

Cyclic Changes along *Posidonia oceanica* Rhizomes (Lepidochronology): Present State and Perspectives

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With 6 figures

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Abstract. Leaf sheaths in the seagrass *Posidonia oceanica* can persist for millenia and they show, according to their insertion rank, cyclic variations in parameters such as thickness and tissue structure. The principal cycles are always annual, but pluriannual cycles can also be detected. Annual cycles may be changed by environmental parameters such as light, temperature, or water movement. In a fashion analogous to the study of annual tree rings (dendrochronology), the study of cyclic changes in *Posidonia oceanica* sheaths is thus a technique allowing the study of past yearly changes in the near-shore environment.

Problem

Posidonia oceanica (LINNAEUS) DELILE, a marine phanerogam abundant in the Mediterranean, grows between the surface and depths of 30 to 40 m in extensive beds called meadows ("herbiers" in MOLINIER & PICARD, 1952). Vertical growth of its rhizomes allows the plant to counter burial by sediments trapped within the leaf canopy (CAYE, 1980; BOUDOURESQUE *et al.*, 1984). Their interlacing rhizomes, together with sediment filling the interstices (BLANC & JEUDY DE GRISSAC, 1978), constitute a most characteristic structure, the "matte" (Fig. 1). When *Posidonia oceanica* leaves die, only the blade falls away; the sheath remains attached to the rhizome and is often wrongly termed a "scale" (GRENIER, 1860; GIRAUD, 1977; PERGENT, 1987). Sheaths and rhizomes decay little and can persist within a matte for millenia (> 4,600 years, using ¹⁴C method; in BOUDOURESQUE *et al.*, 1980).

Sheath thickness has been shown to vary cyclically as a function of position on the rhizome (CROUZET, 1981; PERGENT *et al.*, 1983; PERGENT, 1987). By analogy with dendrochronology (FRITTS, 1976), the study of this periodicity and associ-

ated effects has been termed "lepidochronology" (BOUDOURESQUE *et al.*, 1983; PERGENT *et al.*, 1983; PERGENT, 1987). In fact, the word "lepidochronology" is based on a misleading application of terms (*i. e.*, scale). Another cyclic variation has also been detected in *Posidonia oceanica* rhizomes: the rhizome thickness (PIRC, 1983).

The questions are: (i) Are these cycles a general feature all around the Mediterranean and within the entire depth range of the species? (ii) What is the periodicity (annual?) of these cycles? (iii) What is their origin (endogenous or exogenous)? (iv) Are other anatomical and/or morphological parameters simultaneously changing? (v) What are the possible applications of "lepidochronology"?

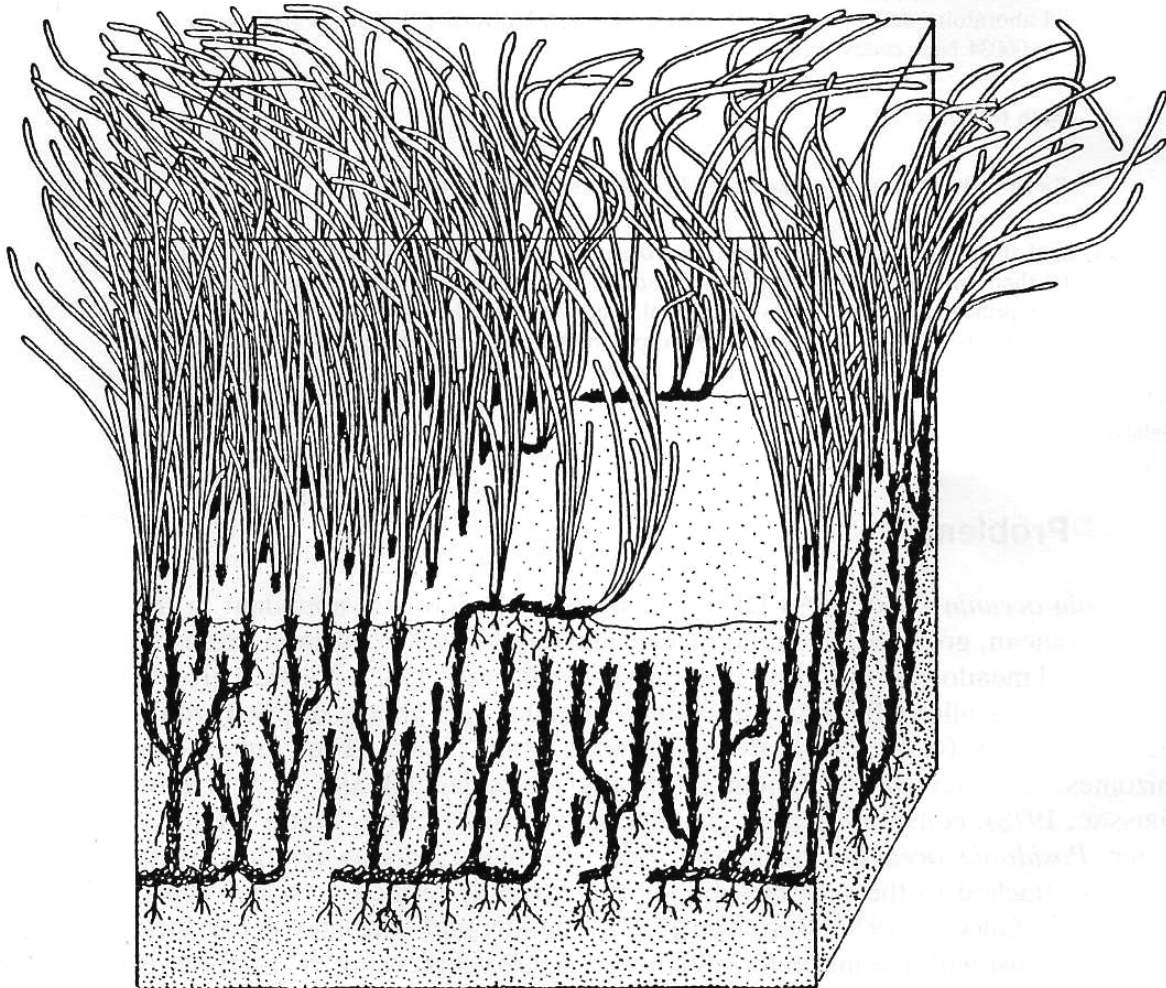


Fig. 1. Schematic diagram illustrating characteristic arrangement of rhizomes with alternating vertical (orthotropic) and horizontal (plagiotropic) growth. This very compact system, comprising dense interlaced rhizomes together with the sediment surrounding them, is known as "matte" (in BOUDOURESQUE & MEINESZ, 1982).

Material and Methods

More than 5,000 rhizomes (orthotropic and plagiotropic) have been sampled and analysed so far from around the Mediterranean, Egypt (THELIN *et al.*, 1985), Turkey (PERGENT, 1987), Tunisia (PERGENT, 1986), Corsica (BOUDOURESQUE *et al.*, 1986 a, b) and mainland France (MOSSE, 1984; PERGENT *et al.*, 1985; PERGENT, 1987), at all seasons and between depths of 0.5 to 32 m.

The sheaths were carefully detached, and the order of occurrence (rank) (Fig. 2) back from the rhizome apex noted. A thin transverse section of each sheath was made between 10 and 12 mm from its point of attachment, and the sheath thickness was measured using a microscope fitted with an ocular micrometer. Anatomical characteristics observed in the sheath section were also noted: number of cell layers in the mesophyllous parenchyma, number of cell layers in the ventral and dorsal sclerenchyma, presence or absence of dorsal sclerenchyma islets, shape of the cells of ventral sclerenchyma (palisadic or rounded), abundance of tannin cells (rare, common, very common). The length of the sheath was measured from its base to the median point of its tip.

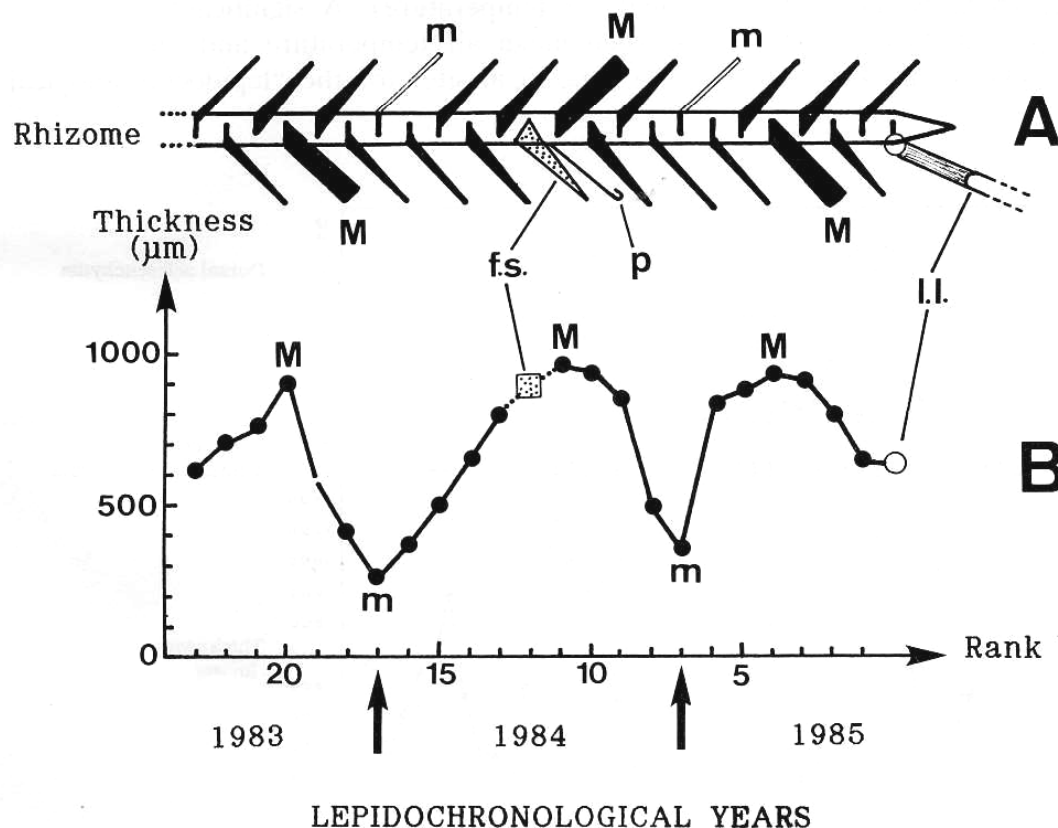


Fig. 2. Arrangement of sheaths along an orthotropic rhizome (A) and corresponding cycles of variation in sheath thickness (B). Chronological significance of cycles ("lepidochronological years") also indicated. M – sheaths of each cycle showing maximal thickness; m – sheaths of each cycle showing minimal thickness; f. s. – floral stalk; p – prophyll; l. l. – living leaf (rank N°0). The flower stalk is only drawn to indicate position, not thickness.

Results

All rhizomes studied (both orthotropic and plagiotropic, from shallow and deep waters), show cycles in sheath thickness (MOSSE, 1984; PERGENT, 1987). These cycles are related to changes in the anatomical structure of certain tissues, such as the number of cell layers in both the sclerenchyma and the mesophyllous parenchyma, as well as changes in the shape and appearance of these cells (Fig. 3; CROUZET, 1984; PERGENT, 1987). Cyclic changes in tannin cell abundance are less conspicuous, although present.

By following month by month the thickness of sheaths newly formed at the rhizome apex (PERGENT, 1987), it has been shown that: (i) generation of these cycles takes place at the apex; (ii) sheath characteristics do not change after initial formation; (iii) the cycles are annual, showing one minimum and one maximum in thickness per year (Fig. 2); (iv) dates of change in sheath thickness are consistent from year to year for a particular station; (v) fine sheaths begin to appear in late winter or early spring, while production of thick sheaths begins in autumn. The term "lepidochronological year" is used to name the time period between two minima. This term prevents any confusion with the calendar years.

Various characteristics of the annual cycles, including amplitude, period, and mean thickness are modulated either internally or by some external means (perhaps water movement, light, or temperature). A significant correlation (BRAVAIS-PEARSON, $k = 1$) between mean air temperature and mean sheath thickness has been observed in superficial sites for the "lepidochronological

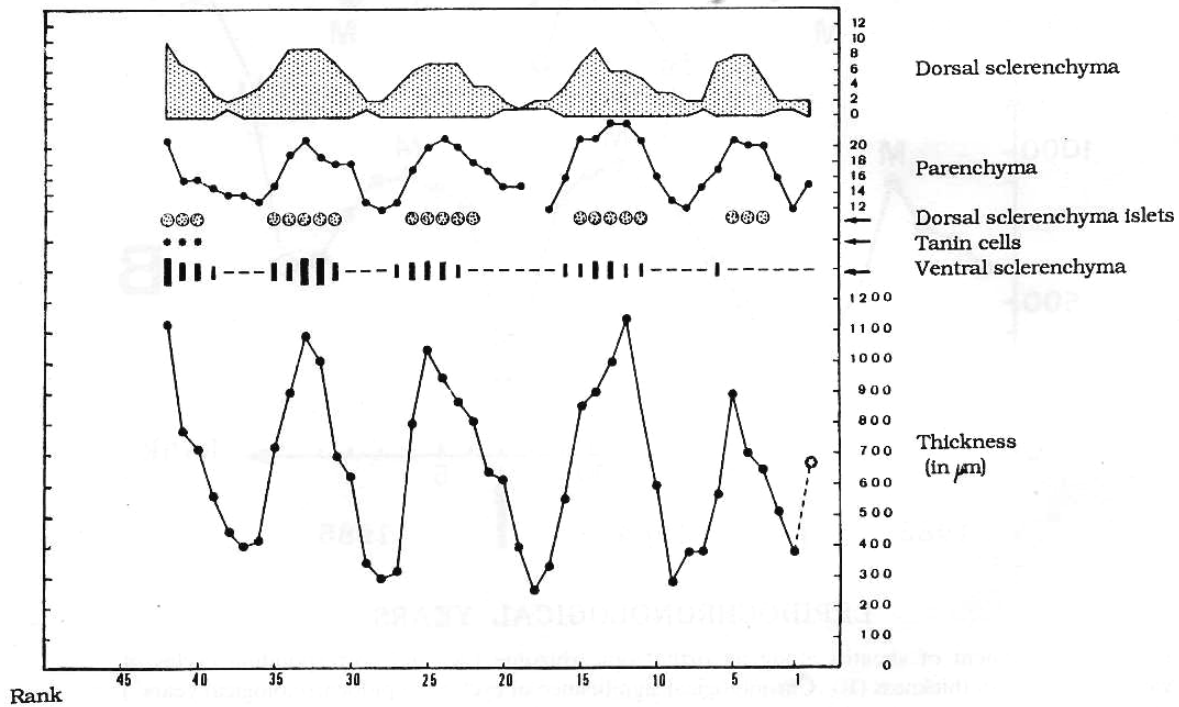


Fig. 3. Cycles of sheath thickness and anatomical parameters according to the insertion rank of the sheaths, for a rhizome sampled at Port-Cros in January 1982 (-3 m). (○) = the oldest living leaf.

year" following the presumed causal phenomenon (Fig. 4). Thus, at any one station, sequences of annual cycles recorded on different rhizomes can be consistent in showing the same type of interannual modulation (Fig. 5).

A large number of annual cycles can be recorded along a rhizome, far more than in growth rings of mollusk shells (LUTZ & RHOADS, 1980); cycles with a longer periodicity are apparent (Fig. 6), although their significance is not yet known. That past differences in growth characteristics can be read by means of "lepidochronology", and that both living and dead parts of rhizomes persist for so long, allows reconstruction of long-term growth and development histories of *Posidonia oceanica*, something apparently not previously possible for marine plants.

Discussion

Numerous applications, of which certain ones have already been successfully tested, are envisaged. Examples are:

- Estimation of growth rate and annual production of rhizomes (BOUDOURESQUE *et al.*, 1983; PERGENT *et al.*, 1983; BOUDOURESQUE *et al.*, 1984; ROMERO-MARTINENGO, 1985; PERGENT, 1987). The mean annual primary production of orthotropic rhizomes was found to range from 32 to 83 mg dry weight per rhizome and 9 to 65 g dry weight · m⁻¹ (PERGENT, 1987), which is consistent with BAY (1984) and OTT (1980). BOUDOURESQUE *et al.*, (1984), by studying growth rate variations from year to year along a rhizome, demonstrated the relation between growth and sediment input.

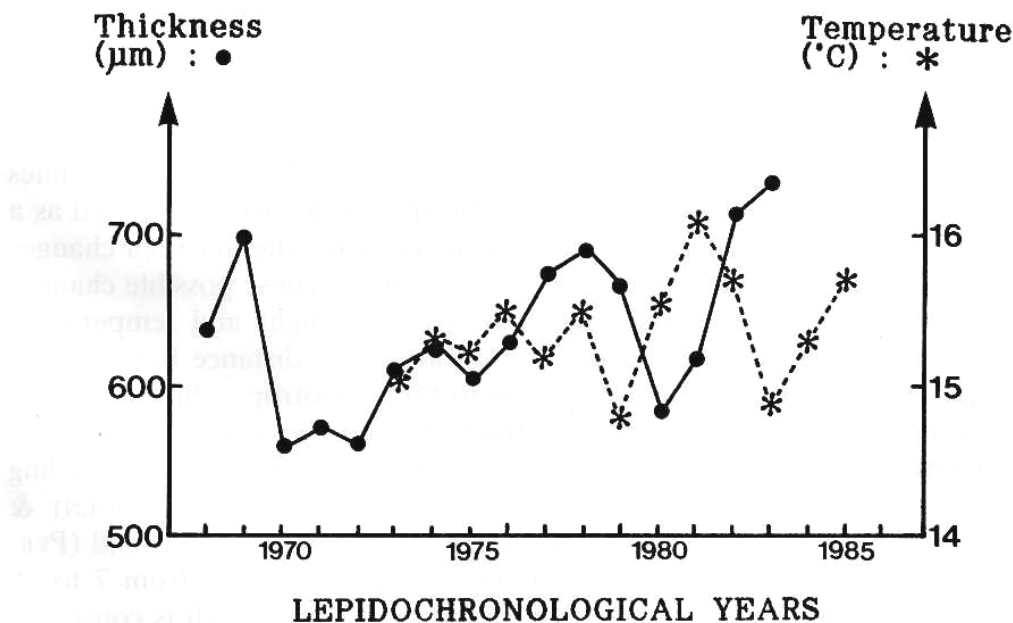


Fig. 4. Changes in mean air temperature and mean sheath thickness in a shallow site at Port-Cros island.

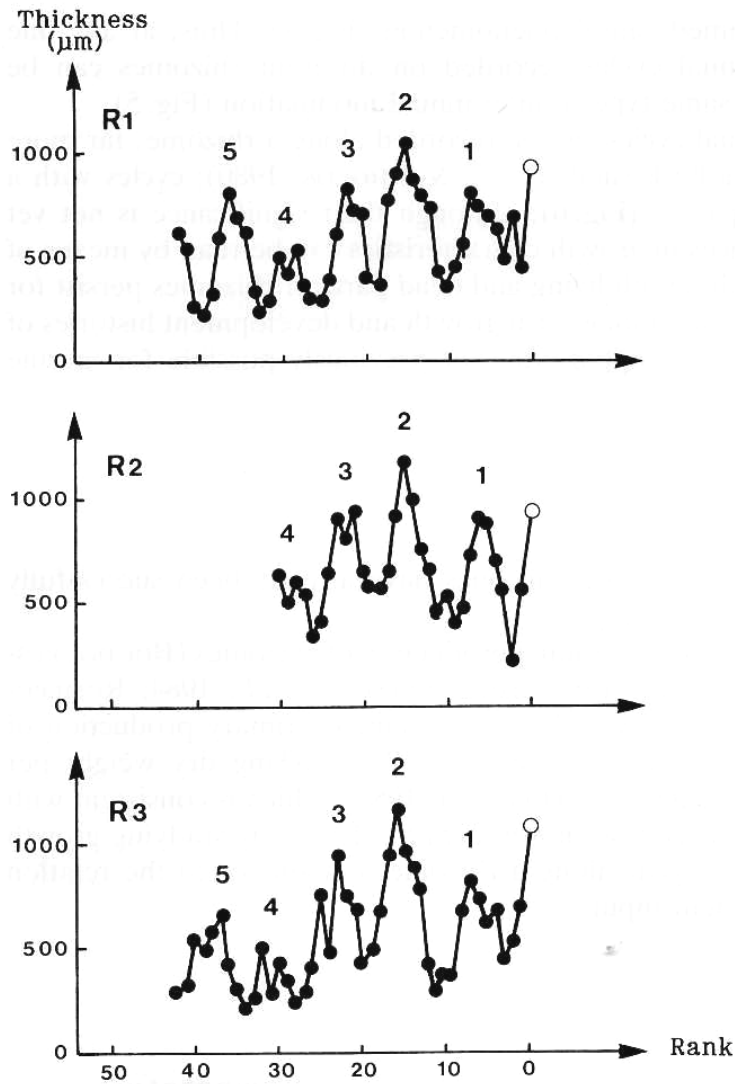


Fig. 5. Sheath thickness on three rhizomes (R1, R2, R3) from a station at Banyuls-sur-Mer, France, in relation to order of occurrence (rank). For all rhizomes, Peak N°2 (formed in 1979) is highest, while Peak N°4 (formed in 1977) is lowest. ○ – first living leaf.

– Enumeration of annual leaf production in both recent and former times (PERGENT *et al.*, 1983; PERGENT, 1987). Significant changes were observed as a function of depth and locality. The question arises as to whether such changes can occur with time along rhizomes of a given meadow. These possible changes could be related to external parameters (*e.g.*, mean light and temperature changes from year to year) or to internal features, like distance between the orthotropic rhizome apex and its connexion to the plagiotropic rhizome.

– Modelling of leaf renewal cycles (rhythms of leaf formation and of leaf fall, leaf longevity): leaf formation exhibits a peak in summer or in autumn (according to depth) and is generally interrupted from February to June (PERGENT & PERGENT, 1985; PERGENT, 1987). Leaf shedding is continuous year round (PERGENT & PERGENT, 1985; PERGENT, 1987). Leaf longevity ranges from 7 to 14 months according to the month of origin (PERGENT, 1987), which is consistent with THELIN & BOUDOURESQUE (1983), OTT (1980), and ROMERO-MARTINENGO (1985).

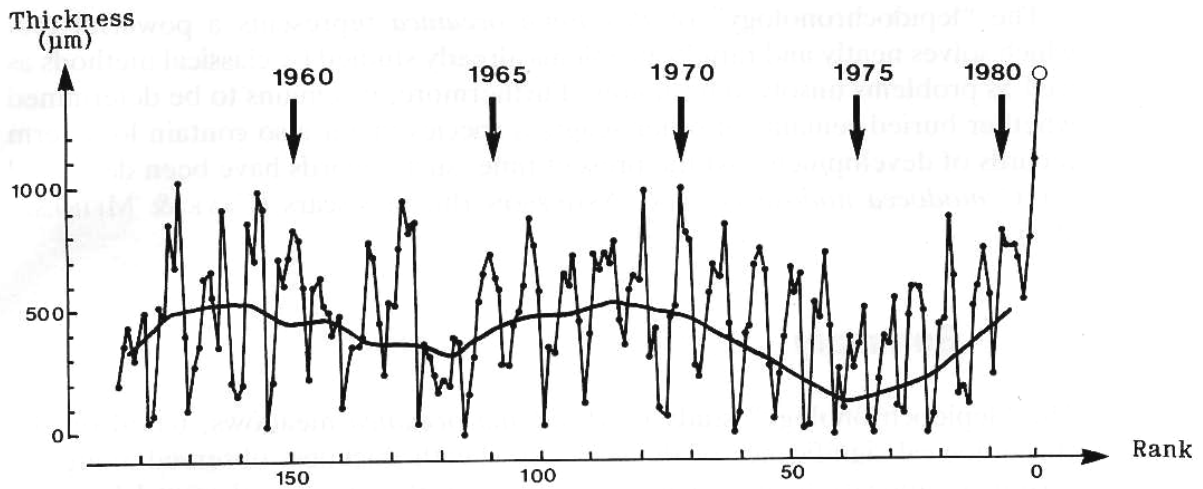


Fig. 6. Sheath thickness of one rhizome sampled at Banyuls-sur-Mer (July 1981, water depth 1 m) in relation to rank, showing multiannual cycles. Time scale of cycles indicated. Mean thickness of sheaths over an annual cycle shown after smoothing using a 3-year moving average. ○ – first living leaf.

– Detection and dating of paleo-flowerings from the remains of flower stalks inserted between the sheaths (BOUDOURESQUE *et al.*, 1986 a; PERGENT, 1987). Flowering is a rare event in recent time (THELIN & BOUDOURESQUE, 1985). Furthermore, it occurs at a season (autumn) in which field observations are usually scarce. At Banyuls-sur-Mer and in Corsica, numerous flowerings, the oldest dating from 1942, which passed unnoticed at the time, were detected (PERGENT, 1987). “Lepidochronology”, in making available an amount of data considerably larger than field observations, should result in a better knowledge of the climatic parameters which control flowering.

– Better understanding of processes involved in the formation and evolution of mattes (BOUDOURESQUE *et al.*, 1986 b). By accurate dating of each rhizome section within the matte, BOUDOURESQUE *et al.*, (1986 b) elucidated the dynamics of a peculiar type of *Posidonia oceanica* meadow, the hill-type meadow (BOUDOURESQUE *et al.*, 1985). The dynamics of two other types of meadows, namely the tiger-type meadow (BLANPIED *et al.*, 1979; BOUDOURESQUE, 1986) and the stairs meadow (BOUDOURESQUE, unpubl.), should be studied in the same way.

– Fast evaluation of primary production (actual and past) by using correlations between sheath thickness and blade length. A preliminary attempt in this direction was performed by MOSSE (1985), but the work is in progress.

– Recording of atmospheric fallout using, for example, ^{137}Cs analysis (CALMET *et al.*, 1988). The maximum activity of ^{137}Cs in sheaths occurred in groups produced between 1960 and 1964, a period corresponding to a fallout peak. The distribution of ^{137}Cs activity in rhizome age groups indicates an apparent lag, perhaps due to transport of material in the rhizome. As a result, sheaths of *Posidonia oceanica* rhizomes appear to be able to memorize a chemical event for at least 30 years, and *Posidonia oceanica* could prove to be a valuable tool for marine pollution surveys.

The "lepidochronology" of *Posidonia oceanica* represents a powerful tool which solves neatly and rapidly problems already studied by classical methods as well as problems unsolved until now. Furthermore, it remains to be determined whether buried remains of other seagrass species might also contain long-term records of development. At the present time, such records have been described for *Cymodocea nodosa* (UCRIA) ASHERSON rhizome scars (CAYE & MEINESZ, 1985).

Summary

The "lepidochronology" study of *Posidonia oceanica* meadows, based on the chronological significance of the cycles of sheath thickness observed along the rhizomes, appears to be a valuable tool. Correlations are observed between sheath thickness and exogenous parameters (light, temperature, water movement) or endogenous parameters (anatomical structure of certain tissues). Furthermore, the "lepidochronology" harbours numerous applications and perspectives: (i) Estimation of growth rate and annual production of rhizomes, (ii) Estimation of annual leaf production, (iii) Modelling of leaf renewal cycles, (iv) Detection and dating of past flowering, (v) Better understanding of the formation and evolution of mattes, (vi) Fast evaluation of primary production, (vii) Detection and dating of chemical events recorded in the sheaths.

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