES	3813.90±457	38.11±0.50	0.64±0.04	0.024±0.002
		ROOTS	2871.14±234	43.25±0.33	0.59±0.02	0.027±0.001
		TOTAL	8322.34			
5 m	**DEAD**	**LEAVES**	10.45±6	32.35±0.41	0.77±0.09	0.052±0.010
		RHIZOMES	3909.78±502	35.83±0.92	0.50±0.03	0.021±0.001
		ROOTS	1047.99±504	43.62±0.49	0.53±0.04	0.019±0.002
		TOTAL	5803.37			
	TOTAL		14125.70			
	LIVING	**LEAVES**	586.00±150	26.90±2.55	1.60±0.16	0.140±0.007
		RHIZOMES	2117.98±601	38.59±1.20	0.66±0.07	0.033±0.000
		ROOTS	503.48±119	41.25±0.38	0.61±0.03	0044±0.003
		TOTAL	3207.46	35.58	0.96	0.072
20 m	**DEAD**	**LEAVES**	31.89±3.82	35.20±037	0.74±0.01	0.032±0.001
		RHIZOMES	2707.29±723	32.44±0.35	0.44±0.04	0.026±0.001
		ROOTS	835.30±148	39.67±0.63	0.51±0.02	0.023±0.002
		FINE	1219.72±141	38.37±0.21	0.58±0.01	0.047±0.002
		TOTAL	4794.20			
	TOTAL		8001.66			

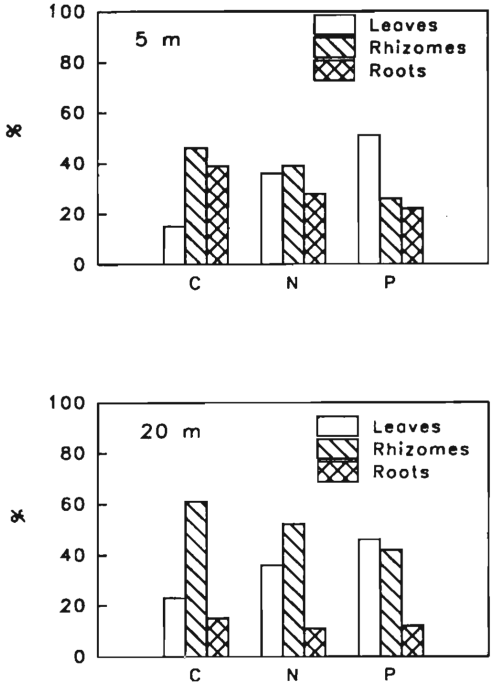


FIGURE 2. Resource allocation (carbon, nitrogen and phosphorus) in the three fractions studied (leaves, rhizomes and roots) at 5 m and 20 m. *Reparto de recursos (carbono, nitrógeno y fósforo) en las tres fracciones estudiadas (hojas, rizomas y raíces) a 5 y 20 m.*

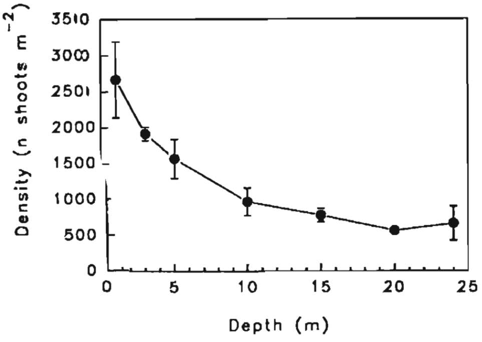


FIGURE 3. Bathymetrical variation of the density of *Posidonia oceanica*. For each depth, the mean and the standard error are gven (n=3). *Variación batimétrica de la densidad de Posidonia oceanica. Para cada profundidad se dan la media y el error típico (n=3).*

Bathymetric variations of leaf nutrient content and shoot density

Shoot density decreased exponentially with depth (Fig. 3). Carbon content in the leaves was depth independent, while N and P clearly increased in the deeper plants (Figs. 4, 5 and 6). In all cases, young leaves showed a higher nutrient concentration than old leaves. The N:P ratio was, in general, very high, ranging from 25 to 35, decreasing with depth, especially in young leaves.

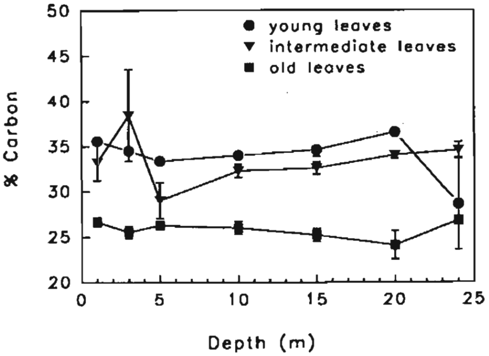


FIGURE 4. Bathymetrical variations in carbon content of young, intermediate and old leaves. The mean and the standard error are given (n=3). *Variaciones batimétricas en el contenido en carbono de hojas jóvenes, intermedias y viejas. Se dan la media y el error típico (n=3).*

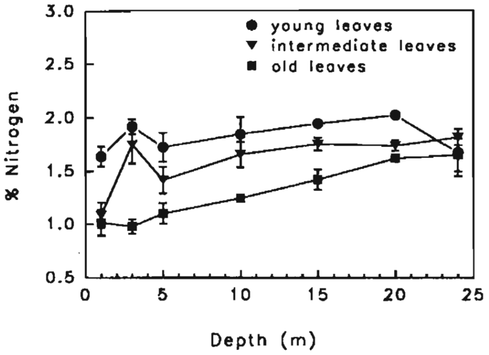


FIGURE 5. Bathymetrical variations in nitrogen content of young, intermediate and old leaves. The mean and the standard error are given (n=3). *Variaciones batimétricas en el contenido en nitrógeno de hojas jóvenes, intermedias y viejas. Se dan la media y el error típico (n=3).*

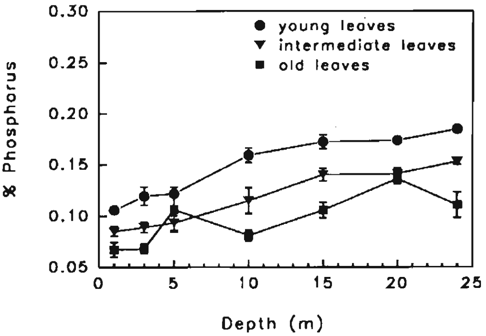
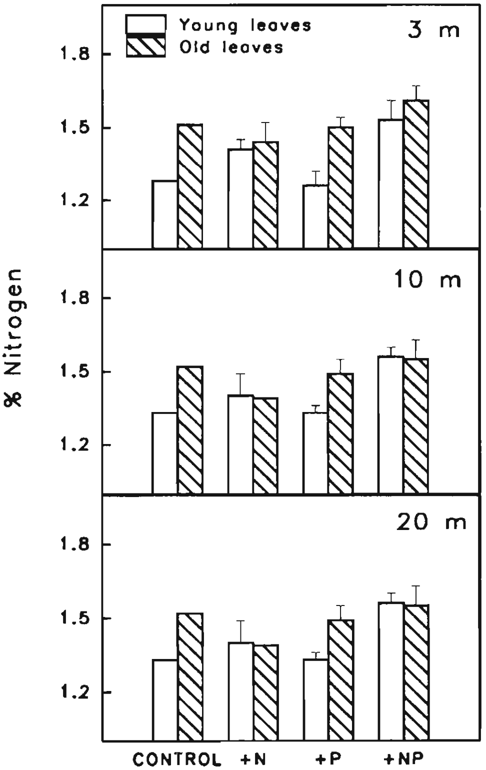


FIGURE 6. Bathymetrical variations in phosphorus concentration of young, intermediate and old leaves. The mean and the standard error are given (n=3). *Variaciones batimétricas en el contenido en fósforo de hojas jóvenes, intermedias y viejas. Se dan la media y el error típico (n=3).*

Nutrient addition experiments

Leaf nutrient concentration following the experimental fertilization are shown in figu-



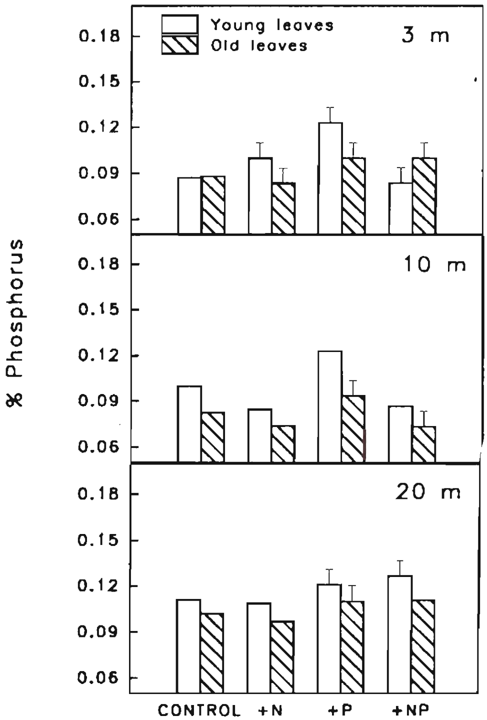


FIGURE 8. Effect of nutrient additions (Control; +N = addition of nitrogen; +P = addition of phosphorus; +NP = addition of nitrogen plus phosphorus) on the phosphorus content of young and old leaves at three depths (3, 10 and 20 m). *Efecto de las adiciones de nutrientes (control; +N = adición de nitrógeno; +P = adición de fósforo; +NP = adición de nitrógeno y fósforo) sobre el contenido en fósforo de las hojas jóvenes y viejas a tres profundidades (3, 10 y 20 m).*

FIGURE 7. Effect of nutrient additions(Control; +N = addition of nitrogen; +P = addition of phosphorus; +NP = addition of nitrogen plus phosphorus) on the nitrogen content of young and old leaves at three depths (3, 10 and 20 m). *Efecto de las adiciones de nutrientes (control; +N = adición de nitrógeno; +P= adición de fósforo; +NP = adición de nitrógeno y fósforo) sobre el contenido en nitrógeno de las hojas jóvenes y viejas a tres profundidades (3, 10 y 20 m).*

res 7 and 8. As mentioned (Figs. 5 and 6), N and P concentration increased with depth. An increase in N and P content was found in treated relative to untreated plants, which was highest for phosphorus at 3 m (more than 30 % relative to controls); maximum increase in nitrogen occurred at 10 m (around 20 % relative to controls).

Mean values for plant growth after treatments are given in figure 9. As shown, growth of shoots from the shallower station (3 m) was lower than that of the deep ones. The addition of N or P did not induce any significant change in shoot growth. In any case, attention is drawn to the very high variability in shoot growth due to random factors, mostly variability within plots (47 % of variance explained) but also between replicate plots (10 % of variance explained).

The contribution of each individual leaf to the overall growth of the shoot depends largely on the leaf age (ranked from 1 to 6, where 1 is the youngest one) and is modified by both nitrogen (increase of the relative contribution of the older leaves) and phosphorus additions (increase of the relative contribution of the younger leaves; Fig. 10).

Finally, the action of both herbivores and

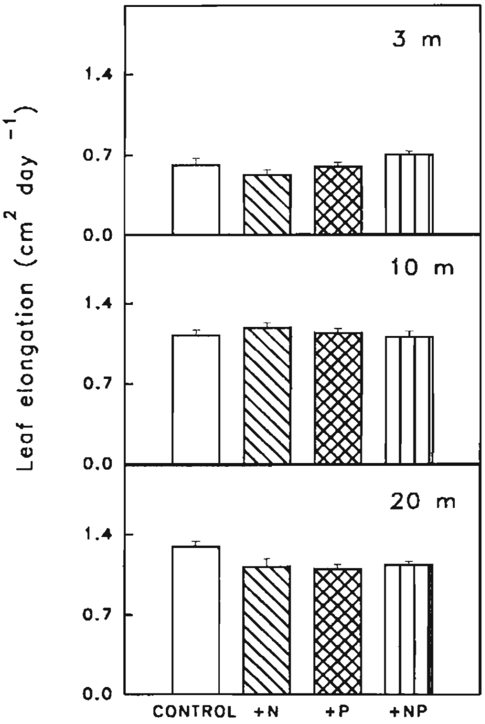


FIGURE 9. Effect of nutrient additions (Control; +N = addition of nitrogen; +P = addition of phosphorus; +NP = addition of nitrogen plus phosphorus) on leaf growth at three depths (3, 10 and 20 m). *Efecto de las adiciones de nutrientes (control; +N = adición de nitrógeno; +P = adición de fósforo; +NP = adición de nitrógeno y fósforo) sobre el crecimiento foliar a tres profundidades (3, 10 y 20 m).*

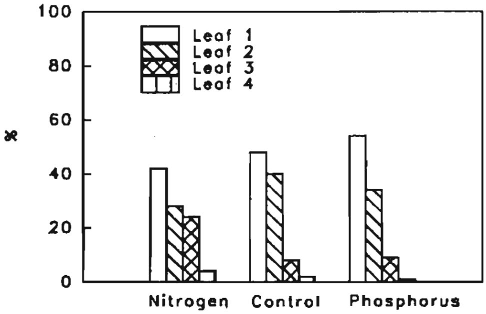


FIGURE 10. Relative contribution of each leaf to the shoot growth in the different treatments at 10 m depth. *Contribución relativa de cada hoja al crecimiento del haz en los distintos tratamientos a 10 m de profundidad.*

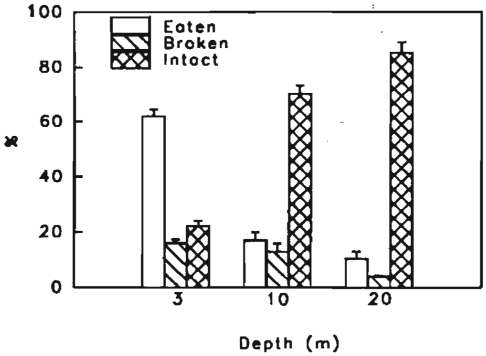


FIGURE 11. Apex state (frequency, in %) at the three stations studied. *Estado del ápice (frecuencia, en %) en las tres estaciones estudiadas.*

hydrodynamism in causing leaf breakage was clearly higher near the surface (Fig. 11).

DISCUSSION

Shoot density values (Fig. 3) are very high, especially in shallow areas, compared to data obtained by other authors (Giraud, 1979; Ott, 1980; Bay, 1984; Romero, 1989b; see more references in Sánchez-Lizaso, 1993). Density decrease with depth is linked to light reduction (Boudouresque et al., 1980; Bay, 1984; Romero, 1985) and also, in the studied meadow, to the damaging effect of trawling fishing below 20 m (Sánchez-Lizaso, pers. obs.).

Belowground biomass also decreases with depth (Table I), and is related to the decrease in shoot density; root plus rhizome weight per shoot remains fairly constant (4-5 g DW shoot^{-1}), and in the same range as that found in other meadows (Pirc, 1983; Romero, 1985).

Leaf litter stocks are very low (Table I), representing less than 1 % of the leaf biomass. Although at this time of year (end of June) the litter stocks are generally very low, values of 8-15 % have been reported under similar conditions of season and depth (Romero et al., 1992; Mateo & Romero, 1997) and may be due either to high export rates or to high decay values. However, high leaf decay values are not likely to occur, due to the low quality of the leaf material (low N and P concentration, Figs. 5 and 6; C:N in the order of 20-30), which has been recognized as a key factor in controlling decay rates (Melillo et al., 1989; Buchsbaum et al., 1991). Thus we conclude that up to 75-80 % of leaf production (computed following Romero et al., 1992) is exported due to the action of the prevailing E winds (Sánchez-Lizaso, 1993). These high export rates should therefore affect the nutrient budget of the system; if 75-80 % of leaf production is exported in the form of old leaves (Figs 2, 3 and Table I), and taking into account the annual production given by Sánchez-Lizaso (1993), we can estimate a total loss of 19.6 g N m^{-2} y^{-1} at 3 m and 5.8 g N m^{-2} y^{-1} at 20 m, and 1.14 g P m^{-2} y^{-1} at 3 m and 0.33 g P m^{-2} y^{-1} at 20 m, which represents, respectively, 88-85 % of N and 75-59 % of P of annual nutrient requirements for leaf growth. These losses, in addition to the general oligothrophy of the area (Prats & Martín, 1991), can cause nutrient shortage.

Consistently with this assertion, N and P concentration of leaves are very low (Figs. 5 and 6), and the N:P atomic ratio is very high compared to other seagrasses (Duarte, 1990) and to *Posidonia oceanica* from other sites (Alcoverro et al., 1995) suggesting a nutrient limitation of growth. This potential limitation is reflected in a number of findings, such as the increase in N and P concentration with depth and the decrease in the N:P ratio (coherent with a P limitation in the shallow areas of the meadow that further switches to a light limitation in the deeper areas) or the preferential allocation to leaves of the most limiting resources (N and P), which is described in nutrient-limited seagrasses (Pérez et al., 1994). Further indirect evidence of nutrient limitation in the shallow zone, higher resource allocation to root development (Fig. 2), needs more critical evaluation, since the role of roots as absorption organs in *Posidonia oceanica* is still controversial (Fresi & Saggiomo, 1980); an alternative explanation can be proposed, based upon the need for a more consistent anchoring system in shallow areas, due to more intense water movement.

In any case, this scenario (nutrient limitation in shallow areas and light limitation in deeper ones) is paradigmatic in aquatic systems (see, for example, Ballesteros, 1989) and depends basically on the availability of these resources (light and nutrients) relative to the demand for them. However, it can be amplified by accelerated leaf losses, which prevents retranslocation. Reclamation of nutrients from old to young, actively growing leaves has been demonstrated as an important process in nutrient economy of seagrasses (Pedersen & Borum, 1993). In our case, the positive correlation (Fig. 12) between shoot size (which depends on the presence or absence of old leaves) and the P concentration of young leaves supports the importance of retranslocation. Leaf loss is enhanced by herbivory and hydrodynamism, and, as shown in figure 11, both effects are clearly stronger near the surface. Thus, nutrient limitation could be severe near the surface due not only to the high demand for growth (higher shoot density; Fig. 3), but also to leaf losses caused by higher herbivore pressure and hydrodynamism forcing (Fig. 11) preventing internal recycling and leaf litter exportation (preventing external recycling).

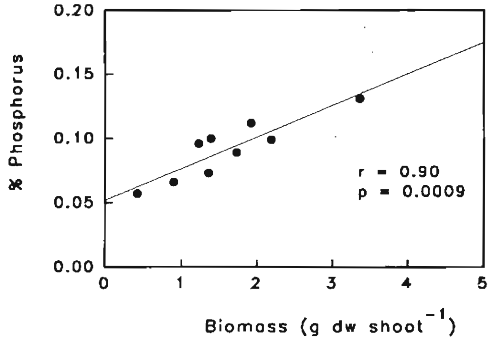


FIGURE 12. Relationship between shoot size (as biomass in g dry weigth) and phosphorus content in leaves (weighted mean of young, intermediate and old leaves). The correlation is significant for the data of the shallow stations (1, 3 and 5 m). *Relación entre tamaño del haz (como biomasa en g de peso seco) y contenido en fósforo en las hojas (media ponderada de hojas jóvenes, intermedias y viejas). La correlación es significativa para los datos de las estaciones someras (1, 3 y 5 m).*

The results of the experimental fertilization showed that all the plants treated with P reached a relatively constant P concentration in tissues, irrespective of depth (about 0.12 % for young leaves; Fig. 8), which is the same concentration found in the deep (20 m) control plants. In the plots treated with both N and P, the atomic N:P ratio was about 25, significantly lower than the control ratios (32 at 3 m and 30 at 10 m). These results, given similar findings reported in the literature (Duarte, 1990, Short et al., 1990, Pérez et al., 1991; Tomasko & Lapointe, 1991), again point to a P limitation, at least at the shallow station. Conversely, the growth data obtained in the experimental fertilization do not support this hypothesis.

The apparent contradiction between most of our results and growth data can be explained by two alternative hypotheses. The first is that the response of *Posidonia oceanica* to nutrient addition is neither simple nor direct, but follows a sequential pattern: increase in assimilation, increase in nutrient content in tissues, increase in leaf elongation, increase in biomass and finally interactions at population and community level (see Pérez et al., 1991, 1994). The duration of this experiment (1 month) is probably not long enough to cover more than the first steps of this sequence.

At the shoot level there is a high heterogeneity (leaf material of 0 to 100 days of age; Romero, 1989b), which can also affect the plant response. Our data show that the growth differences between shallow and deep shoots are due to differences in the growth of leaves 2 and 3 (leaf 1 being the youngest). At 10 m, nitrogen seems to enhance growth of leaves 2 and 3 while phosphorus enhances growth of leaf 1 (Fig. 10). This response does not appear at 3 m.

An alternative hypothesis is based upon the fact that from June to September most of the products of higher plant photosynthesis are allocated to starch and sucrose synthesis (Pirc, 1989; Alcoverro, 1995), with a reduced leaf growth. As has recently been shown (Sánchez-Lizaso, 1993), such a decrease in leaf growth occurs in March-April in Nueva Tabarca, revealing an early beginning of starch synthesis. Thus when a nutrient increase occurs, nutrients are assimilated and not used for growth but stored, which is coherent with our results. The internal growth rhythm demonstrated by Ott (1979) reinforces this hypothesis.

In summary, our results point to a nutrient limitation of *Posidonia oceanica* growth in shallow areas of the Nueva Tabarca meadow, due to three concurrent factors: (i) high demand relative to nutrient availibility. (ii) high leaf litter export which prevents in situ recycling, and (iii) high leaf losses due to herbivory and hydrodynamism, which prevents retranslocation of nutrients (internal recycling).

The response of the plant to nutrient addition shows an increase in nutrient assimilation following fertilization in the shallow area, but not growth enhancement, which can be explained either by the short duration of our experiment or by a certain independence of *Posidonia* growth strategy from environmental factors.

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