



Anthesis effects on *Posidonia oceanica* (L.) Delile phenology in the Bay of Calvi (Corsica, Mediterranean Sea)

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Abstract

In *Posidonia oceanica* (L.) Delile, anthesis induces a decrease in the number of juvenile leaves resulting in a significant reduction in the number of leaves on the flowering shoots. All the leaves of the flowering shoots are narrower than the leaves of nonflowering shoots. A modification of the leaf growth also appears in flowering shoots: the oldest leaves are longer and the leaves induced during or after anthesis are shorter. At 10 m depth, in the Bay of Calvi, anthesis lasts roughly 3 months and the flowering is induced 7 months before anthesis.

Introduction

Endemic to the Mediterranean Sea, the marine phanerogam *Posidonia oceanica* (L.) Delile covers the soft substrate of the sea bed between 5 and 40 m depth and forms monospecific meadows which represent one of the most productive Mediterranean ecosystems (Boudouresque et al., 1984, 1989). The annual leaf growth cycle and biometry are well documented (Boudouresque et al., 1984, 1989) in the *Posidonia* ecosystem (Panayotidis & Giraud, 1981; Caye & Rossignol, 1983; Bay, 1984; Pergent & Pergent-Martini, 1988, 1991; Buia et al., 1992), while little is known about the sexual reproduction which has been 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), but the factors inducing flowering remain uncertain (McConchie &

Knox, 1989). Bathymetric and geographical variations appear regarding the flower occurrence and the flower time apparition (Boudouresque & Meinesz, 1982; Mazzella et al., 1984). Flowers have a patchy distribution (Pergent, 1985; Pergent & Pergent-Martini, 1988; Buia & Mazzella, 1991) and appear only on orthotropic rhizomes which generally have longer leaves and a smaller number of leaves than plagiotropic ones (Caye, 1980a,b). The inflorescence is a spike of three or four spikelets, each done with two or three hermaphrodite flowers and one male flower with reduced gynoeceum (den Hartog, 1970; Caye & Meinesz, 1984).

Recently, the genetic structure of the population and the seedling conditions have been investigated (Capiomont et al., 1996; Procaccini & Mazzella, 1998; Piazza et al., 1999; Sandmeier et al., 1999), but the biometry of flowering shoots has been poorly studied (Caye & Meinesz, 1984). Nevertheless, following the flower formation, a change in the physiology of the shoots has been pointed out with a modification of leaf growth. After flowering, the intermediate leaves of the shoots were, on average, shorter than those of the non-flowering ones (Giraud, 1977). This difference in leaf

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length is the result of a shift to a lateral meristem from the main ones after the flowering and a preferential use of photosynthetates by the inflorescence (Panayotidis, 1986; Pergent & Pergent-Martini, 1988).

In the Bay of Calvi (Corsica), from 1975 to 1993, flowers were rarely observed (Bay, 1984, Gobert, unpublished data) but from 1994 onwards, flowering was regularly observed (Gobert et al., submitted). In this work, we have investigated the effects of anthesis (time or process of expansion of a flower) on both the biometrical characteristics of *P. oceanica* shoots and the leaves' renewal, to evaluate its impact on the meadow phenology.

Material and methods

This work was carried out in the *P. oceanica* meadow near the marine research station STARESO (in the Bay of Calvi, Corsica; 42° 35' N, 8° 43' E) (Fig. 1). Ten flowering and ten nonflowering shoots from different patches were collected in October 1998 at 10 m depth by SCUBA diving in areas displaying similar light, temperature and hydrodynamical conditions. Plants were weighed, measured and separated, their biomass (g shoot^{-1}) and leaf area (cm^2 of leaf area shoot^{-1}) were calculated according to Giraud (1979).

The Kolmogorov–Smirnov test was used to assume the normality of the data. The *t*-test and Mann–Whitney *U*-test were used to compare the data sets. Results were judged significant when $P \leq 0.05$.

Results

The biometry of the nonflowering shoots presented in this study (Table 1 and Fig. 2) is in good agreement with data obtained since 1990 in the same period of the year at 10 m depth (i.e., 9.0 ± 1.0 leaves and $160 \text{ cm}^2 \text{ shoot}^{-1}$, Gobert et al., 1995).

On average (Fig. 2), the nonflowering shoots display one more leaf (8.8 ± 1.1 leaves) than the flowering ones (7.8 ± 0.4 leaves, $P \leq 0.05$). This is the result of a significant decrease in the number of juvenile leaves ($P \leq 0.05$) while the number of intermediate and adult ones remains constant.

The width of both intermediate and adult leaves are significantly smaller in the flowering shoots (Table 1). In spite of a modification of both width and number of leaves in the flowering shoots, the leaf surface and shoot biomass (without any consideration of the

flower weight and surface in the calculation) remain unchanged.

The flowers, which are chlorophyllous organs, contribute up to 16% (i.e., $0.13 \pm 0.04 \text{ g}$ of the dry weight) of the total shoot biomass. The total leaf weight of flowering shoots is smaller (8% of the dry weight) (Table 1) resulting in no significant difference in the total weight of both types of shoot.

Discussion and conclusion

The juvenile leaves, elaborated simultaneously with the floral peduncle, are scarce on the flowering shoots. This suggests that the energy required for the juvenile leaf growth is used for the elaboration of the inflorescence. Thus, the biometry of flower carrying shoots appears to be modified and the production of the inflorescence could reduce the emergence of juvenile leaves. This statement is in good agreement with what is observed in terrestrial monocotyledons (see, e.g., Nozeran & Neville, 1971) but is in disagreement with the observations of Pergent (1987), who by lepidochronological method, found a higher number of leaves on the flowering shoots of *P. oceanica*. He suggested a higher activity of the apical meristem with preferential transfer of photosynthetates to the flowering shoots as shown by Harrison (1978) in *Zostera marina* den Hartog. This kind of resource allocation shifting from vegetative to reproductive structures resulting in a modification in plant growth has also been observed for other Mediterranean seagrasses (Marbà et al., 1996). However, Pergent (1987) has shown that the year following flowering, the shoots were not affected and the number of leaves did not change. The stability of the number of leaves suggests that in the meadow of Calvi a limitation of one or some factors operates on the growth when flowering. This could be related to the very low nitrogen contents of *P. oceanica* tissues in Calvi Bay (Gobert et al., 1995).

To evaluate the impact of anthesis and of flowering on the shoot phenology, we have classified the leaves according to their insertion rank (1–*n*, beginning from the youngest) (Fig. 3). Considering a mean growth of 3 mm day^{-1} (data for the juvenile leaves in October 1998), we have calculate that the anthesis last for 3.3 months (3 months according to Buia & Mazzella, 1991), the floral axis being $30 \pm 5 \text{ cm}$ ($n=10$) long. Thus the first visible parts of the inflorescence appeared in August.

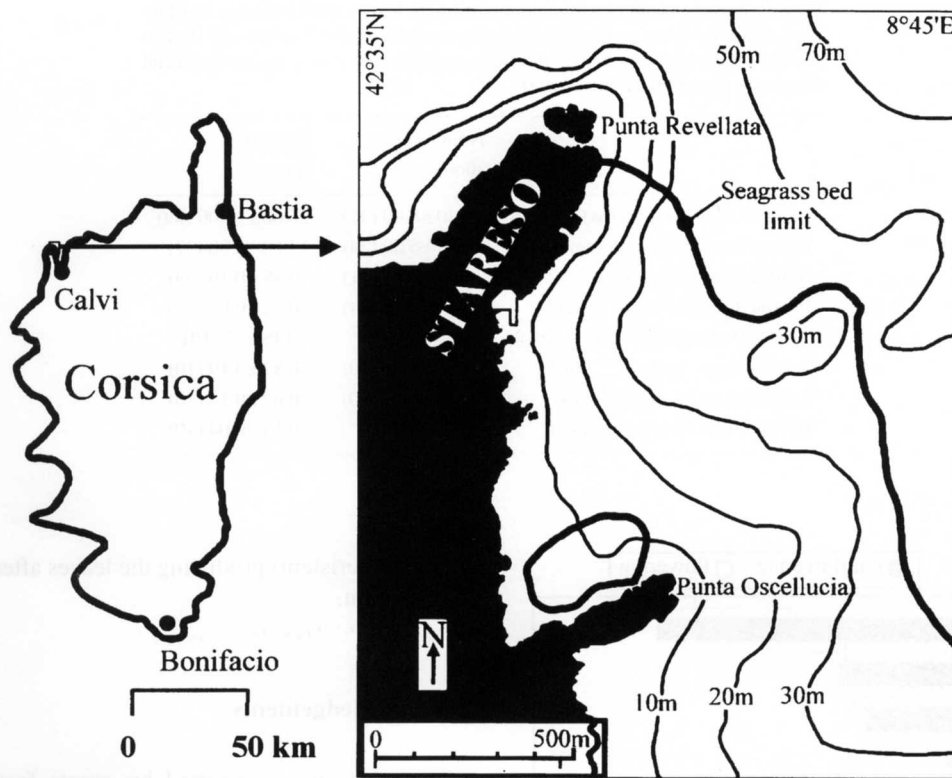


Figure 1. Location of the Bay of Calvi and of the marine research station STARESO.

In October, the shoots presented leaves that we have classified in three categories (Fig. 3): (1) leaves number 8 and 9 which are significantly longer in the flowering shoots than in nonflowering ones; (2) leaves 2, 3 and 4 which are significantly shorter in the flowering shoots than in nonflowering ones; and, finally, (3) leaves 5, 6 and 7 without significant difference between both two shoot types. Leaf 1 is the first juvenile leaf and this leaf do not exist on the flowering shoot.

At the beginning of anthesis, leaves 8 and 9, being significantly longer than in the nonflowering shoots, were 6 and 7 (considering a plastochrone for *P. oceanica* leaves of 43 days according to Duarte et al., 1998). These adult leaves are 7 months old (Caye & Rossignol, 1983; Pergent & Pergent-Martini, 1991), and are longer and narrower than in the nonflowering shoots and so bear the effects of the flowering before the actual flowers appear. Therefore, at 10 m depth in the northern Mediterranean, flowering induction occurs about 7 months before anthesis. Our results suggest that before anthesis, the shoots which will bear the flowers have a modified physiological activity in-

ducing an increase of the leaf length and a decrease of the leaf width.

Leaves 2, 3, 4 are significantly shorter in flowering shoot than the leaves of the same rank in nonflowering ones ($P \leq 0.05$). They have been formed during or after anthesis (their mean daily growth is 2.1 ± 0.6 mm ($n=31$), unpublished data). They are 40–120 days old and have been formed on a secondary axis, a lateral meristem (Giraud, 1977). This confirms the previous observations of Caye (1980a,b) who has shown that the first leaves of this lateral meristem always bear narrower and smaller leaves than the main one.

No significant difference appeared on the leaf length for leaves 5, 6 and 7.

To conclude, the comparison of flowering and nonflowering shoots indicates that the flower induction of *P. oceanica*, at 10 m depth in the Bay of Calvi, starts about 7 months before the flower occurrence. This flowering induces a range of changes in the biometrical characteristics of the shoots: general reduction of the leaf width, increase of the length of the older leaves and reduction of the length of the young leaves. On the whole these changes have no effect on the total

Table 1. Length, width of adult and intermediate leaves, total leaf area, leaf biomass of nonflowering and flowering shoots and inflorescence biomass at 10 m in October 1998 (mean \pm standard deviation (number of sample); ns, no significant difference; *: significant difference)

| | Nonflowering shoots | Flowering shoots |
|---|-----------------------|------------------------|
| Adult leaf length (cm) (ns) | 24.30 \pm 8.00 (41) | 26.60 \pm 13.00 (39) |
| Intermediate leaf length (cm) (ns) | 14.50 \pm 6.00 (34) | 13.60 \pm 5.50 (37) |
| Adult leaf width (cm) (*) | 1.04 \pm 0.10 (41) | 0.98 \pm 0.10 (39) |
| Intermediate leaf width (cm) (*) | 0.99 \pm 0.10 (34) | 0.92 \pm 0.07 (37) |
| Total leaf area (cm ² shoot ⁻¹) (ns) | 159 \pm 36 (10) | 148 \pm 35 (10) |
| Total biomass (g shoot ⁻¹) (ns) | 0.75 \pm 0.26 (10) | 0.82 \pm 0.19 (10) |
| Leaf biomass (g shoot ⁻¹) (ns) | 0.75 \pm 0.26 (10) | 0.69 \pm 0.17 (10) |
| Inflorescence biomass (g shoot ⁻¹) | – | 0.13 \pm 0.04 (10) |

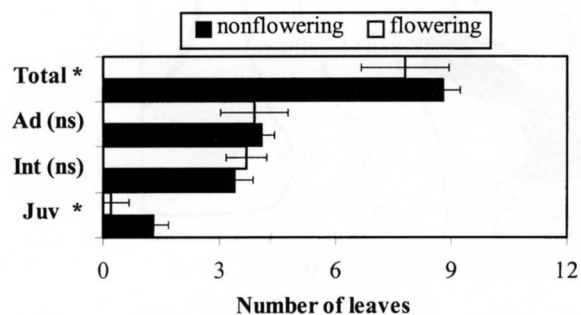


Figure 2. Number of leaves (total, adult, intermediate and juvenile) per shoot in flowering ($n=10$) and nonflowering ($n=10$) *P. oceanica* shoots (*significant difference; ns, no significant difference).

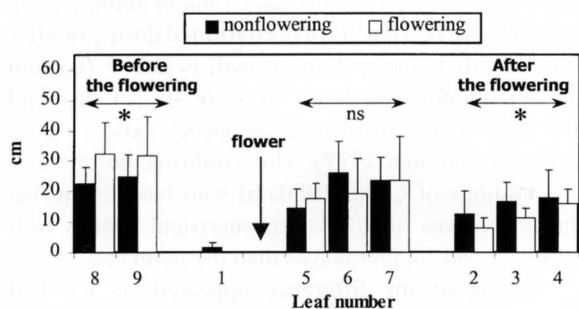


Figure 3. Comparison between the leaf length of nonflowering (black bars) and flowering (white bars) shoots classified according to their insertion (1–9 starting with the youngest) in October 1998 (mean \pm standard deviation; *significant difference, ns, non significant difference).

biomass and leaf surface. They 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 flower apparition.

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