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Long-term stability in the production of a NW Mediterranean *Posidonia oceanica* (L.) Delile meadow

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ABSTRACT

Long-term changes in leaf net production of the seagrass *Posidonia oceanica* (L.) Delile, and in the irradiance arriving at the meadow canopy, were investigated in a NW Mediterranean meadow using a palaeoecological approach. We conducted *in situ* shade experiments to find the relationships between the carbon stable isotope ratio (δ^{13}C) of plant tissues, leaf net production, and ambient irradiance. The relationships were highly significant and fitted the Michaelis–Menten equation and power functions. These functions were used to reconstruct light and net production using the δ^{13}C of *P. oceanica* detritus as a palaeoecological proxy along a 150 cm core of *P. oceanica* matte (a peat-like deposit formed by this endemic seagrass species). The δ^{13}C values of sheath detritus along the core (i.e., the net leaf production) showed a weak but significant decrease towards the present time ($R=0.308$; $P=0.02$) probably as a result of (1) an increase in DIC availability, and/or (2) a progressive change in the carbon isotopic signature of DIC, both of which are consistent with a rise in anthropogenic atmospheric CO_2. The canopy irradiance, reconstructed for the last 1200 years, showed a mean value of 128 μE m^{-2} s^{-1} with a range of 12.5–280 μE m^{-2} s^{-1}. The reconstruction of the net leaf production for the same period yielded a mean value of 2.5 mg dw day^{-1} $shoot^{-1}$ with a range of 2.0–2.7 mg dw day^{-1} $shoot^{-1}$. Both ranges are within the values reported in the literature for present day studies. The absence of significant fluctuations or sudden changes through time suggests remarkable ecosystem stability during the last millennium.

1. Introduction

Seagrass beds are among the most productive and complex oceanic ecosystems (McRoy and McMillan, 1977). This high productivity and complexity is the result of an overall annual positive carbon balance at the ecosystem level that renders a substantial surplus of energy available to feed a high diversity of communities (Cebrián, 2002; Mateo et al., 2006). Perturbations, either natural or anthropogenic, at local or regional levels, either strong and episodic or weaker but persistent in time, can potentially compromise meadow gains leading to meadow decline or disappearance (Marbà et al., 1996). This is particularly critical for climax, slow-growing seagrass species such as *Posidonia oceanica*. Therefore elucidating the range and time scales of variability in climax seagrass ecosystem productivity, the frequency and magnitude of perturbations, and species capacity to maintain an overall stability or to recover from perturbations, should constitute a priority for ecologists and environmental managers when elaborating conservation action plans for seagrass-dominated ecosystems (Short and Wyllie-Echeverria, 1996). Because these processes and phenomena take place at a very long time scale, the study of seagrass-dominated ecosystems is difficult and usually has to rely on relatively short time-series of variables and models (Duarte et al., 20062).

Palaeoenvironmental reconstructions are of interest as they provide data about longer-term ecosystem dynamics such as natural fluctuations and succession (Indermuhle et al., 1999; Petit et al., 1999; Arnand, 2000). At the shorter temporal scale of centuries, these studies have useful applications, especially within the framework of recent global environmental change (Crutzen and Stoermer, 2000). In fact, the palaeoecological approach can be considered a short-cut to fulfilling some of the objectives of costly monitoring plans (i.e. identifying general trends and potential future scenarios). The possibility of creating such reconstructions critically depends upon the availability of adequate palaeo-records and proxies.

Records may be abiotic (lacustrine or oceanic sediments, stalagmites and icecaps), biotic (peat bogs, corals, tree-rings and shells) or a mix of these two. Their quality usually depends on adequate long-term preservation of their chronological and chemical structure after formation. Such conditions are rarely encountered in temperate coastal ecosystems, even in well-protected bays, because of the characteristic tension at the interface between marine and terrestrial systems (hydrodynamism and bioturbation). One of the exceptions is the peat-like sediments accumulated by the endemic Mediterranean seagrass *Posidonia oceanica* (L.) Delile. These sediments, known as "mat" or "matte", constitute a unique bio-construction formed by debris from the

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belowground organs of the plant (sheaths and roots). Carbon dating has revealed that they span several thousand years (Boudouresque et al., 1980; Romero et al., 1994; Lo Iacono et al., 2008) and that they accurately record chronology of deposition (Mateo et al., 1997; Mateo et al., 2002). Hence, the detailed analysis of cores from these deposits may provide a new way to study local and regional broad changes in key environmental and biological variables during the Holocene.

Palaeoecological transfer functions are empirically derived equations for making quantitative estimates of past environmental conditions from palaeontological data (Sachs et al., 1977). They are generally obtained by calibration against datasets of extensive modern sample sets (Birks, 1998; Sejrup et al., 2004). However, when the gradient of data sampled under natural conditions is not wide enough, or when the relationship between past environment and palaeontologial data is poor, it is necessary to take an experimental approach (Tilman et al., 1994).

The recognised relationship between carbon stable isotopes and primary production (Craig, 1954a; Park and Epstein, 1960; O'Leary, 1981; Farquhar et al., 1982), together with its conservative nature through time, has allowed its use as a proxy of past production in planktonic organisms (Rau et al., 1989; Singer and Shemesh, 1995), corals (Knutson et al., 1972; Erez, 1978; Reynaud-Vaganay et al., 2001) and trees (Craig, 1954b; Pearman et al., 1976; Francey and Farquhar, 1982; McCornac et al., 1994; Trimborn et al., 1995). To our knowledge, only one attempt has been made to use $\delta^{13}C$ to link seagrass ecology to palaeoecology at the decadal scale (i.e., lepidochronology; Mateo et al., 2000) with no information available for longer temporal scales.

The central hypothesis of this work is that the climax seagrass *P. oceanica*, through a high dynamism that combines processes that operate at various spatial and temporal scales, and in the absence of severe catastrophic natural or human-induced disturbances, can maintain one of its key processes, i.e. primary production, rather stable during centuries or millennia. The present paper reports a first attempt to couple experimental field ecology and palaeoecology for seagrass ecosystems. *In situ* shading experiments and isotope analysis have been used to calibrate a palaeoecological proxy trough the development of transfer functions that, in turn, allowed the reconstruction of changes in light reaching the canopy and the net leaf production of *P. oceanica* over the last thousand years. Despite of this mechanistic approach, at this stage our work does not aim at providing a detailed quantitative description of how were those parameters in the past. We propose that *P. oceanica* mattes hold information susceptible to palaeo-reconstruction methods which, by outlining past scenarios, may provide key knowledge to better understand present and future climate and ecosystem dynamics. Although our work is focussed on a Mediterranean seagrass, the principles unravelled from this species may be valid for other low-turnover seagrass species of the world accumulating refractory organic matter.

2. Materials and methods

2.1. Sampling site

A 150 cm core of *P. oceanica* matte was obtained in the summer of 2000 in Portlligat Bay, Natural Parc of Cap de Creus (NW Mediterranean, Girona, Spain; Fig. 1). From ortho-photo images of the bay (316-82 and 316-83, 1:5000, issued by the Institut Cartogràfic de Catalunya) and direct observations using SCUBA it has been estimated that the bottom of the bay is ca. 68% covered in by living *P. oceanica* meadows (ca. 9 ha) with shoot densities ranging from 100 to 900 shoots m^{-2}; dead *P. oceanica* matte is found in small areas adding up around 4% of the bottom of the bay (ca. 5 ha). In some areas

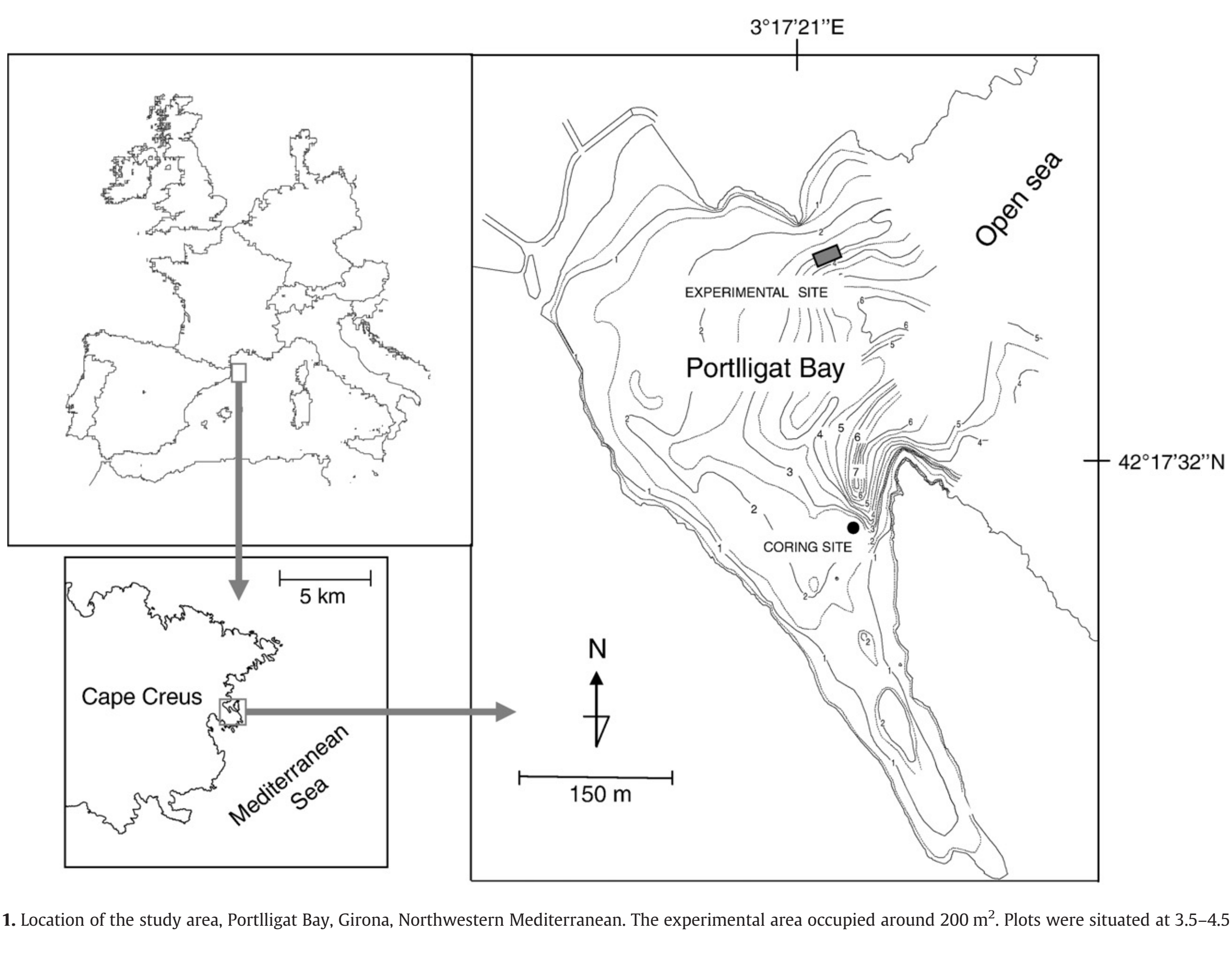

Fig. 1. Location of the study area, Portlligat Bay, Girona, Northwestern Mediterranean. The experimental area occupied around 200 m^2. Plots were situated at 3.5–4.5 m depth.