

Photosynthetic activity buffers ocean acidification

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Photosynthetic activity buffers ocean acidification in seagrass meadows

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Abstract

Macrophytes growing in shallow coastal zones characterized by intense metabolic activity have the capacity to modify pH within their canopy and beyond. We observed diel pH ranges in shallow (5–12 m) seagrass (*Posidonia oceanica*) meadows from 0.06 pH units in September to 0.24 units in June. The carbonate system (pH, DIC, and aragonite saturation state (Ω_{Ar})) and O_2 within the meadows displayed strong diel variability driven by primary productivity, and changes in chemistry were related to structural parameters of the meadow, in particular, the leaf surface area available for photosynthesis (LAI). LAI was positively correlated to mean and max pH_{NBS} and max Ω_{Ar} . Oxygen production positively influenced the range and maximum pH_{NBS} and the range of Ω_{Ar} . In June, vertical mixing (as Turbulent Kinetic Energy) influenced Ω_{Ar} , while in September there was no effect of hydrodynamics on the carbonate system within the canopy. Ω_{Ar} was positively correlated with the calcium carbonate load of the leaves, demonstrating a direct link between structural parameters, Ω_{Ar} and carbonate deposition.

There was a direct relationship between Ω_{Ar} , influenced directly by meadow LAI, and $CaCO_3$ content of the leaves. Therefore, calcifying organisms, e.g. epiphytes with carbonate skeletons, might benefit from the modification of the carbonate system by the meadow. The meadow might be capable of providing refugia for calcifiers by increasing pH and Ω_{Ar} through metabolic activity. There is, however, concern for the ability of seagrasses to provide this refugia function in the future. The predicted decline of seagrass meadows may alter the scope for alteration of pH within a seagrass meadow and in the water column above the meadow, particularly if shoot density and biomass decline, both strongly linked to LAI. Organisms associated with seagrass communities may therefore suffer from the loss of pH buffering capacity in degraded meadows.

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1 Introduction

5 Forecasts predict that ocean acidification will become a significant threat to calcifying organisms in the near future (Orr et al., 2005; Gazeau et al., 2007; Talmage and Gobler, 2010; Waldbusser et al., 2011), many of which live in coastal habitats. However, coastal ecosystems are characterized by large temporal and spatial variability in carbonate chemistry and pH (Hofmann et al., 2011; Mercado and Gordillo, 2011; Duarte et al., 2013), many of which regularly exceed predicted decreases in pH. In highly productive ecosystems this variability follows daily and seasonal cycles as O₂ and DIC concentrations in the water column are modulated through metabolic activity, with a signal that often prevails over physical forcing (Delille et al., 1997; Duarte et al., 2013). Hence, metabolically intense coastal ecosystems, such as seagrass meadows (Duarte and Chiscano, 1999; Duarte et al., 2010), may not conform to the trends in pH forecasted for open-ocean waters (Duarte et al., 2013).

15 Mediterranean *Posidonia oceanica* meadows are able to modify pH in the water column by as much as 0.2–0.7 pH units diurnally through photosynthetic activity and community metabolism (Frankignoulle and Distèche, 1984; Frankignoulle and Bouquegneau 1990; Invers et al., 1997). The diurnal range in pH is greatest in shallow sites and the influence on the water column is diluted with increasing distance from the meadow (Invers et al., 1997), although the influence of the meadow stretches far beyond the canopy itself (Frankignoulle and Distèche, 1984; Gazeau et al., 2005). The magnitude of diurnal variations is largest in summer, coinciding with the peak in productivity, and decreases during the winter (Frankignoulle and Distèche, 1984). Whereas the capacity of Mediterranean *P. oceanica* meadows to affect pH is well characterised, the relationship between pH variability within seagrass meadows and the metabolic and structural traits believed to drive these changes have not yet been resolved.

25 Metabolic activity in highly productive seagrass meadows exposes marine organisms to pH environments that can differ greatly from those of the surrounding bulk water. Seagrasses may therefore provide chemical “refugia” for vulnerable organisms

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where photosynthetic activity may raise pH above the thresholds for impacts on calcification and/or limit the time spent below some critical pH threshold. There is evidence that organisms associated with seagrass meadows might benefit from this function. High pH values modified due to seagrass photosynthesis enhanced calcification rates of calcareous red macroalgae (*Hydrolithon* sp. and *Mesophyllum* sp.) and the green macroalga *Halimeda renschii* growing within a tropical seagrass bed (Semese et al., 2009). A recent model based on records of seagrass metabolism in the Indo-Pacific suggested that pH increases of up to 0.38 units, and Ω aragonite (Ω_{Ar}) increases of up to 2.9 in seagrass meadows could potentially enhance calcification of scleratinian corals downstream of seagrasses by 18 % (Unsworth et al., 2012). The drawdown of dissolved inorganic carbon (DIC) due to photosynthesis of algae can result in a local net increase of pH and Ω_{Ar} , while the spatial patterns of the benthic community structure (i.e. percent cover of algal and coral communities) affects the upstream – downstream patterns of carbonate chemistry and impacts overall calcification rates on reef flats (Kleypas et al., 2011). However, field investigations linking the mitigating capacity of metabolically intense macrophyte ecosystems to their structural parameters are lacking.

Here, we evaluate the effect of structural parameters (shoot density, leaf area index, biomass) of the meadow and the interaction with physical forcing (hydrodynamics) on the resulting carbonate system in the meadow. We demonstrate that the metabolic effects of *P. oceanica* meadows on pH along the coast of Mallorca (Balearic Islands, Spain) are closely related to structural parameters of the meadow. These effects are large enough as to possibly help mitigate the impacts of future ocean acidification for calcifying organisms associated with these meadows.

2 Methods

We examined pH and O_2 fluctuations in six *P. oceanica* meadows off the coast of Mallorca (W. Mediterranean, Spain). Measurements were made in June (5–15 June 2012),

at the peak of *P. oceanica* production (Frankignoulle and Disteche, 1984) and in September (7–23 September 2011), just before leaf shedding and removal by autumn storms. Three meadows were visited in September and four in June with one meadow (Magalluf) sampled in both seasons (Fig. 1). We chose shallow (5–12 m depth) meadows with a wide range of shoot densities (Table 1) to evaluate the influence of structural parameters. At each meadow we carried out measurements in two relatively dense *P. oceanica* patches separated by at least 20 m. Additionally, in September we took measurements in the centre of one bare patch (2–20 m diameter) per station.

2.1 Carbonate system and oxygen measurements

A multiparametric sensor (Hydrolab DS5X) was deployed within the seagrass canopy 0.1 m above the bottom at each site and recorded local pH_{NBS} , O_2 , salinity and temperature every 15 min. A central cleaning system was attached to avoid fouling of the sensors. The oxygen sensors (Hach LDO@Sensor) were calibrated with the water-saturated air method and the pH sensors (with Integrated Reference) with a two-point calibration (before and after each deployment) using NBS standard buffers of 7.00 and 10.00 pH_{NBS} . During the September 2011 we campaign were unable to obtain oxygen data from one vegetated and one bared site due to instrument malfunction. During the June 2012 deployments, one instrument was flooded, leading to the loss of those data. Total alkalinity samples were taken at the bottom and surface before and after each deployment, fixed with 20 μL HgCl_2 and measured within 3 months (using the Metrohm Titrand 808 after SOP3b of Dickson et al., 2007). Light conditions were registered with a HOBO data logger (Pendant[®], Onset Computer Corporation) attached to the Hydrolab. Additionally, we obtained irradiance data (W m^{-2}) from the meteorological station at Ses Salines (located at the South-eastern point of Mallorca) as an additional measure of the light conditions on the surface during our campaigns. The maximum, minimum, and average pH_{NBS} were extracted from data obtained during the full deployment while the diel range of the pH fluctuation was calculated as the average difference from the lowest pH_{NBS} during the night time to the maximum pH_{NBS} during the next day

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over each 24 h period. Additional parameters of the carbonate system were calculated from the in situ pH_{NBS} , temperature, and salinity data, and the discrete total alkalinity samples, which were linearly interpolated across the deployment time. DIC and the saturation state of aragonite (Ω_{Ar}) were calculated using CO2SYS excel program (Pierrot et al., 2006) with the K1 and K2 constants from Mehrbach et al. (1973), as modified by Dickson and Millero (1987), and the K_{HSO_4} constant from Dickson (1990).

Strong diel variability in pH and O_2 were observed in all data collected (see Fig. 2), indicating that the observed changes were related to community productivity. However, we refrained from calculating metabolic rates as we were unable to quantify lateral advection and air-sea gas fluxes, and instead focus on changes in pH and O_2 .

2.2 Hydrodynamic regime

We approximated the water residence time on the local pH_{NBS} regime within seagrass meadows. At every site, water velocity in 3-D was measured during bursts programmed in time (every 15 min; in sync with the Hydrolab measurements) at 32 Hz, with a total of 5000 samples using Acoustic Doppler Velocimeters (Nortek, Vector). Measurements were taken just above the canopy level, at 1.2 m above the bottom. Absolute water velocity (non-directional) was calculated for each site (Table 1) as well as Turbulent Kinetic Energy (TKE), and Reynolds Stress. As obtaining a full profile through the canopy was not logistically possible, we approximated the volumetric flow of water (Q_{approx} in $\text{m}^3 \text{s}^{-1}$) through the canopy by extrapolating the water flow from our values in the water column above the canopy taking into account the given canopy height. To generate a profile through the vegetation we used a generic profile (from Hendriks et al., 2008) measured at 0.02 m s^{-1} free stream velocity, not taking into account the different shoot densities at each site, as $Q_{\text{approx}} = \sum_0^{Q_j z_c}$ and $Q_j = (z_j - z_{j-1})\bar{u}z_j$ (Morris et al., 2008), where z_c is the height of the canopy, z_j the height of the measurement and Q_j the

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volumetric flow rate of water through the layer ($z_i - z_{i-1}$), and $\bar{u}z_i$ the double-averaged horizontal (u) component of the velocity at depth z_i .

2.3 Meadow characterization

At each sampling location we characterized the structural parameters of the meadow. Shoot density was estimated in eight replicate 0.0625 m^2 quadrats in September and six replicate 0.05 m^2 quadrats in June. To determine biomass and Leaf Area Index (LAI), twelve shoots were randomly collected at each sampling site. The length and width of all leaves were measured, and the mean total leaf area per shoot multiplied by the shoot density to obtain the LAI ($\text{m}^2 \text{ leaves m}^{-2}$). All leaves were dried at 60°C for 48 h and the aboveground dry weight (g m^{-2}) was determined as the product of the average shoot weight and density.

To obtain the total leaf carbonate load, dried shoots were burned at 550°C for 4 h and weighed to determine organic matter (OM) content and organic carbon. Shoots were then combusted at 1000°C for 2 h and weighed again. The weight lost between 550 and 1000°C represents the carbonate load (Smith and Atkinson, 1984). We assume that the bulk of the carbonate can be attributed to the associated epiphytes on the leaf surface. Internally precipitated inorganic carbonate is also included with this method, although internal content of carbonates in the leaves should be negligible (Gacia et al., 2003).

2.4 Statistical analyses

We tested (1) the effect of oxygen production and structural parameters of the meadow and (2) the effect of hydrodynamics on the carbonate system (pH_{NBS} and Ω_{Ar}) using univariate ANOVA in separate Models in JMP (SAS) and (3) the effect of Ω_{Ar} (min, max, mean) on the carbonate load of the leaves with an ANOVA considering all carbonate parameters (min, mean, max, range). Model selection using Akaike's Information Criterion (AIC) was used to evaluate the best model for predictions.

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3 Results

Oxygen concentrations in the water column followed the diurnal cycle of daylight and photosynthetic activity of the plants with highest concentrations observed in the afternoon and the lowest around sunrise. In September, oxygen concentrations were overall lower and typically ranged from 6.04 to 7.23 mg O₂ L⁻¹ (Table 2) . The highest value measured in September was 8.02 mg O₂ L⁻¹ and the lowest 4.18 mg O₂ L⁻¹ (111 % and 66 % saturation, respectively, mean water temperature 26.5 ± 0.23 SD °C). In June, the range was larger and the overall values higher with a mean range from 7.62 to 9.94 mg O₂ L⁻¹ . The highest value measured in June was 11.7 mg O₂ L⁻¹ and the lowest 5.29 mg O₂ L⁻¹ (161 % and 77 % saturation, respectively, mean water temperature 23.4 ± 0.18 SD °C).

Clear diurnal patterns in pH_{NBS}, following those of oxygen, were observed (Fig. 2a and b, Table 2). Oxygen production by photosynthesis, or metabolic activity of the plants during the day directly influenced the carbonate system in the meadow, as there was a strong correlation between O₂ (in μmol kg⁻¹) and DIC (in μmol kg⁻¹) in the canopy with an average daytime relationship for all the experimental sites of -0.96 μmol DIC/μmol O₂ in June and -0.97 μmol DIC/μmol O₂ in September (average mean *r*² of 0.90). During the night time, when respiration is dominant, this relationship was -0.92 μmol DIC/μmol O₂ in June and -1.13 μmol DIC/μmol O₂ in September (average mean *r*² of 0.88). The mean pH_{NBS} for all sites was similar in June (8.06 ± 0.22) and September (8.03 ± 0.02; *t* = -0.95, *p* = 0.36). However, the maximum observed pH_{NBS} during the daily cycles was higher in June (8.19 ± 0.09) than in September (8.09 ± 0.02; *t* = -3.44, *p* < 0.01), driven by the higher productivity of the plants, while the minimum pH_{NBS} was very similar in both seasons (7.97 ± 0.03 and 7.97 ± 0.03 in June and September, respectively, *t* = 0.08, *p* = 0.93). Consequently, the mean range in pH was greater in June (0.16 ± 0.01) than in September (0.08 ± 0.01, *t* = -4.41, *p* = 0.001). The smallest diel ranges of 0.06 pH units were observed in the meadows of Magalluf and St. Elm

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in September and maximum diel ranges of 0.24 pH units were observed in the bay of Palma (Cala Blava) in June (Table 2).

Measurements of pH_{NBS} and oxygen in bare areas adjacent (max. 10 m from the nearest edge) to the seagrass meadows ($n = 3$; September campaign only) demonstrated clear diurnal patterns similar to those found in the seagrass canopy (data not shown), indicating a large spatial footprint for seagrass metabolic effects on O_2 and pH. Oxygen ranged from 5.72 to 6.95 $\text{mg O}_2 \text{L}^{-1}$, which is comparable to the values measured inside the meadow during September. Mean pH_{NBS} was 8.02 ± 0.04 SD, ranging diurnally between 0.06 to 0.21 units, significantly lower than the mean pH_{NBS} in the vegetated sites (8.03 ± 0.02 , $t = 13.98$, $p < 0.001$).

The leaf surface available for photosynthesis (LAI) affects both max ($r^2 = 0.60$, $F = 13.71$, $p < 0.01$), and mean ($r^2 = 0.60$, $F = 13.51$, $p < 0.01$) oxygen concentrations and affects the flow of water through the meadow ($r^2 = 0.48$, $F = 9.1345$, $p = 0.01$). LAI (Table 1) emerged as the most consistent driver of pH variability (Table 3; Fig. 3). In contrast, the observed differences in mean pH_{NBS} within seagrass canopies (Table 2) could not directly be attributed to differences in biomass or shoot density between meadows (Table 3). The maximum pH_{NBS} was related to biomass and LAI, and the average daily range of pH to LAI (Table 3), while the minimum pH_{NBS} was independent of structural meadow parameters (Table 3). LAI also influenced maximum Ω_{Ar} , and its daily range (Fig. 4, Table 3), while no correlation was found with biomass and shoot density.

We found strong relationships between oxygen within the canopy and pH suggesting photosynthetic rates and metabolism are important drivers of the carbonate system within the meadow. Oxygen concentration (max and mean) were correlated to the maximum pH_{NBS} measured during the deployments ($F = 10.68$, $p < 0.01$ and $F = 23.28$, $p < 0.001$ for max and mean respectively). The range of pH measurements was also influenced by oxygen concentrations (max and mean; $F = 61.86$, $p < 0.0001$ and $F = 18.29$, $p < 0.01$, respectively), probably as a direct result of the higher maximum pH_{NBS} . The range of Ω_{Ar} was correlated to oxygen concentrations (maximum and

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mean O_2 ; $F = 20.61$, $p < 0.01$ and $F = 16.44$, $p < 0.05$, respectively), but the maximum saturation state in the meadow was not significantly influenced ($F = 4.71$, $p = 0.06$) by the mean oxygen concentration.

The volumetric flow through the canopy Q_{approx} was $19.4 \text{ m}^3 \text{ h}^{-1}$ in June and $6.4 \text{ m}^3 \text{ h}^{-1}$ in September, equivalent to canopy water residency times of approximate 0.05 and 0.16 h in June and September, respectively. This estimate is based on extrapolation of the flow velocities measured in the water column above the seagrass bed at the sites with complete modelled profiles measured in a laboratory flume with low shoot density ($120 \text{ shoots m}^{-2}$ Hendriks et al., 2008). As flow profiles are dependent on shoot density (Peralta et al., 2008) and the densities at the field sites were considerably higher, actual residency times are likely to be longer. Since water velocity was different between June and September ($t = -5.61$, $p < 0.001$) we separated the analyses of the effect of hydrodynamics on the carbonate system by season (Fig. 5, Table 4). In September, no significant effect of water velocity or mixing on the carbonate system was found. In June vertical mixing (as TKE) affected the mean ($F = 77.54$, $p < 0.001$) and minimum ($F = 17.31$, $p = 0.01$) Ω_{Ar} positively, raising the saturation state with higher mixing intensities. A higher absolute water velocity lowered the mean Ω_{Ar} in June ($F = 12.01$, $p < 0.05$).

Even though the full model for Ω_{Ar} (max, min and mean) vs CaCO_3 was not significant ($r^2 = 0.56$, $p = 0.05$), the maximum Ω_{Ar} within the canopy was correlated with the calcium carbonate load of the leaves ($F = 5.73$, $p < 0.05$, Fig. 6), thereby providing a direct link between Ω_{Ar} and net carbonate deposition on the leaf surfaces.

3.1 Model selection

The best models predicting Ω_{Ar} (max, min and mean) always included meadow metabolic activity (as range O_2 concentration; Table 5). For minimum and maximum Ω_{Ar} meadow structural parameters were important, providing a direct link with the available surface for photosynthesis, while the mean and range of Ω_{Ar} were best determined

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by models combining advective processes and productivity (Table 5). The best model to predict CaCO_3 content per m^2 of the leaves included hydrodynamics (TKE, U, Re stress) and the range of oxygen concentration within the canopy (Table 6). Including structural parameters had a slightly higher score, possibly pointing to an indirect effect of meadow structure mainly through modification of the water flow by the canopy.

4 Discussion

We observed dynamic changes in pH_{NBS} and Ω_{Ar} within *P. oceanica* meadows, implying that the epiphytic calcifiers on seagrass leaves of highly productive meadows will experience a variable pH environment and carbonate chemistry very different from that predicted by climate models derived for open ocean conditions (Duarte et al., 2013). We found highly temporally variable pH environments in seagrass ecosystems driven by metabolic activity and directly related to the leaf area index of the plants, which reflects the density of photosynthetic tissues. The magnitude of diurnal pH variation was strongly related to seagrass productivity, with the largest ranges coinciding with the peak in seagrass productivity. Diurnal fluctuations in pH in a *P. oceanica* meadow can drop to as low as zero in winter, reflecting the much lower biological activity in the meadow at this time of the annual cycle (Frankignouille and Distèche, 1984). The ranges in pH_{NBS} measured here are very similar to those found in *P. oceanica* meadows by Invers et al. (1997) of 0.17 and 0.3 pH units. We found strong evidence that structural and metabolic parameters of the seagrass meadows influence the mean and maximum pH_{NBS} within the canopy through positive relationships between the amount of photosynthetic leaf area per m^2 (LAI) and pH_{NBS} . Meadows with high LAI were associated with the highest pH values and higher mean pH during the diurnal cycle. These observations demonstrate the capacity of seagrasses to buffer the pH environment within the meadow.

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4.1 Potential for buffering of the carbonate system in seagrass-dominated coastal ecosystems

Oxygen dynamics driven by seagrass metabolic activity positively influenced mean and max pH and the range of Ω_{Ar} , confirming that metabolically intense seagrass meadows actively control the carbonate system in their canopies. The metabolic signal varies seasonally and the influence on carbonate chemistry is likely to be most pronounced at the peak of seagrass production, in June. Our results also highlight an important role for hydrodynamic processes in modulating the carbonate system within the canopy. Hydrodynamics control fluxes in and out of the meadow and may modify or dampen the metabolic signal. High community metabolism in seagrass meadows is common, with higher primary productivity rates in tropical meadows as compared to temperate ones (Duarte et al., 2010). The capacity to modify coastal pH in shallow near-shore water with submerged vegetation is therefore wide-spread, in areas with seagrass as well as in macrophyte habitats in general, such as kelps (Frieder et al., 2012), but the magnitude of buffering will depend on both structural and metabolic parameters and hydrodynamic processes of each system.

4.2 Potential for buffering of the carbonate system in adjacent sites

Our results support the argument that metabolic processes can regulate pH in coastal habitats, possibly deviating the local pH trajectories from those expected under ocean acidification (Duarte et al., 2013). We observed clear diurnal patterns in oxygen and pH in bare sandy areas adjacent to the seagrass meadows demonstrating that the footprint of seagrass metabolism on pH extended several meters beyond the limits of the meadow. The size of this footprint depends on local hydrodynamics, seasonality and the overall meadow size. A low productivity meadow with a long water residence time could achieve the same effect on pH as a highly productive meadow with short water residence time. The properties of the emerging canopy of the meadow simultaneously control photosynthetic rates and affect hydrodynamic processes (Gutierrez et

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al., 2012). The same measure used to express the amount of photosynthetic surface area, LAI, is directly linked to the influence of the meadow on water flow and had a positive influence on both oxygen (max and mean) and water flow through the meadow. The influence on the water column is likely to be attenuated with increasing distance from the meadow (Invers et al., 1997), but a clear signal can be detected in surface waters above deep (> 8 m) *P. oceanica* meadows (Frankignoulle and Distèche 1984; Gazeau et al., 2005) showing that the influence of seagrass meadows stretches far beyond the canopy itself. The photosynthetic uptake of CO₂ and the associated pH buffering capacity of highly productive seagrass meadows may, therefore, benefit adjacent habitats that include components vulnerable to ocean acidification (Duarte et al., 2013). An example are patchy landscape configurations including metabolically intense macrophyte communities and calcifiers, where calcifying organisms like bivalves and coral reefs may benefit from the increase in pH by the metabolism of the adjacent seagrass meadow (e.g. Kleypas et al., 2011; Unsworth et al., 2012).

4.3 Future potential for calcifiers living in the meadow

The changes in pH and Ω_{Ar} associated with *Posidonia oceanica* meadows are sufficiently large to facilitate calcification processes. This effect is driven by structural parameters of the meadow, with LAI being the best predictor, as this affects both metabolic activity and hydrodynamic regimes. LAI is a relative measure including both shoot length and density and therefore takes both seasonality (leaf length) and meadow health (shoot density) into account. LAI is therefore a key parameter that should be measured during experiments. The leaf-inhabiting calcifying epiphytes can directly benefit from the modification of the carbonate system by the meadow as suggested by the positive relationship between Ω_{Ar} and the carbonate load of the leaves found in this study. These results clearly suggest that the present-day meadow provides refugia for calcifiers.

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There is, however, concern for the ability of seagrasses to continue to provide this function in the future. Seagrass meadows are declining worldwide (Waycott et al., 2009) and, in the Mediterranean, shoot densities are diminishing at an alarming rate (Marbà and Duarte, 2010). Since the pH modification is directly linked to the structural parameters of the meadow the ability of seagrass meadows to provide pH “refugia” in the Mediterranean and globally is threatened.

Future increased levels of CO₂ in the atmosphere and a subsequent increase in dissolved CO₂ are predicted to have significant direct effects on aquatic plant communities (Wetzel and Grace, 1983; Edwards, 1995; Short and Neckles, 1999). At present seagrass photosynthesis is frequently limited by DIC availability under natural conditions (Beer, 1989; Durako, 1993; Madsen et al., 1993; Koch, 1994; Beer and Koch, 1996). Photosynthetic rates (Durako, 1993; Zimmerman et al., 1997) and growth and biomass (Zimmerman et al., 1997) might increase with increasing CO₂ concentrations, although long-term evidence for this is lacking (Short and Neckles, 1999). Acclimation following prolonged exposure to elevated CO₂ may lead to down-regulation (Durako, 1993; Madsen et al., 1996) or up-regulation (Zimmerman et al., 1997) of photosynthesis. Long-term responses are therefore likely to depend on the degree of physiological and morphological adaptation to increased CO₂ (Drake, 1992; Dahlman, 1993; Amthor, 1995). It is therefore difficult to predict how this may affect the ability of seagrass meadows to buffer the pH environment within their canopies.

Measurements of diurnal pH cycles in volcanic vent systems of the Mediterranean Sea indicate that the ability of the meadows to modulate pH will be significant. The maximum diurnal range in a *P. oceanica* meadow in the Ischia CO₂ vent system was very large, at 1.0–1.6 of pH units at high pCO₂ sites (Duarte et al., 2013). These large diurnal fluctuations are probably the result of a combination of high productivity and photosynthesis in shallow DIC-rich meadows and variability produced by stochastic changes in CO₂ venting rates and hydrodynamic conditions, but, in any case, the capacity of seagrasses to modulate pH through their metabolic activity does not appear to be diminished, and is possibly enhanced, under conditions of increased pCO₂.

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Even though seagrass productivity might be enhanced in a high- $p\text{CO}_2$ world, other stresses associated with global change might play a negative role. Like other seagrasses, *P. oceanica* meadows are highly vulnerable to coastal deterioration and are currently threatened by eutrophication, invasive species, coastal erosion and mechanical impacts (Williams, 2007; Diaz-Almela et al., 2008; Boudouresque et al., 2009). Declines of *P. oceanica* have been reported across the entire Mediterranean basin and it has been estimated that 13–50% of *P. oceanica* area may have been lost, and that shoot density has declined in the remaining areas, with little scope for recovery, provided the very slow growth of this species (Marbà and Duarte, 1998). Rapid warming of the Mediterranean is enhancing seagrass decline further (Marbà and Duarte, 2010) and will enhance shoot mortality and trigger population decline as critical temperature thresholds are exceeded (Marbà and Duarte, 2010; Jordà et al., 2012).

The predicted global decline of seagrass meadows (Orth et al., 2006; Waycott et al., 2009) may alter the ability of the meadows to modify pH in the water column, in particular if meadows suffer declines in shoot density and biomass. The mean dry weight of the meadows at the height of their production (in June) is very close, even below, the predicted threshold for autotrophy of *P. oceanica* meadows (694.1 vs. 735.3 g DW m⁻² in Duarte et al., 2010). The on going shoot density decrease of seagrass meadows could bring the meadows around Mallorca closer to the threshold for the functional role of *P. oceanica* meadows as a refuge for calcifying. Organisms associated with seagrass communities will therefore be exposed to lower pH regimes in the future as pH decreases through ocean acidification and pH-buffering capacity is lost in declining meadows. Effective conservation of seagrass meadows is not only required to preserve these habitats under threat, but also the role they can play in the future in providing refuge from ocean acidification for calcifying organisms.

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Table 1. Mean (\pm SD) environmental parameters (temperature, light intensity), hydrodynamics (\pm SE) and characteristics of the seagrass meadows (shoot density, biomass, LAI) at the sites sampled in this study.

station	Plot	Mean Temp (°C)	light intensity (lux)	shoot density (m ⁻²)	biomass wt (g dry m ⁻²)	LAI	U (m s ⁻¹)	TKE (10 ⁻⁶ m ² s ⁻²)	Re Stress (10 ⁻⁶ m ² s ⁻²)
September									
Sta Maria	1	26.6 (\pm 0.16)	6644 (\pm 841)	582	515.48	1.23	0.012 (\pm 3 10 ⁻⁴)	21 (\pm 2 10 ⁻⁵)	-290 (\pm 7 10 ⁻⁶)
Sta Maria	2	26.5 (\pm 0.16)	6644 (\pm 841)	778	419.57	1.22			
St Elm	1	26.8 (\pm 0.07)	5442 (\pm 414)	368	465.75	0.69	0.013 (\pm 5 10 ⁻⁴)	19 (\pm 1 10 ⁻⁵)	160 (\pm 2 10 ⁻⁶)
St Elm	2	26.8 (\pm 0.08)	5442 (\pm 414)	456	647.37	1.39	0.012 (\pm 5 10 ⁻⁴)	19 (\pm 1 10 ⁻⁵)	-91 (\pm 2 10 ⁻⁶)
Magalluf	1	26.4 (\pm 0.20)	6711 (\pm 1097)	580	606.02	1.35	0.018 (\pm 6 10 ⁻⁴)	21 (\pm 2 10 ⁻⁵)	-50 (\pm 2 10 ⁻⁶)
Magalluf	2	26.3 (\pm 0.20)	6711 (\pm 1097)	582	793.42	2.1	0.019 (\pm 6 10 ⁻⁴)	21 (\pm 2 10 ⁻⁵)	-77 (\pm 2 10 ⁻⁶)
June									
Son Veri Nou	1	23.4 (\pm 0.33)	8230 (\pm 1525)	607	714.85	1.9	0.007 (\pm 3 10 ⁻⁴)	2.8 (\pm 8 10 ⁻⁶)	-0.46 (\pm 2 10 ⁻⁶)
Son Veri Nou	2	23.4 (\pm 0.30)	8230 (\pm 1525)	577	417.34	1.1			
Cala Blava	1	23.2 (\pm 0.35)	7056 (\pm 842)	624	1012.86	2.9	0.006 (\pm 2 10 ⁻⁴)	2.4 (\pm 1 10 ⁻⁵)	-140 (\pm 1 10 ⁻⁶)
Cala Blava	2	23.2 (\pm 0.35)	7056 (\pm 842)	537	648.51	2.47	0.007 (\pm 3 10 ⁻⁴)	2.5 (\pm 1 10 ⁻⁵)	9.6 (\pm 1 10 ⁻⁶)
Magalluf	3	23.4 (\pm 0.24)	8752 (\pm 2348)	467	712.99	2.76	0.004 (\pm 2 10 ⁻⁴)	7.5 (\pm 1 10 ⁻⁵)	-17 (\pm 1 10 ⁻⁶)
Magalluf	4	23.7 (\pm 0.40)	8752 (\pm 2348)	587	623.02	2.41	0.003 (\pm 1 10 ⁻⁴)	7.4 (\pm 8 10 ⁻⁶)	-31 (\pm 1 10 ⁻⁶)
Portals	1	23.6 (\pm 0.25)	8646 (\pm 2894)	440	636.78	2.42	0.002 (\pm 1 10 ⁻⁴)	7.7 (\pm 8 10 ⁻⁶)	0.4 (\pm 1 10 ⁻⁶)
Portals	2	23.6 (\pm 0.24)	8646 (\pm 2894)	610	807.46	3.48	0.002 (\pm 1 10 ⁻⁴)	8.2 (\pm 4 10 ⁻⁶)	-7.8 (\pm 3 10 ⁻⁷)

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Table 2. Observed biogeochemical parameters (pH_{NBS} measured, pCO_2 , DIC and Ω_{Ar} calculated with the excel version of CO2SYS), oxygen concentration in the canopy (mg L^{-1}) and CaCO_3 content of seagrass leaves in the meadows.

station	Plot	$\text{CaCO}_3 \text{ m}^{-2}$ (Mean O_2 (mg L^{-1})	Range O_2 (mg L^{-1})	Mean pH	pH Range
Sta Maria	1	51.72			7.99	0.11
Sta Maria	2	45.41	5.84	2.78	8.00	0.11
St Elm	1	35.70	6.12	1.51	8.02	0.06
St Elm	2	54.17			8.06	0.10
Magalluf	1	88.05	6.02	1.34	8.06	0.06
Magalluf	2	94.44	6.41	2.30	8.06	0.09
Son Veri Nou	1	113.46	7.44	2.75	8.03	0.17
Son Veri Nou	2	83.48	7.19	2.99	7.99	0.15
Cala Blava	1		7.70	6.41	7.98	0.23
Cala Blava	2	123.97	7.68	5.53	8.02	0.24
Magalluf	3	75.15	7.70	2.74	8.14	0.13
Magalluf	4	68.09				
Portals	1	73.68	7.87	4.72	8.14	0.17
Portals	2	58.26	7.77	4.33	8.14	0.17

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Table 2. Continued.

station	Plot	$p\text{CO}_2$ mean	$p\text{CO}_2$ range	mean DIC	range DIC	mean Ω_{Ar}	range Ω_{Ar}
Sta Maria	1	490.42	272.32	2155.21	138.24	3.63	1.28
Sta Maria	2	468.62	183.11	2143.71	89.62	3.74	0.81
St Elm	1	446.17	85.98	2118.16	71.18	3.82	0.54
St Elm	2	396.17	144.63	2089.26	85.10	4.11	1.00
Magalluf	1	396.32	77.00	2105.53	53.75	4.09	0.54
Magalluf	2	396.26	112.72	2105.24	73.46	4.10	0.77
Son Veri Nou	1	435.72	325.19	2167.53	177.55	3.59	1.83
Son Veri Nou	2	491.81	206.90	2198.38	90.82	3.30	0.91
Cala Blava	1	503.27	370.11	2194.37	169.22	3.23	1.64
Cala Blava	2	452.65	356.71	2172.03	196.20	3.46	1.96
Magalluf	3	317.81	112.72	2095.95	97.86	4.30	0.94
Magalluf	4						
Portals	1	319.01	205.53	2087.30	157.64	4.32	1.59
Portals	2	325.55	193.85	2096.26	149.38	4.27	1.51

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Table 3. Results from univariate ANOVA in separate models testing the effect of structural parameters of the meadow on the resulting carbonate system. Models from JMP; D.f. are 1 for all results.

pH	Shoot density			Biomass			LAI		
	<i>F</i>	<i>p</i>	<i>R</i> ²	<i>F</i>	<i>p</i>	<i>R</i> ²	<i>F</i>	<i>p</i>	<i>R</i> ²
Mean	1.8358	0.20	0.14	0.8446	0.38	0.07	4.9701	0.05*	0.31
Max	0.6992	0.42	0.06	5.3362	0.04*	0.33	30.9739	< 0.001***	0.74
Min	2.7791	0.12	0.20	0.1023	0.76	0.01	0.8006	0.39	0.07
range	0.2769	0.61	0.02	3.3465	0.09	0.23	8.1708	0.02*	0.43
Ω_{Ar} Mean	1.6083	0.23	0.13	0.0649	0.80	0.01	0.6957	0.42	0.06
Max	0.8933	0.36	0.08	3.3123	0.10	0.23	9.8041	< 0.01**	0.47
Min	1.7485	0.21	0.14	0.0680	0.80	0.01	0.0261	0.87	0.00
range	0.1432	0.71	0.01	3.0739	0.10	0.22	6.4881	< 0.05*	0.37

Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

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Table 4. Results from univariate ANOVA in separate models testing the effect of hydrodynamics on the carbonate system (Ω_{Ar}) JMP. Models from JMP; D.f. are 1 for all results.

		TKE			Normalised U			Reynolds stress		
		F	p	R^2	F	p	R^2	F	p	R^2
September	Mean	0.0378	0.01	0.17	1.1330	0.37	0.27	0.04347	0.56	0.13
	Max	0.04775	0.14	0.15	0.1220	0.75	0.04	0.8567	0.42	0.22
	Min	0.0550	0.02	0.18	2.8500	0.19	0.49	1.8777	0.26	0.39
	range	0.4356	0.13	0.02	1.0879	0.37	0.27	8.9514	0.06	0.75
June	Mean	77.5370	< 0.001***	0.95	12.0136	< 0.05*	0.75	0.0788	0.79	0.02
	Max	5.2935	0.08	0.57	2.5994	0.18	0.39	0.4580	0.54	0.10
	Min	17.3095	0.01*	0.81	4.0196	0.12	0.50	0.5000	0.52	0.11
	range	3.3367	0.14	0.46	1.3318	0.31	0.25	5.6920	0.08	0.59

Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

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Table 5. Model selection for GLM models predicting Ω_{Ar} with normal distribution and link identity with main effects of the predictors. Aikake's information criterion (AIC) is as less-is-better. Figures highlighted in bold indicate the models with the highest predictive power.

Model	predictors	range Ω_{Ar}	min Ω_{Ar}	max Ω_{Ar}	mean Ω_{Ar}	
hydrodynamics structural	TKE, xvel, Restress	24.64	41.994	50.121	45.912	
	biomass, density, LAI	20.886	22.677	10.021	17.142	
	metabolism & structure	biomass, density, LAI, Range O ₂	15.902	2.030	9.656	8.174
structural & hydrodynamics	biomass, density, LAI, TKE, xvel, Restress	10.546	15.434	8.766	11.474	
	metabolism	Range O ₂	10.405	13.471	16.971	15.502
	met&struct&hydro	biomass, density, LAI, TKE, xvel, Restress, Range O ₂	8.062	-17.164	1.087	7.693
hydrodynamics & metabolism	TKE, xvel, Restress, Range O ₂	7.989	0.223	5.351	-4.936	

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Table 6. Model selection for GLM models (main effect) predicting $\text{CaCO}_3 \text{ m}^{-2}$ with normal distribution and link identity with main effects of the predictors. Aikaike's information criterion (AIC) is as less-is-better.

Model	Predictors	AIC	
structural	biomass, density, LAI	119.564	
	LAI	116.833	
metabolism	Range O_2	98.723	
hydrodynamics	TKE, xvel, Restress	83.448	
	struct + hydro	biomass, density, LAI, TKE, xvel, Restress	79.186
	hydro + met	TKE, xvel, Restress, Range O_2	54.978

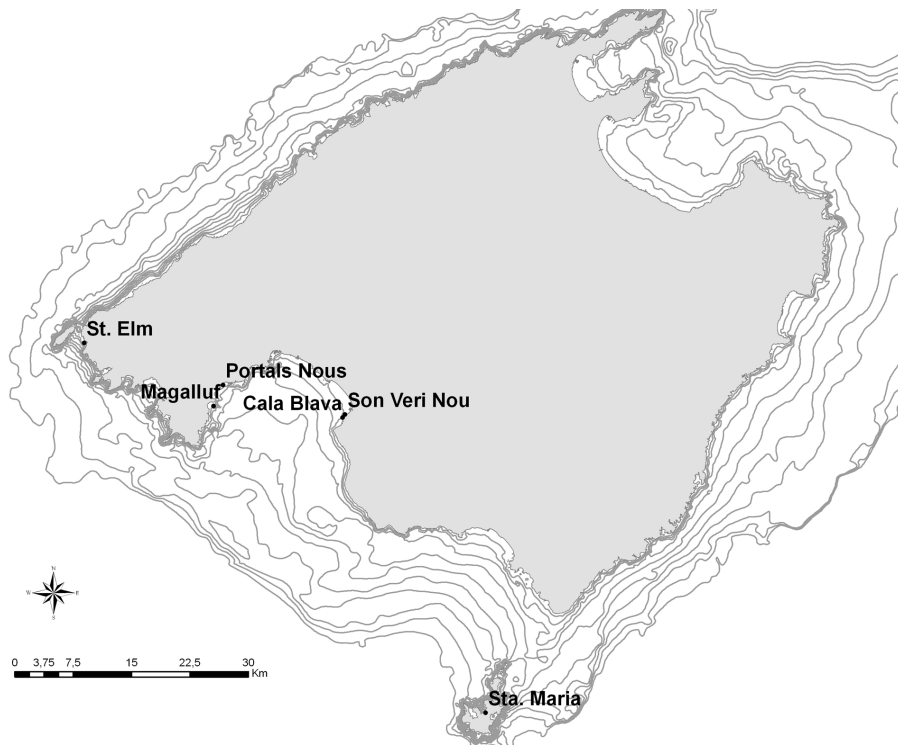


Fig. 1. Sampling sites in the south of Mallorca, Balearic Islands, Spain.

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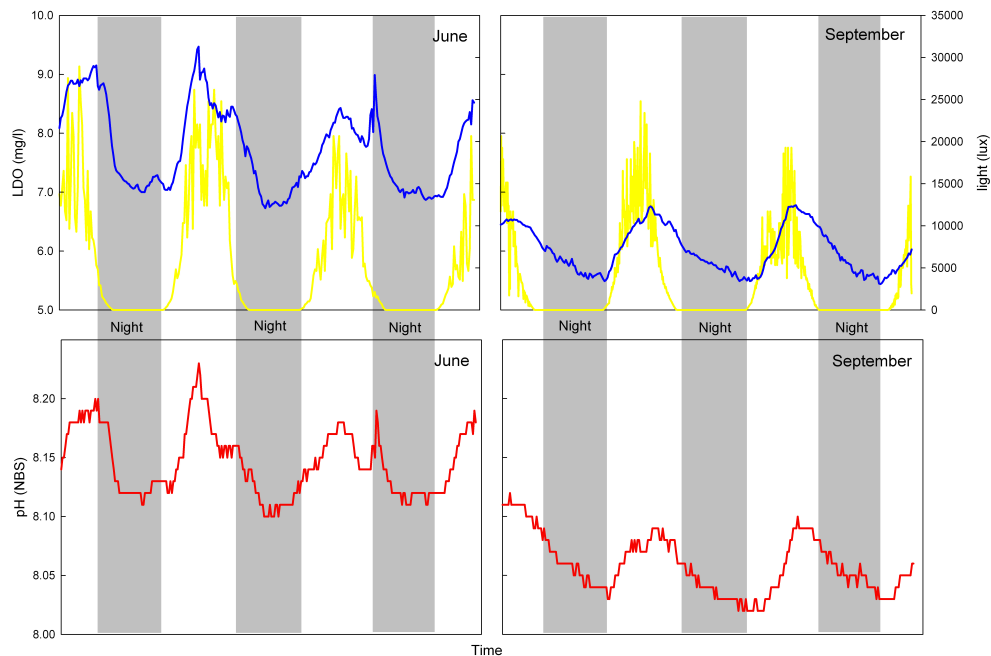


Fig. 2. Diurnal profiles of light levels (lux) and evolution of oxygen (mg L^{-1} ; upper panels) and pH (lower panels) in the canopy during the June (left panels) and September campaigns (right panels) in Magaluf.

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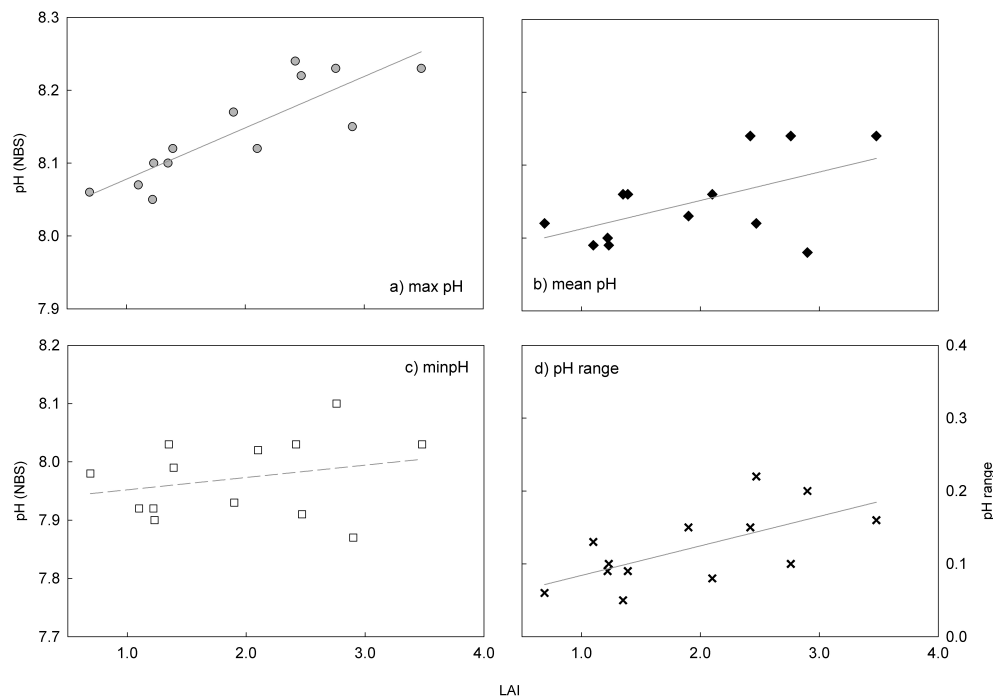


Fig. 3. The relationships between leaf area index (LAI) and **(a)** max, **(b)** mean, **(c)** min pH and **(d)** pH range. Non-significant relationships are dotted lines. Mean pH (black diamonds) is described by $0.04 \text{ LAI} + 7.97$ ($r^2 = 0.33$) maximum pH (grey circles) is $0.07 \text{ LAI} + 8.01$ ($r^2 = 0.75$) Minimum pH are white squares while the range of pH (right y-axis) are crosses.

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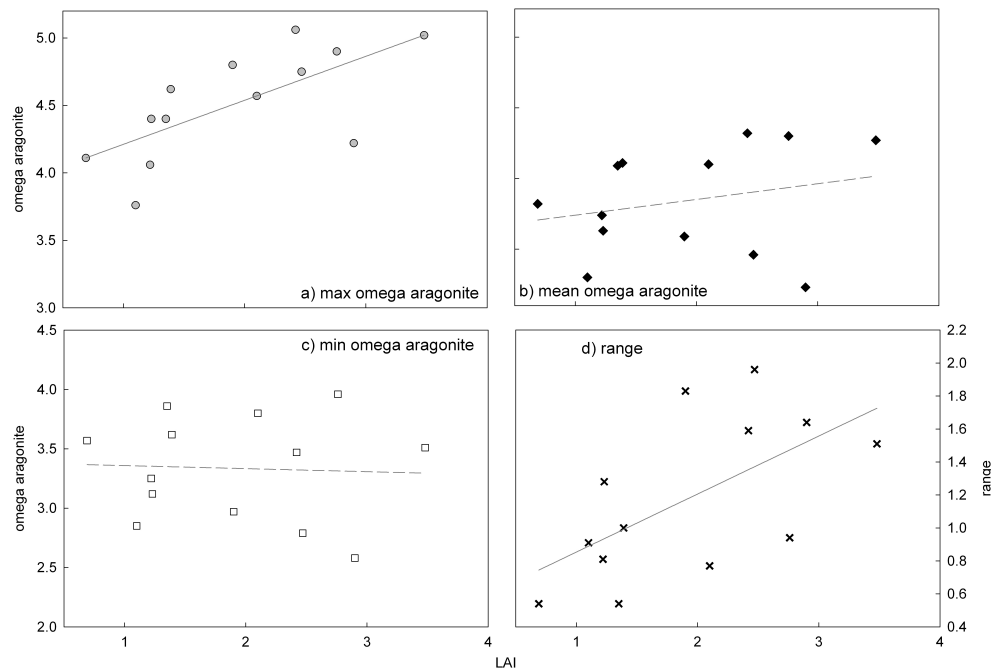


Fig. 4. The relationship between leaf area index (LAI) and mean, max, min and the range of Ω_{Ar} . Non-significant relationships are dotted lines. Maximum Ω_{Ar} (grey circles) is $0.33 \text{ LAI} + 3.89$ ($r^2 = 0.47$). Mean Ω_{Ar} are black diamonds, Minimum Ω_{Ar} are white squares while the range of Ω_{Ar} (right y-axis) are crosses.

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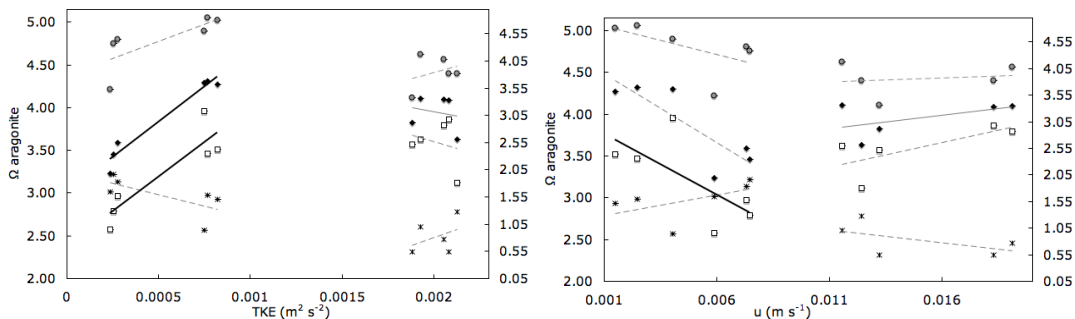


Fig. 5. The relationship between **(a)** TKE ($\text{m}^2 \text{s}^{-2}$) and **(b)** u (m s^{-1}) and mean, max, min and the range of Ω_{Ar} . Non-significant relationships are dotted lines. Maximum Ω_{Ar} is represented with grey circles, Mean Ω_{Ar} are black diamonds, Minimum Ω_{Ar} are white squares while the range of Ω_{Ar} (right y-axis) are crosses.

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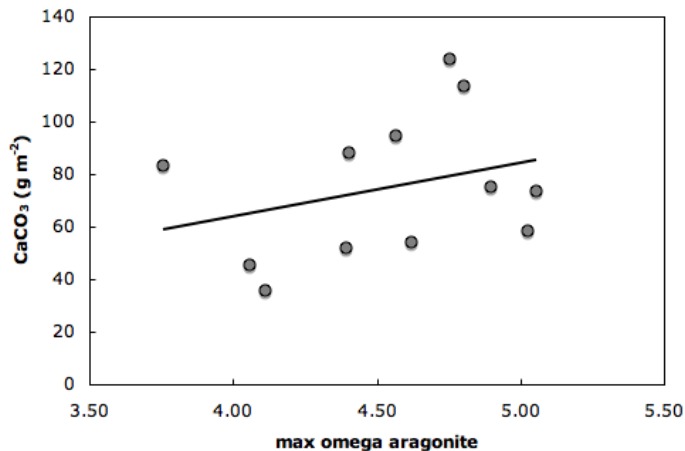


Fig. 6. Calcium carbonate content of the leaves vs. the saturation state of Aragonite (Ω_{Ar}) in the meadow. The linear regression is described as $\text{CaCO}_3 = 20.12 \Omega_{Ar} - 16.48$.

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