Research Article

Flowering of the seagrass *Posidonia oceanica* in the NW Mediterranean: is there a link with solar activity?

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Abstract

Time series analysis of the leaf biometry and rhizome production of the endemic Mediterranean seagrass *Posidonia oceanica* (L.) Delile was performed for a meadow in the Ligurian Sea (NW Mediterranean) in order to assess changes in plant growth during a massive flowering event that occurred in 2003 and coincided with the warmest summer temperatures recorded in the last centuries. *P. oceanica* exhibited the highest values of leaf surface area during the flowering year and the highest values of rhizome production in the previous year. The years immediately following the flowering event were characterized by a decrease in both parameters. Comparison of the years of massive flowering events reported in the literature for the entire Mediterranean with the historical series (spanning the last 50 years) of air temperature and sunspot number suggests that intense solar activity, and not warmer temperature *per se*, is likely to be the main trigger of massive *Posidonia oceanica* flowering events.

Keywords: *Posidonia oceanica*, flowering, solar activity, shoot morphometry, Ligurian Sea, NW Mediterranean.

Introduction

Virtually all biological phenomena have annual cycles and are influenced by the timing of abiotic events, such as light, temperature, lunar phase, rainfall, etc. (Forrest & Miller-Rushing, 2010). Flowering of plants are only one of many examples of physiological rhythms that are observed in nature. It is commonly accepted that light and temperature are the two environmental signals that can provide a consistent timing message for the vegetative and reproductive growth of plants (Johansson & Bolmgren, 2013); however, the former provides the most reliable and noise-free signal to start physiological processes, or in other words acts as a "*Zeitgeber*" (from German *Zeit* = time and *geber* = giver) (Brady, 1979; Migaud & Davie, 2010). A *Zeitgeber* synchronizes rhythms by determining their period (i.e. the length of a process) and their phase (i.e. the time when the cycle occurs). Temperature, being extremely variable, constitutes an imprecise signal and does not determine the precise time of the year to start the processes (Jackson, 2008; Johnsson, 2008), while it acts more as the regulator of the pace of the response. Also, the starting time of flowering is kept synchronized by a *Zeitgeber*, which is often regulated by light (Bailly *et al.*, 2011). Various cosmic cycles, such as sunspot periods, have been advocated as *Zeitgebers*, even if such correlations are more difficult to prove (Sollberger, 1962).

The endemic *Posidonia oceanica* (L.) Delile (1813) is the dominant seagrass in the Mediterranean Sea, where it forms extensive meadows that play a key role in coastal ecosystems (Boudouresque *et al.*, 2006; Montefalcone, 2009). Like all marine Magnoliophyta, *P. oceanica* shows both asexual and sexual reproduction. Asexual reproduction is the most common modality adopted by the plant and may occur through: 1) stolonization (i.e. the growth of horizontal, plagiotropic shoots), which allows for the colonization of bare substrata and the expansion over new areas (Boudouresque *et al.*, 2006); 2) dispersal of vegetative fragments that remain on the seafloor after disturbance events (Di Carlo *et al.*, 2005). Sexual reproduction, with the production of flowers and fruits, is a rare phenomenon that ensures greater genetic variability within meadows (Micheli *et al.*, 2010) and allows for the distribution of the plant over large spatial scales. Flowering usually occurs during autumn, while fruiting occurs in the late spring of the following year (Peirano *et al.*, 2001). Sexual reproduction seems to be unpredictable and highly variable, both in space and time, and changes in environmental conditions over large spatial scales are likely to be involved in the control of flowering induction (Balestri, 2004). Although the factors influencing the flowering of *P. oceanica* remain largely unexplored, water temperature has been showen to be one of the most important (Diaz-Almela *et al.*, 2006, 2007). Earlier reports

(Molinier & Picard, 1953; Semroud, 1993) showed that the southern meadows flower more frequently and abundantly than northern meadows; the latter, developing at the highest and coldest latitudinal range for this species, are thus able to reproduce sexually only in particularly favourable years (Balestri, 2004 and reference therein). Only recently, Diaz-Almela *et al.* (2006) found that the flowering probability was not correlated with latitude and hypothesized temperature variations as the main triggers of *P. oceanica* flowering rather than absolute temperature values. However, all these previous studies did not explore the synchronizer, i.e. the *Zeitgeber*.

The Ligurian Sea is one of the coldest sectors of the northern Mediterranean Sea (Morri & Bianchi, 2001). Some records of sporadic events of flowering and fruiting of *P. oceanica* in the Ligurian Sea are available (Bussotti & Guidetti, 1996; Stoppelli & Peirano, 1996; Sandmeier *et al.*, 1999; Aliani *et al.*, 2006; Micheli *et al.*, 2010), derived from either studies based on retrospective analyses or observations in the field. Flowering events all around the Mediterranean Sea have been reported in the last century (see for instance Giraud, 1977 and reference therein; Panayotidis *et al.*, 1989; Balestri & Vallerini, 2003; Calvo *et al.*, 2006), but events defined as "massive", i.e. involving most of the Mediterranean meadows at a wide-scale, have been reported only in years 1971, 1982, 1993 and 2003, suggesting a periodicity of about 11 years for such single important events (Diaz-Almela *et al.*, 2006). The highest proportion of flowering meadows was observed in 2003 (Diaz-Almela *et al.*, 2007), coinciding with the highest summer temperatures recorded since 1500 CE (Common Era) (Luterbacher *et al.*, 2004).

Peaks in solar activity show a periodicity of about 11-years (Ma *et al.*, 2009); boosting cosmic and UV rays, they reduce cloud formation and runoff, and increase irradiance and Earth temperature (McCabe & Wolock, 2008). Increases of sea surface temperature linked to peaks in solar activity have been particularly evident (Southward *et al.*, 1995; Roy & Haigh, 2009). Many biological phenomena are known to be linked to fluctuation in solar activity over the 11-year solar cycle such as, for instance, the effects on epidemics (Stoupel *et al.*, 1995), the life-cycle of *Lepus americanus* Erxleben (1777) (Sinclair *et al.*, 1993), pelagic fishes (Guisande *et al.*, 2004), macroalgae (Walker & Richardson, 1957), and plankton (Southward *et al.*, 1995).

This paper aims at: i) analysing leaf growth and rhizome production in a *P. oceanica* meadow of the Ligurian Sea using a time series of data collected at the time of the massive sexual reproductive event in 2003; ii) investigating the potential link between *P. oceanica* massive flowering events and two major climatic variables: air temperature, which has been shown to be a proxy of sea surface temperature (Astraldi *et al.*, 1995; Bianchi & Morri, 2004), and sunspot number.

Materials and Methods

The study was carried out in the *Posidonia oceanica* meadow of Prelo Cove (Ligurian Sea, NW Mediterranean) (Fig. 1). Three stations were identified along a permanent depth transect: one station at 4 m depth, near the meadow upper limit; one at 9 m depth, in the intermediate zone of the meadow; one at 14 m depth, corresponding to the meadow lower limit. At each station, 10 randomly selected *P. oceanica* orthotropic shoots were collected
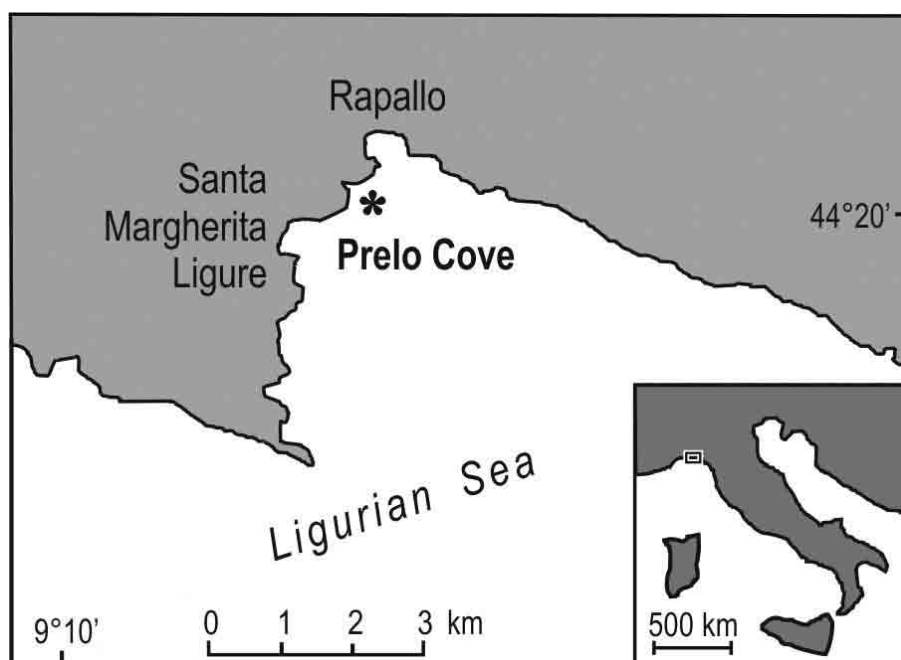

Fig. 1: Geographic location of the study area.

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monthly from January 2002 to December 2006. Shoots were collected at a minimum distance of 10 m from each other to minimise the possibility of being part of the same horizontal rhizome. In June 2006, a greater amount of shoots were collected (35 shoots for each station) to be analysed using the lepidochronology technique (Pergent, 1990). This reconstructive method has been recommended as a tool for assessing rhizome production for several years preceding the sampling dates.

At the laboratory, the leaves were removed from each shoot respecting the distich order of insertion, and then separated into the three growth categories defined by Giraud (1979): juvenile, intermediate, and adult leaves. To assess the leaf surface area of each shoot, the following leaf biometry parameters were measured: the number of adult and intermediate leaves per shoot, leaf length and leaf width. The mean annual leaf surface area (± standard error) was then computed from 2002 to 2006.

When *P. oceanica* leaves die and fall, their basal portions (sheaths) remain attached to the rhizome and are preserved within the matte for several years (Boudouresque *et al.*, 1980). The thickness of the sheets shows cyclical variations, with a minimum and a maximum every year (Crouzet, 1981). The minimum thickness is reached in February-March, while the maximum in September-October (Crouzet *et al.*, 1983). The number of sheets recorded between two minima represents the number of leaves produced during one lepidochronological year. Similarly, the portion of the rhizome between two minima corresponds to the amount of tissue produced in one year, and thus represents the rhizome annual production (Pergent, 1990; Montefalcone *et al.*, 2008). The portions of the rhizome produced between two minima were cut and then dried for 48 h at 70 °C, until constant dry mass (DM) was achieved. Rhizome production was reconstructed for the previous 7 years (1999 to 2005) for all the 105 shoots collected. The annual flowering prevalence (FP, flowering records per total records) was calculated for the 7 reconstructed years, counting the number of modified floral sheets, indicating past flowering events, encountered in each rhizome (Diaz-Almela *et al.*, 2007).

Univariate analysis of variance (2-way ANOVA) was used to assess differences in rhizome production and in leaf surface area among different years. To ensure statistical independence of the data (Underwood, 1992), mean values of rhizome production were calculated on different sets of 5 shoots randomly selected among the 35 shoots for each of the 7 reconstructed years. The model of the analysis consisted of two factors: Year (seven levels for rhizome production, five levels for leaf surface area, fixed) and Depth (three levels, fixed and orthogonal), with $n = 5$ replicates for rhizome production, $n = 120$ replicates for leaf surface area. Prior to analysis, homogeneity of variance was tested by Cochran's C-test and data were ln(x) transformed. When a factor was significant, the differences between levels were determined

using the Student-Newman-Keuls test (SNK test).

The years of massive flowering events reported in the literature at the entire Mediterranean-wide spatial scale (Diaz-Almela *et al.*, 2007) were compared to the historical series (from 1960 to 2012) of the average annual summer values of air temperature recorded by the Meteorological Institute of the University of Genoa and to the historical series (from 1961 to 2012) of the average annual number of sunspots (SN) recorded by NOAA (USA National Oceanic and Atmospheric Administration) and available at http://www.ngdc.noaa.gov/stp/SOLAR/ftp-sunspotnumber.html. The historical series of the average annual number of sunspots was also compared with available data on the average annual flowering prevalence (FP, flowering records per total records, calculated for years when observations were available for a minimum of 10 localities) reported for the NW Mediterranean by Diaz-Almela *et al.* (2007) from 1973 until 2004, and included in our own archives from 2005 until 2013.

Pearson's correlation coefficient (r) was used to investigate relationships between flowering prevalence, air temperature and sunspot number.

Results

In the *Posidonia oceanica* meadow of Prelo Cove, the number of sheets per year ranged from 5 to 10 in the shallow and intermediate stations and from 5 to 9 in the deep station. The highest mean number of sheets was found during 2003 (8.2±1.2 at 4 m, 8.5±0.8 at 9 m and 7.6±0.7 at 14 m), i.e. in the year of flowering. Rhizome production was higher at the shallow and intermediate stations than at the deep station (Table 1). The highest mean value of rhizome production (0.132±0.004 g_{DM} year^{-1}) was recorded during 2002 in correspondence with the intermediate station (Fig. 2). At all depths, the mean values of rhizome production in 2002 (i.e. the year before the massive flowering event) were significantly higher than in the three previous years and than in the three following years (Table 1).

The leaf surface area showed the highest values in 2003 (i.e. in the massive flowering year), with mean values of 182.17±9 cm² shoot^{-1} at the shallow station, 196.24±8 cm² shoot^{-1} at the intermediate station and 210.33±9 cm² shoot^{-1} at the deep station (Fig. 2). In the year before the massive flowering event (2002) and in the three years following the flowering event (2004, 2005, and 2006) the leaf surface area decreased significantly in correspondence with the shallow and the deep stations (Table 1).

Flowering prevalence (FP) in the Prelo Cove meadow reached the highest value in 2003 (FP = 0.65), whilst it was irrelevant (FP < 0.02) during all the other 7 reconstructed years.

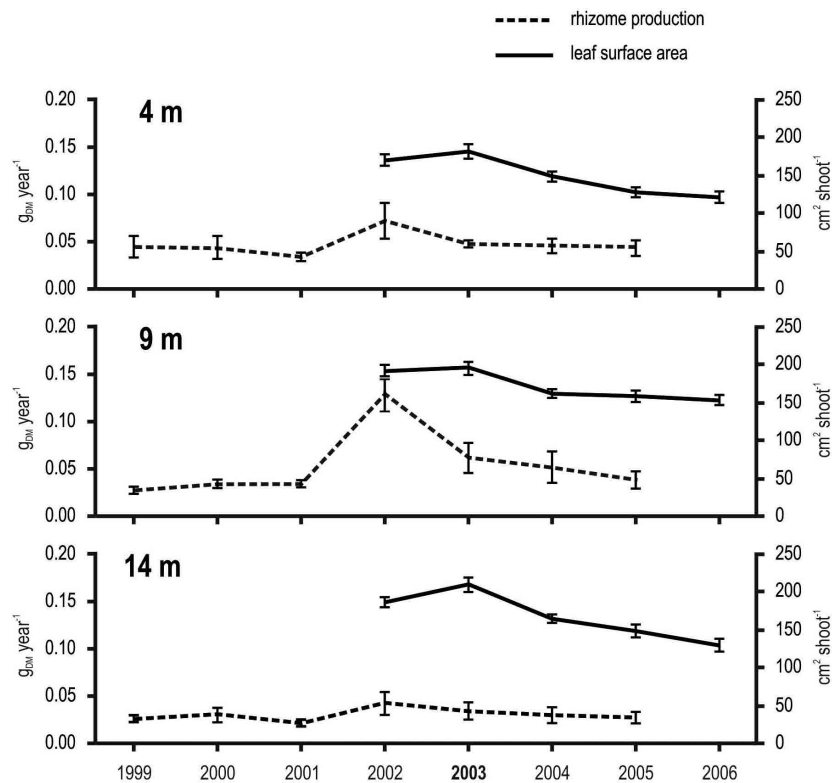Massive flowering events occurred at basin-wide

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Fig. 2: Mean annual leaf surface area (cm^2 shoot^{-1}) and mean annual rhizome production (g$_{DM}$ year^{-1}) at three depths (4 m, 9 m, 14 m) in the *Posidonia oceanica* meadow in Prelo Cove. The year corresponding to the massive flowering event is in bold.

Table 1. Results of 2 way-ANOVAs on the rhizome production and the leaf surface area. df = degrees of freedom; MS = mean square; *F* = value of the F-statistic test; *p* = value of significance; n.s. = not significant.

Source of variation	Rhizome production				Leaf surface area			
	df	MS	*F*	*p*	df	MS	*F*	*p*
Year	6	2.9547	7.17	0.0000[a]	4	0.3090	1.49	0.2167
Depth	2	4.4675	10.84	0.0000[b]	2	0.3582	1.72	0.1790
Year × Depth	12	0.5133	1.25	0.2661	8	2.1512	10.34	0.0000[c]
Residual	162	0.4122			1428	0.2080		
Tot	219				1559			
Cochran's *C*-test	*C* = 0.1047, n.s.				*C* = 0.1075, n.s.			
Transformation	ln(x)				ln(x)			

SNK tests:
a) Year: 2002 > 1999**, 2002 > 2000 **, 2002 >2001**, 2002 > 2003*, 2002 >2004*, 2002 >2005*
b) Depth: 4 m > 14 m **, 9 m > 14 m **
c) Year × Depth: 4 m) 2002 < 2003**, 2004 < 2003**, 2005 < 2003**, 2006 < 2003**
     9 m) n.s.
    14 m) 2002 < 2003**, 2004 < 2003**, 2005 < 2003**, 2006 < 2003**

scale in autumn 1973, 1983, 1994, 2003, and 2012 (the latter being followed by a massive fruiting event in May 2013). All these years of massive flowering were always characterised by warm summers, but not all air temperature maxima corresponded to flowering events (Fig. 3). On the contrary, peaks of sunspot number (SN) always occurred two to three years before the massive flowering events. From the year of the peak in sunspot number (SN), the annual flowering prevalence (FP) always starts increasing (Fig. 4). A significant correla-tion was found between FP and summer air tempera-ture (r = 0.61, p < 0.01) (Fig. 5a), whilst no significant correlations were found between FP and SN (r = 0.40) and between summer air temperature and SN (r = 0.03). Furthermore, no significant correlations were found be-tween SN shifted by two years and both FP (r = 0.30) and summer air temperature (r = 0.40). On the con-trary, correlation between sunspot numbers shifted by three years (SN$_{t-3}$) and FP resulted significant (r = 0.85, p < 0.01) (Fig. 5b).
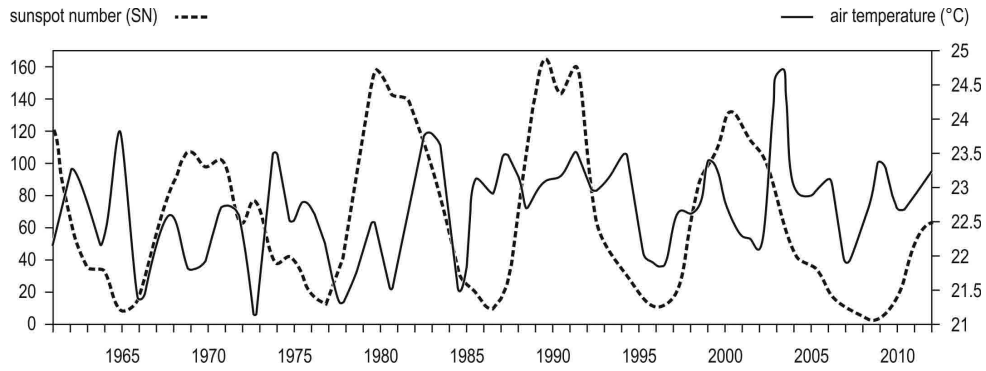
Fig. 3: Mean air temperature in the summer season and the 2-year average of the number of sunspots (SN) from 1960 to 2012.
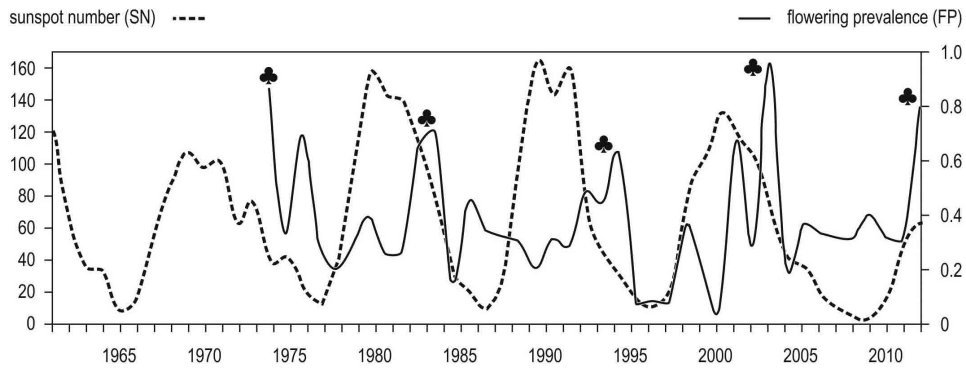

Fig. 4: The 2-year average of the flowering prevalence (FP) from 1973 to 2012 and the 2-year average of the number of sunspots (SN). The symbols indicate massive flowering events.
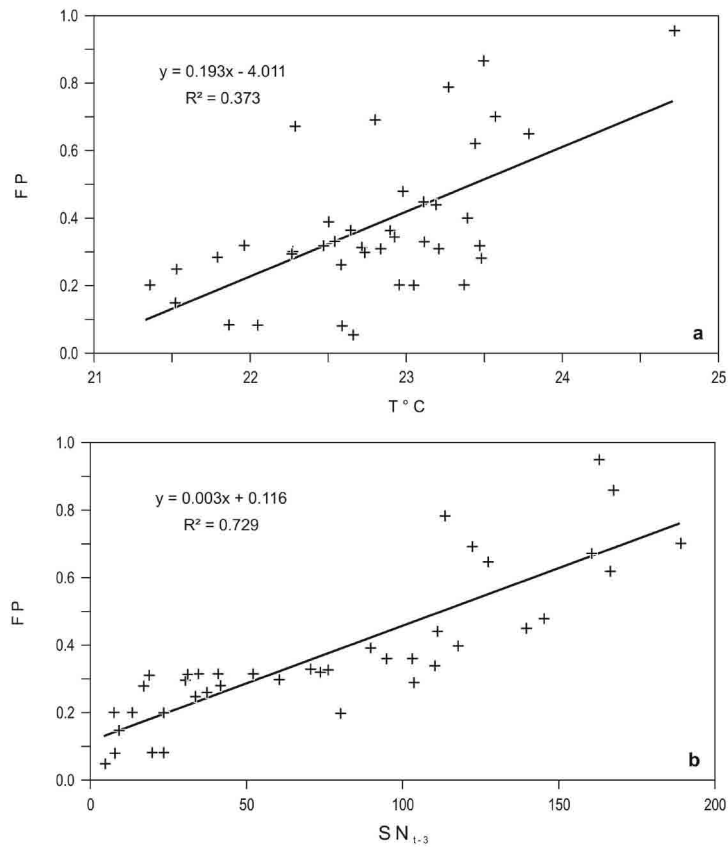

Fig. 5: Relationship between flowering prevalence (FP) and summer air temperature (T°C) and between sunspot number shifted by three years (SN_{t-3}) and flowering prevalence (FP); n = 40 in both cases.

Discussion

Values of leaf surface and rhizome production in the *Posidonia oceanica* meadow of Prelo Cove were comparable to mean values obtained in other meadows of the Ligurian Sea (Peirano *et al.*, 2005; Montefalcone *et al.*, 2006; Giovannetti *et al.*, 2008, 2010), as well as along the Mediterranean Sea (Buia *et al.*, 1992; Pergent-Martini *et al.*, 1994). The massive flowering event that occurred in 2003 at basin-wide spatial scale involved the meadow of Prelo Cove, where nearly two-thirds of the shoots reproduced sexually during this year. Although some sporadic records of flowering were reported in the previous (i.e. from 1999 to 2002) and the following (i.e. 2004-2005) years in other Mediterranean meadows (Diaz-Almela *et al.*, 2007), sexual reproduction in Prelo Cove was negligible during these years. Flowering of *P. oceanica* at the Mediterranean basin scale is subject to large-scale control and to high variability due to the presence of significant regional differences in the meadows. Diaz-Almela *et al.* (2006, 2007) based their analyses on data from the Balearic Islands mainly. In Tuscany, a massive flowering event occurred in 1993 (Balestri & Vallerini, 2003), while in Sicily a major flowering event occurred in 1998 (Calvo *et al.*, 2006). The time series of flowering records (i.e. FP) in the meadow of Prelo cove, although rather short and at a small spatial scale, showed clear trends between flowering and environmental forces. This Ligurian meadow, developing in one of the coldest sectors of the northern Mediterranean Sea (Morri & Bianchi, 2001), showed a massive flowering event during the warmest year 2003, but only sporadic events of flowering in a number of years before and after, thus suggesting the influence of an environmental 'signal' other than temperature on such a single massive event.

Sexual reproduction implies a very high energy cost for *P. oceanica* (Calvo *et al.*, 2006); plants in Prelo Cove coped with such a costly event by enhancing rhizome production in the year before flowering. Energy storage in the rhizomes possibly allowed the plant to reach the highest values of leaf surface area and leaf number during the flowering year (Pergent, 1985). An alternative interpretation might assume a storage strategy, i.e. the plant stores starch and nutrients within the rhizomes, rather than increases rhizomes production. If the plant presents a capacity to store energy in the year before the flowering event, there must be an environmental signal that triggers such a metabolic modification. A signal that can synchronize the start of the flowering process, i.e. the *Zeitgeber*, may well be represented by peaks in solar activity, which regularly occur two-three years before, and extend until the massive flowering events. The time lag between this *Zeitgeber* and the highest values in rhizome production is consistent with the time needed by *P. oceanica* to complete the growth of its rhizomes, as

rhizomes continued to grow and enlarge for 3 years before lignification (Boudouresque *et al.*, 1983; Peirano, 2002).

The delay between the peaks in sunspot number and the consequent peaks in cosmic ray intensity ranges between 3-10 months (Ma *et al.*, 2009), one year after the cosmic ray intensity peak is necessary to the plant for enhancing rhizome growth and energy storage, while another 7 months are required for the induction of flower development and fruit maturation (Gobert *et al.*, 2001): the whole process may require a period between 22 and 30 months. Thus, from the beginning of the second summer after the solar activity peak, the plant is ready for sexual reproduction, and the warm conditions during the following months may just play the final regulatory role in order to ensure flower appearance at the end of the summer, as confirmed by the significant correlation found between flowering prevalence and mean summer air temperature. The existence of a time lag of about 3 years between peak in solar activity and massive flowering event was confirmed by the significant correlation found between flowering prevalence and the sunspot number shifted by three years, while no correlation was found between flowering prevalence and sunspot numbers.

Many climatic factors have been shown to influence *P. oceanica* phenology (Peirano *et al.*, 2011). A significant correlation between flowering prevalence and air temperature had already been found (Diaz-Almela *et al.*, 2007). For many seagrass species, increased temperature often enhances positive physiological response (Short & Neckles, 1999); however, high temperature values might represent a stress-factor for plant growth as recent insights evidenced negative effects of increased global temperatures on the vitality of *P. oceanica* meadows (Marbà & Duarte, 2010). Although high temperatures are indirectly required for *P. oceanica* flowering, massive events are probably triggered by peaks in solar activity, which represent the most reliable and noise-free signals to start physiological processes.

This study suggests that *P. oceanica* flowering events are timed with solar activity and, in particular, sunspot number maxima, which regularly show an 11-year cycle. An 11-year cycle has also been observed in the scale characteristics of *P. oceanica*, in French Catalonia, using lepidochronology (Pergent *et al.*, 1985). At Prelo, the last two flowering episodes were separated by 10 years rather than by 11 as in the previous three records. Based on these results, we predict a next massive flowering episode in the NW Mediterranean for the year 2022.

As solar activity influences climate (Friis-Christensen & Lassen, 1991), the positive link between flowering and sea water temperature (Diaz-Almela *et al.*, 2007) may be indirect: sunspot cycles are much more regular and predictable than climate fluctuations and are therefore a better *Zeitgeber* (Brady, 1979) than temperature.

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