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Short research note

C, N, P concentrations and requirements of flowering *Posidonia oceanica* shoots

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Abstract

The carbon, nitrogen and phosphorus contents in flowering and nonflowering shoots were compared after an important flowering event occurred in the *Posidonia* meadow of the Bay of Calvi. The flower formation caused a significant increase of C and a significant decrease of N concentrations in intermediate and adult leaves. Minimum daily requirements in mg shoot^{-1} day^{-1} of 3.4 and 4.8 of C, 0.09 and 0.09 N, 0.01 and 0.02 of P respectively for nonflowering and flowering shoots were calculated. It shows that additional quantities of C and P are required for the inflorescence elaboration. The unchanged quantity of N required by the shoot for the inflorescence elaboration and the significant modification of N concentration in intermediate and adult leaves suggests that N is limited in the environment and that an efficient resorption of N occurs from leaves to ensure the inflorescence formation.

The marine phanerogam *Posidonia oceanica* (L.) Delile, endemic to the Mediterranean Sea, is a key species of the marine littoral zone. It forms meadows which rank amongst the most productive ecosystems (Boudouresque et al., 1984, 1989). This species can colonize very low concentration nutrients areas (i.e. Gobert et al., 2002, 2003) but is adapted face this situation and has carried a series of adaptation. On an annual average, 60% of the total nitrogen uptake occurs in roots and 40% in leaves (Lepoint et al., 2002a), rhizomes contribute to the total shoot nitrogen assimilation by 32–54% between autumn and spring (Invers et al., 2002). Rhizomes are organs for N storage both inorganic and organic (Invers et al., 2002; Lepoint et al., 2003). The leaves, comprising the adult leaves which have low metabolic demand, participate in nitrogen uptake. Adult leaves quickly transfer incorporated nitrogen to growing tissues or storage organs (rhizomes or young leaves) (Lepoint et al., 2002b). *P. oceanica* plants are able to take up inorganic nitrogen as nitrate or ammonium (see Touchette & Burkholder, 2000), even at very low concentrations in the water (i.e. 0.05 μmol L^{-1}) (Lepoint et al., 2002b). Marbà et al. (2002) showed that strong physiological integrations occur between clonal ramets. This integration allows the transfer of photosynthates and amino-acids along rhizomes over a distance of 20–30 cm. The translocation is mainly directed from parent ramets to young and growing ramets. This mechanism could be very important to ensure the N needs and expansion of young ramets which are not rooted during the first months of their growth (Alcoverro et al., 1997, 2000; Lepoint et al., 2002a, b).

The vegetative propagation is the most important mode of *P. oceanica* to spread. The vegetative growth of *P. oceanica* shows very slow rates ranging from 0.4 to 1.1 cm y^{-1} and from 0.4 to 7.4 cm y^{-1} for orthotropic and plagiotropic

rhizomes respectively (Boudouresque & Jeudy de Grissac, 1983), with a new shoot produced every 213 days (Hemminga & Duarte, 2000).

Sexual reproduction is observed in both the northern and southern parts of the Mediterranean Sea (den Hartog, 1970; Bay, 1984; Pergent, 1985). The reproduction cycle in relation to environmental parameters has been studied both in the laboratory (Buia & Mazzella, 1991) and *in situ* (Mazzella et al., 1983, 1984; Pergent, 1985; Pergent & Pergent-Martini, 1988; Balestri & Cinelli, 2003), but the factors inducing flowering remain uncertain (McConchie & Knox, 1989). The flower occurrence and the flower time apparition present bathymetric and geographical variations (Boudouresque & Meinesz, 1982; Mazzella et al., 1984). Flowers have a patchy distribution (Pergent, 1985; Pergent & Pergent-Martini, 1988; Buia & Mazzella, 1991). The causes of the spatial variation in flowering frequency are presently unknown but may be influenced by genetic variation or shoot age (Balestri & Vallerini, 2003), distribution of active meristems or small-scale differences in the environment or by temperature (Marbà & Walker, 1999; Campey et al., 2002). The flowering occurs more frequently in shallow sites than deeper ones (Pergent & Pergent-Martini, 1988).

The production of reproductive shoots is an episodic phenomenon. It seemed that *P. oceanica* flowering was rare in the cold waters along northwestern shores, and on the other hand, flowering was thought to be frequent or even annual in the southern and eastern regions of the Mediterranean basin (Molinier & Picard, 1952). Flowering of *P. oceanica* appeared in the entire Mediterranean basin, in 1961, 1967, 1971, 1972, 1973, 1975, 1979, 1981, 1982 and 1983 (Pergent & Pergent-Martini, 1990) and in 1994 (Sandmeier et al., 1999). Flowers and fruits of *P. oceanica* have been observed at many localities within the Mediterranean basin (den Hartog, 1970; Giraud, 1977; Mazzella et al., 1983; Pergent, 1985; Buia & Mazzella, 1991; Gobert et al., 2001), but the establishment of seedlings is episodic. Germination begins with the development of the plumule following by the protusion of a white primary root at the radical pole, all occurring within the pericarp. There is no seed bank in *Posidonia*. After about 10 days, the apical meristem grows and produces 2 or 3 green leaves and several adventitious white roots. After 9 months, seedlings have 12–13 leaves, one primordial tap-root and 3–4 adventitious roots. At this stage, a wide proportion of mortality occurs (Balestri et al., 1995). *P. oceanica* seedlings begin to develop their own rhizome, growing horizontally at a rate of about 5–10 cm year^{-1} (Boudouresque & Meinesz, 1982). Grazing of inflorescences could affect the success of sexual reproduction (Piazzi et al., 2000).

The flowers appear generally on orthotropic rhizomes, but in case of important flowering, plagiotropic rhizomes issued from orthotropic ones could bear flowers (Caye, 1980). Floral development in *P. oceanica* is initiated during April–June. Development of flowering lasts 3 months when the temperature is high. Anthesis (time or process of expansion of a flower) began in July–September and continued over several weeks, followed by fruit and seed development, with fruits being shed in November–January. Anthesis induces biometrical and growth modifications on the flowering shoot (Gobert et al., 2001). These changes are probably the result of a physiological modification of the flower-bearing shoots, occurring before and during anthesis but also due to a change of the meristematic zone (terminal to lateral meristem) producing the leaves after the inflorescence apparition.

The Calvi Bay (Corsica) is a nutrient poor area characterized by quasi permanent low level of nutrient related to unimportant agricultural and industrial activities, small local population, low rainfall regime and low runoff from river. The nutrients and the chlorophyll *a* concentrations in the water column were low, even during the winter-spring phytoplankton bloom (i.e. 0.2–0.3 mol l^{-1} for nitrate and <0.4 μg l^{-1} chlorophyll *a* concentrations in February–March) (Gobert et al., 2002; Goffart et al., 2002). The nitrogen levels in the sediment pore water are also very low (i.e. 1.0 and 3.3 μmol l^{-1} for the nitrites + nitrates and for the ammonium respectively) (Gobert et al., 2003).

In the Bay of Calvi, from 1975 to 1993 on, flowers were rarely observed (some isolated shoots). However, in 1998, the meadow blossomed, and since this first event, the *Posidonia* meadow blossomed regularly.

In this paper we investigated the effects of anthesis on the carbon (C), nitrogen (N) and phosphorus (P) contents of *P. oceanica* flowering shoots and we calculated the C, N and P quantities required for flowering in the nutrient poor Calvi Bay.

This work was carried out in 1998, in the Bay of Calvi near the marine research station STARESO (Mediterranean Sea, Corsica-France, 42° 35′ N, 8° 43′ E), at 10 m depth. An extensive *P. oceanica* meadow covers about 180 ha of the sandy seafloor, reaching 38 m depth (Bay, 1984). This seagrass bed has been studied since 1970s (i.e. Bay, 1984; Lepoint et al., 2002a; Gobert et al., 2003).

In October 1998, 10 flowering and 18 nonflowering shoots (the shoot is defined as the aboveground part of *P. oceanica*: the leaves and the flowers as the whole) were collected at 10 m depth in areas displaying similar light, temperature as well hydrodynamic conditions. Shoots were collected in the same patches. The leaves (juvenile, intermediate and adult) were separated and measured according to Giraud (1979), this method clearly establishes criteria to separate and measure the different types (juvenile, intermediate and adult) of leaves on a shoot. Adult leaf presents two distinct regions: the basis (sheath) and the blade, intermediate leaf has no sheath and juvenile leaf are shorter than 5 cm.

The leaves were then scraped with a razor blade to remove epiphytes (Dauby et al., 1994). Biometrical, biomass and growth data (according the method of Zieman) were noted for each shoot (see Gobert et al., 2001). The leaves marking technique method of Zieman (1974) is based on marking the shoot at a fixed reference height, relocating the marks at a later time, and measuring the weight of the new leaf material produced during the interval (Short & Duarte, 2001). For each shoot, the leaves were pooled according to type. The samples were lyophilized and ground to a fine powder. Subsamples were used for the determination of C and N (2.5 mg) and for P (60 mg) concentrations respectively. C and N concentrations of the tissues were determined using a C-N-S elemental analyzer (Carlo Erba, Italy). The P concentration was determined by ICPMS (Inductive Coupled Plasma Mass Spectrometry) after nitric acid digestion. Elemental concentrations are expressed in % relative to dry weight of tissues ($\%_{dw}$).

Parametric and nonparametric tests were used, Kolmogorov–Smirnov test was used to assess the normality of the data. *T*-tests were performed to compare the sets of data (flowering and nonflowering shoots). Results were judged significant when $p \leq 0.01$. Data are presented as mean ± standard deviation.

The relative concentrations of carbon, nitrogen and phosphorus ($\%_{dw}$) in the nonflowering and flowering shoots are shown in Table 1. Our data for C and P concentrations in nonflowering shoots match those previously described in Calvi Bay and in other areas at the same period of the year (Velimirov, 1987; Alcoverro et al., 1995; Mateo & Romero, 1997). The nitrogen values in the Calvi Bay are generally lower than those recorded in other Mediterranean sites: i.e. 2.8% (Augier & Santimone, 1982), 2.2% (Pirc & Wollenweber, 1988), 1.7–2.4% (Alcoverro et al., 1995) and 2.0% (Velimirov, 1987).

The comparison of relative C, N and P concentrations in flowering and nonflowering shoots shows that $\%_{dw}$ C are higher and $\%_{dw}$ N are lower in all the types of leaves in flowering shoots than in nonflowering ones. The inflorescence has relatively low C concentrations while the N and P concentrations are similar in the inflorescence and in the intermediate leaves of flowering shoots.

Using biomass data (i.e. 0.82 ± 0.19 and 0.75 ± 0.26 g DW for flowering and non flowering shoot biomasses respectively, Gobert et al., 2001) and the relative C, N and P concentrations, we calculated the C, N and P contents by shoot (mg shoot^{-1}). The data for juvenile leaves have been discarded in the total budget because of lack of sufficient tissue. Compared to nonflowering ones, the C and P contents of flowering shoots are higher by 30% and 42% respectively ($p < 0.01$). However, the N content by shoot remained unchanged (Table 1).

Furthermore, we have calculated the minimal quantities of C, N and P required in October for the flowering and nonflowering shoots (mg shoot^{-1} day^{-1} – leaf part). Knowing the mean growth rate of the different parts of the shoots during autumn (i.e. 2.5 ± 1.4 mg shoot^{-1} day^{-1} for juvenile leaves; 2.3 ± 0.8 mg shoot^{-1} day^{-1} for intermediate leaves; 0.6 ± 0.7 mg shoot^{-1} day^{-1} for adult leaves and 2.5 mg shoot^{-1} day^{-1} for inflorescence), taking into account the respective biometry of flowering and nonflowering shoots (Gobert et al., 2001), using our CNP concentration measurements (Table 1), we have calculated a daily requirement of 3.4 ± 1.4 and 4.8 ± 1.6 mg C; 0.09 ± 0.04 and 0.09 ± 0.04 mg N; 0.01 ± 0.006 and 0.02 ± 0.007 mg P for nonflowering and flowering shoots respectively. Additional quantities of C and

Table 1. C, N and P concentrations ($\%_{dw}$) and contents per shoot (mg shoot^{-1}) in nonflowering and flowering leaves

		Nonflowering			Flowering		
		C	N	P	C	N	P
Juvenile	$\%_{dw}$	33.3 ± 3.3 (6)	1.1 ± 0.3 (6)	nd	40.9 (1)	0.6 (1)	nd
	mg shoot^{-1}	1.1 ± 0.1 (2)	0.03 ± 0.01 (2)	nd	0.4 (1)	0.01 (1)	nd
Intermediate	$\%_{dw}$	35.2 ± 2.2 (18)	1.0 ± 0.2 (18)	0.13 ± 0.02 (18)	37.1 ± 1.6 (10)$^{0.002}$	0.8 ± 0.1 (10)$^{0.007}$	0.14 ± 0.01 (9)
	mg shoot^{-1}	49.3 ± 3.8 (18)	1.4 ± 0.4 (18)	0.18 ± 0.03 (18)	55.7 ± 2.4 (10)$^{0.000}$	1.6 ± 0.5 (10)$^{0.006}$	0.32 ± 0.05 (10)
Adult	$\%_{dw}$	32.1 ± 2.1 (18)	0.5 ± 0.1 (18)	0.06 ± 0.01 (18)	35.2 ± 2.2 (10)$^{0.001}$	0.3 ± 0.1 (10)$^{0.000}$	0.05 ± 0.08 (10)
	mg shoot^{-1}	173.3 ± 11.3 (18)	2.7 ± 1.1 (18)	0.32 ± 0.05 (18)	186.6 ± 11.7 (10)$^{0.007}$	1.6 ± 0.5 (10)$^{0.006}$	0.32 ± 0.05 (10)
Inflorescence	$\%_{dw}$				33.6 ± 2.1 (9)	0.7 ± 0.3 (9)	0.13 ± 0.02 (9)
	mg shoot^{-1}				47.0 ± 2.9 (9)	1.0 ± 0.4 (9)	0.18 ± 0.03 (9)

Mean ± standard deviation (number of sample); *significant difference between nonflowering and flowering parts ($p \leq 0.01$); nd: not determined.

P are therefore required for the inflorescence elaboration. For C, an accumulation in the leaves of the flowering shoots occurs (see Table 1) while for P, the stock in the leaves remains unchanged and the additional quantity serves for the inflorescence elaboration (Table 1). The unchanged quantity of N required for the inflorescence elaboration could mean that the N is unavailable in the environment or/and is easily drawn from leaves (resorption). Similar results are obtained for *Zostera marina* with a significant N resorption from leaves for the flowering and seed production (Lent & Verschuure, 1995).

By using ^{15}N as tracer, Lepoint et al. (2002a, b) calculated that leaf and root would contribute respectively 40 and 60% of the annual N uptake. These uptake represent about 60% of the annual N need of a nonflowering plant. The remaining needs are ensured by N recycling.

Our results suggest that, in flowering shoots, a part of the nitrogen required for the inflorescence elaboration needs to be translocated from both intermediate and adult leaves of the flowering shoots.

In the Bay of Calvi, from 1975 to 1993 on, flowers were rarely observed. However, since 1998, the meadow blossomed. The inflorescence elaboration affects the shoots' biometry: decrease in the number of juvenile leaves, decrease in length of intermediate and small adult leaves, increase in length of long adult leaves, and decrease of both widths in intermediate and adult leaves (Gobert et al., 2001). This work emphasized that elemental C, N concentrations of the flowering shoots are modified (higher C and lower N concentrations in all the types of leaves) in comparison to nonflowering shoots. In flowering shoots, additional quantities of C and P are required for the inflorescence elaboration. A part of the necessary additional C is probably provided (and translocated) by the leaves or by the inflorescence which could acquire part of resources needed. The shoot concentrations of P are not modified during the flowering, it seems to be available directly in the environment. The additional C and P could also be provided by neighbouring shoots by the way of the rhizomes. *P. oceanica* grows in nutrient-poor areas; the availability of nitrogen is probably one of the factors which limit the flowering in the Calvi Bay.

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