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Highlights

(a) Dynamics assessment of anhydrosugars in seawater
(b) Assimilation and mineralization of anhydrosugars by marine bacteria
(c) Levoglucosan is a substrate that can be used for cell maintenance
(d) Anhydrosugars showed the selection of Roseobacter clade in seawater
(e) Anhydrosugars are semilabile compounds compared to glucose

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Revised Version

10 October 2023

ABSTRACT

Wildfires, controlled burns, and biofuel combustion (biomass burning or BB) are major contributors to particulate matter in the atmosphere and thus have an impact on climate, human health, and ecosystems. Once emitted, the particulate matter derived from BB can be taken up by the oceans. However, the fate and impact of BB in the marine biological carbon pump, and carbon cycle are largely unknown. This work presents the first attempt to investigate the bioavailability of two BB tracers, levoglucosan and galactosan, in seawater inoculated with marine prokaryotes. Levoglucosan and galactosan were incubated with a marine bacterial inoculum and monitored for six weeks under controlled laboratory conditions. Along with the anhydrosugar concentrations, multiple chemical and biological parameters were monitored over time. The results indicate that levoglucosan and galactosan can be assimilated by marine prokaryotes as their concentrations decreased by 97 ± 4% and 36 ± 21% (n = 3) of their initial values. However, this decrease occurred only after a 9 and 15 days from the beginning of the experiment, respectively. The decrease in the levoglucosan and galactosan concentrations was accompanied by an increase in both heterotrophic prokaryotic production, and abundance. These results demonstrate that these anhydrosugars have the potential to be assimilated by heterotrophic prokaryotes and thus contribute to the microbial food web functioning. Under our experimental conditions, levoglucosan exhibited a bacterial growth efficiency of 17 ± 5% (n = 3), suggesting that most of the levoglucosan is mineralized into CO_2. Prokaryotic diversity analyses revealed the predominance of a few bacterial genera from the Roseobacter clade that were selected after the addition of the anhydrosugars. The presence of this widespread marine bacterial clade reflects its ability to process semilabile compounds (here levoglucosan and galactosan) originating from BB and contribute to the dissolved organic matter pool in surface seawaters.

keywords: biomass burning, anhydrosugars, marine biological carbon pump, carbon cycle, semilabile dissolver organic matter, Roseobacter clade

1. Introduction

Wildfires, controlled burns, and biofuel combustion (biomass burning, BB) are major contributors to the emission of particulate matter in the atmosphere (up to 90% of primary organic aerosol (Bond et al., 2004) and thus have an impact on climate, human health, and ecosystems. Furthermore, the importance of BB emissions can potentially increase in the future due to the climate change-driven rise in wildfire occurrence in several regions of the world (Dennison et al., 2014; Ponomarev et al., 2021; Sierra-Hernández et al., 2022), including the Mediterranean Basin (Durrieu de Madron et al., 2011), and the parallel increase in fire severity in high biomass-containing woody vegetation (Daniau et al., 2012; Nolde et al., 2021; van Wees et al., 2021; Walker et al., 2020).

Once emitted, BB particulate matter can be deposited in the terrestrial ecosystem or eventually transported to the ocean. Although previous investigations showed the presence of BB tracers (PAHs and anhydrosugars) in several compartments of aquatic ecosystems including sinking particles (Castro-Jiménez et al., 2012; Schreuder et al., 2018; Simoneit and Elias, 2000; Theodosi et al., 2013), concentrated dissolved organic matter (Panagiotopoulos et al., 2013), and sediments (Froehner et al., 2010; Guigue et al., 2017; Hopmans et al., 2013; Schreuder et al., 2018; Theodosi et al., 2013) the fate of BB particulate matter in the marine environment is currently unknown, particularly its link with the microbial food web and the biological carbon pump (BCP). Recent investigations have demonstrated that wildfires can potentially trigger phytoplankton blooms (Tang et al., 2021) and modify the composition of their communities (Kramer et al., 2020) pointing to a possible utilization of such substrates by marine planktonic microorganisms. Conversely, the survival and the persistence of these substrates in sediments (Froehner et al., 2010; Hopmans et al., 2013) may imply a slow degradation mechanism in the marine environment which may be compound dependent. The above contrasting results clearly demonstrate that there is a gap in knowledge on the dynamics of BB particulate matter in seawater.

Several studies have highlighted the importance of atmospheric nutrient input in oligotrophic regions (Letelier et al., 2019; Van Wambeke et al., 2021) whereas incubation experiments comprising organophosphate compounds (Vila-Costa et al., 2019) atmospheric particulate matter (i.e., Saharan dust and anthropogenic aerosols; Djaoudi et al., 2020) and fossil fuel particles (i.e diesel, ship soot; Martinot et al., 2023) have shown an active response by marine heterotrophic prokaryotes. Interestingly, the former study on organophosphate compounds showed that in seawater bacteria (particularly Flavobacteria) exist with a high potential to utilize such organophosphate substrates, while the latter study on atmospheric aerosols highlighted significant differences in the metabolic response of heterotrophic prokaryotes between Saharan dust and anthropogenic aerosol substrates.

This work presents the first attempt to investigate the bioavailability of two BB-produced molecules (i.e., levoglucosan and galactosan) in seawater inoculated with marine microorganisms. These anhydrosugars are produced during wildfires and/or BB events and are due to the pyrolysis of cellulose and hemicellulose occurring at temperatures > 300 °C (levoglucosan represents > 90% of the anhydrosugars). Since cellulose and hemicellulose account for 60 – 80% of the dry weight of wood, levoglucosan is very abundant in BB emitted particles and thus is an unequivocal tracer of these processes (Bhattarai et al., 2019).

To investigate the bioavailability of these two molecules, a novel method was developed to extract these anhydrosugars from their salty matrix and monitor their evolution for 44 days under controlled laboratory conditions. Along with the anhydrosugar concentration, multiple parameters (dissolved organic carbon or DOC, inorganic nutrient concentrations, heterotrophic prokaryotic production, abundances of heterotrophic prokaryotes, and heterotrophic prokaryotic diversity) were monitored to achieve a complete picture of their fate in seawater in relation to the physiological responses and changes in the taxonomic composition of the prokaryotic communities. Furthermore, two experiments (one with a reference labile substrate, glucose; and one control, a nonamended substrate with an organic molecule) were run in parallel for comparison purposes.

2. Materials and methods

2.1. Experimental outset

2.1.1. Seawater sampling

Seawater was pumped at 30 m depth at the SOLEMIO station (26 March 2021) in the Bay of Marseille (43.24°N; 5.29°E), filtered online through GF/F glass-fiber filters and then transferred to two 20 L Nalgene Carboys (previously washed with 5 % HCl, Milli-Q water and seawater). Seawater was allowed to stand in the dark at 5 °C for approximately two months to allow labile organic matter to be degraded (DOC concentrations dropped from 70±1 to 65±1 µM C) and then filtered through a

Whatman Polycap cartridge (0.2 µm) to remove any particles or microorganisms. This 'prokaryotic free' seawater was used as background for the biodegradation experiments, and hence, it can be considered as 'recalcitrant' marine DOC.

2.1.2. Preparation of bacterioplankton inoculum

The bacterioplankton inoculum was prepared with seawater collected at the same site one day before the experiments were run. First, 10 L of seawater was filtered at 0.8 µm using polycarbonate filters (precleaned with 10% HCl solution and Milli-Q water) to remove bacterioplankton predators, phytoplanktonic organisms, and detrital particles. Then, this 0.8 µm filtrate was further concentrated to reach high bacterial abundances by filtration through 0.2 µm polycarbonate filters until a final volume of 0.9 L, in which we resuspended the 0.2 µm filters. The bacterioplankton inoculum contained 3.95×10^6 heterotrophic prokaryotes as indicated by flow cytometry. The DOC concentration of the inoculum was 100 ± 6 µM C (n = 2).

2.1.3. Batch preparation

Biodegradation experiments were performed in 2 L precombusted Schott bottles (450 °C, 6 h) containing 1.95 L of 'prokaryotic free' seawater and the natural prokaryotic community (i.e., 0.05 L of bacterioplankton inoculum). Anhydrosugars and glucose standards were added to each incubation bottle at a final concentration of 10 µM C resulting in initial DOC concentrations of ~ 70 µM C in the bottles, typical carbon concentrations of surface water at this sampling site. Control experiments were run in triplicate without the addition of any organic substrate. To avoid nutrient limitation throughout the experiments and maintain a C/N/P ratio of approximately 106/16/1, nitrate ($NaNO_3$), and phosphate (NaH_2PO_4) were added to each bottle, including the triplicate controls, to achieve final concentrations of 3.32 ± 0.04 µM N and 0.20 ± 0.01 µM P. Incubations were run for 44 days in the dark at 21 °C to ensure the degradation of substrates. To prevent oxygen depletion, the bottles were opened for a few seconds every 2-3 days and stirred quickly by hand. Several parameters were monitored at selected time points for a duration of approximately 6 weeks (Table S1). These parameters included the anhydrosugar concentrations, dissolved organic carbon concentration ([DOC]), inorganic nutrient (nitrate, nitrite, phosphate and silicate) concentrations, heterotrophic prokaryotic production (HPP), heterotrophic prokaryote abundance (HPA), and heterotrophic prokaryotic diversity (HPD).

2.2. Sample analyses

2.2.1. Anhydrosugars

Anhydrosugars were sampled from bottles after filtration on precombusted (450 °C, 6 h) Whatman GF/F (retention size, 0.7 µm) and stored at −20 °C until analysis. Anhydrosugars were extracted from their salty matrix using a mixed anion−cation exchange resin (Amberlite® IRN-150). First, a 2.5 g bed of resin was packed in a 20 mL glass syringe. Prior to use, the resin was conditioned using successively of acetonitrile, methanol, and water (3×15 mL each). A 2 mL volume of sample was loaded and allowed to stand for 20 min, and the anhydrosugars were then eluted with 30 mL of Milli-Q water. The sample was freeze-dried and redissolved in 1 mL of an acetonitrile/water mixture (90/10, v/v) containing 0.01% TEA, and 2 µM deuterated levoglucosan (internal standard for MS).

Analyses were performed by an Agilent LC-ESI-Q-TOF/MS system equipped with an LC system (Agilent 1290 Infinity) coupled to a Q-TOF (Agilent 6530 Accurate-Mass). Separation was performed with a Luna® 3 µm NH_2 100 Å (150 x 2 mm, Phenomenex) at 25 °C. Both solvents, acetonitrile (A) and water (B) contained 0.01% TEA. The flow rate was set at 200 µL min^{-1} and the gradient elution was as follows: 97% of A for 7 min; it gradually goes to 80% of A for 6 min; held for 2 min; returns to initial conditions in 1 min and is held until the end of the analysis (20 min since injection). The injection volume was 10 µL. Detection was performed in negative mode under the following conditions: drying gas flow 5 L min^{-1} at 275 °C, sheath gas flow 11 L min^{-1} at 250 °C, nebulizer pressure 60 psig, capillary voltage 5000 V, nozzle voltage 2000 V, fragmentor voltage 100 V, skimmer voltage 65 V, and octopole RF 750 V. MS data were recorded at full scan in the range of 50 to 350 m/z at a rate of 1 spectrum min^{-1}.

2.2.2. Quality assurance/quality control

The extraction efficiencies of levoglucosan and galactosan were 89 ± 8 and 71 ± 6% (n = 14), respectively, at a concentration of 2 µM. To correct for extraction variability, 2 µM galactosan (surrogate) was added to the levoglucosan subsamples before extraction, and vice versa. Then, the anhydrosugar concentration was calculated as follows:

$$[anhyd.]_{inc} = \frac{[anhyd.]_{sample}}{i \cdot j \cdot [surrogate]_{sample}} \quad (1)$$

where $[anhyd.]_{inc}$ is the concentration of the anhydrosugar in the incubation batch, $[anhyd.]_{sample}$ is the concentration provided by the LC-Q-TOF, $[surrogate]_{sample}$ is the concentration of surrogate, i is the preconcentration factor of 2, j is extraction efficiency ratio between the two anhydrosugars (which was necessary since levoglucosan systematically present higher extraction efficiencies than galactosan). The latter factor was fairly constant in each extraction. The detection limits of levoglucosan and galactosan in the LC-Q-TOF were 100 and 60 nM, respectively.

2.2.3. Dissolved organic carbon

DOC subsamples were filtered through a 25 mm precombusted (450 °C, 6 h) Whatman GF/F filter (nominal retention size, 0.7 µm) and 15 mL of filtrate was acidified with 21 µL of pure H_2SO_4 (95-98%) and stored at 5 °C until analyses. DOC concentration was measured by high-temperature combustion on a Total Carbon Analyzer (Shimadzu TOC 5000) (Para et al., 2013; Sohrin and Sempéré, 2005). To avoid random errors associated with day-to-day instrument variability, all samples from a given biodegradation experiment were analyzed in a single day. The procedural blanks (i.e., Milli-Q water) ranged from 1 to 2 µM C and were subtracted from the values presented here. Deep seawater reference samples (provided by D. Hansell, Univ. of Miami) were run daily (43.5 µM C, n = 4) to check the accuracy of the DOC analyses. The concentrations represent the average of two replicates, ensuring a coefficient of variance (CV) below 2%.

2.2.4. Inorganic nutrients

Inorganic nutrient subsamples were filtered with a precombusted GF/F filter (450 °C, 6 h) and stored at −20 °C until analyses. Concentrations of nitrite, nitrate, phosphate and silicate were measured by colorimetry using a gas-segmented continuous flow analyzer (Aminot and Kérouel, 2007). The detection limits of nitrite, nitrate, phosphate, and silicate were 0.03, 0.05, 0.02, and 0.05 µM, respectively. In-house standards, which were regularly compared to commercially available products, were analyzed to ensure the reproducibility of the analyses. The standard deviation of triplicate measurements was generally better than 5% at the 0.5 µM level for all nutrients.

2.2.5. Hetrotrophic prokaryotic production

Heterotrophic prokaryotic production (HPP) was immediately estimated after sampling by ^{3}H-leucine incorporation using the centrifugation method (Smith and Azam, 1992). The detailed protocol has been described elsewhere (Djaoudi et al., 2020). Briefly, 1.5 mL samples were incubated in the dark for 1−2 h after the addition of ^{3}H-leucine at a final concentration of 20 nM, with the standard deviation of the triplicate measurements being on average 9%. Isotopic dilution was checked and was close to 1 (Van Wambeke et al., 2018); and thus, a conversion factor of 1.5 kg C mol leucine^{-1} was applied to convert leucine incorporation to carbon equivalents (Kirchman, 1993).

2.2.6. Heterotrophic prokaryote abundance

Subsamples (1782 µl) for heterotrophic prokaryote abundances (HPA) were immediately fixed with 18 µL of mix of glutaraldehyde and pluronic acid (0.25% and 0.01%, respectively of final volume) and then stored at −80 °C upon analyses. Analyses were performed using an Accuri C6 (BD Biosciences) flow cytometer with an error measurement < 5%, as described elsewhere (Layglon et al., 2020).

2.2.7. Hetrotrophic prokaryotic diversity

Polycarbonate filters (0.2 µm) were used to collect prokaryotes from 300 mL of sample. The filters were stored at −80 °C. After thawing, they were cut with sterile scissors into small pieces, immersed in 750 µL of sterile saline TSE buffer (50 mM Tris-HCl, 750 mM sucrose, 20 mM EDTA, 40 mM NaCl, pH = 9.0) and vortexed horizontally for 5 min at ambient temperature. Cell lysis was performed with lysozyme, SDS and proteinase K as reported elsewhere (Boström et al., 2004). DNA was precipitated in 70% ethanol, 0.1 M sodium acetate (pH = 5.2) and linear polyacrylamide (Genelute-LPA, Sigma−Aldrich) (Gaillard et al., 1990). After 2 rinsing steps with 70% ethanol, DNA pellets were air-dried, resuspended in Milli-Q water, and stored at −20 °C. Amplification of the V4-V5 region of 16S rRNA gene was performed with primers 515F-Y/926R (Parada et al., 2016) as described previously (Misson et al., 2021). Extraction and amplification negative controls did not yield any amplification product. After purification (Nucleospin Gel and PCR clean-up, Macherey-Nagel), PCR products were paired-end sequenced (2×300 bp) with an Illumina MiSeq sequencer by Eurofins (Germany). Sequencing reads were deposited in the National Center for Biotechnology Information Sequence Read Archive (NCBI SRA) under the accession number PRJNA908786. MiSeq raw reads were analyzed with DADA2 (Callahan et al., 2016) in RStudio (R Team, 2021) as described previously (Misson et al., 2021). Taxonomic information was assigned to amplicon sequence variants (ASV) with the SILVA database v.138.1 (Quast et al., 2013). Sequences classified as mitochondria or chloroplasts were removed from the dataset. Alpha and beta diversity analyses were performed with RStudio using the *phyloseq* (McMurdie and Holmes, 2013) package and represented using *ggplot2* (Wickham, 2016) and *metacoder* (Foster et al., 2017) packages. Differences in alpha and beta diversity metrics were tested for significance (P value < 0.05) using ANOVA with Tukey post hoc tests and PERMANOVA with *stats* and *microbial* (Guo K. and Gao P, 2021) packages, respectively.

3. Results & Discussion

3.1. General observations

The results of this study showed that levoglucosan concentrations decreased from 15 ± 4 to 0.4 ± 0.5 µM C (n = 3) throughout the experiment (Fig. 1a). This decrease was also mirrored by the corresponding decrease in DOC concentrations, which dropped from 73 ± 2 to 61 ± 1 µM C (Fig. 1b). In contrast, the decrease in galactosan concentrations was less pronounced and dropped from 14 ± 2 to 9 ± 4 µM C (Fig. 1c), while DOC concentrations remained relatively unchanged (initial: 69±2 and final: 68±3 µM C; Fig. 1d). In a parallel biodegradation experiment run with glucose, the results showed that DOC concentrations rapidly decreased during the first two days of incubation, dropping from 67.6 µM C to 59.4 µM C (n = 3) and then remained stable until the end of the experiment (Fig. 1e). Overall, DOC concentrations in the glucose experiment dropped by 10 ± 3 µM C indicating a complete depletion of the molecule as 10 µM C was initially added to the batch as a glucose substrate. These results agree with laboratory incubation experiments (Djaoudi et al., 2020) and field studies indicating the rapid utilization of glucose by marine heterotrophic prokaryotes (Kirchman et al., 2001). Finally, in the control experiments (no added organic substrate), DOC concentrations remained fairly constant at ~ 60 µM C throughout the experiment (Fig. 1b, d, and e) indicating that changes in DOC concentrations for the other experiments were associated with heterotrophic bacterial activities that were ignited from the addition of a degradable substrate (anhydrosugar/glucose).

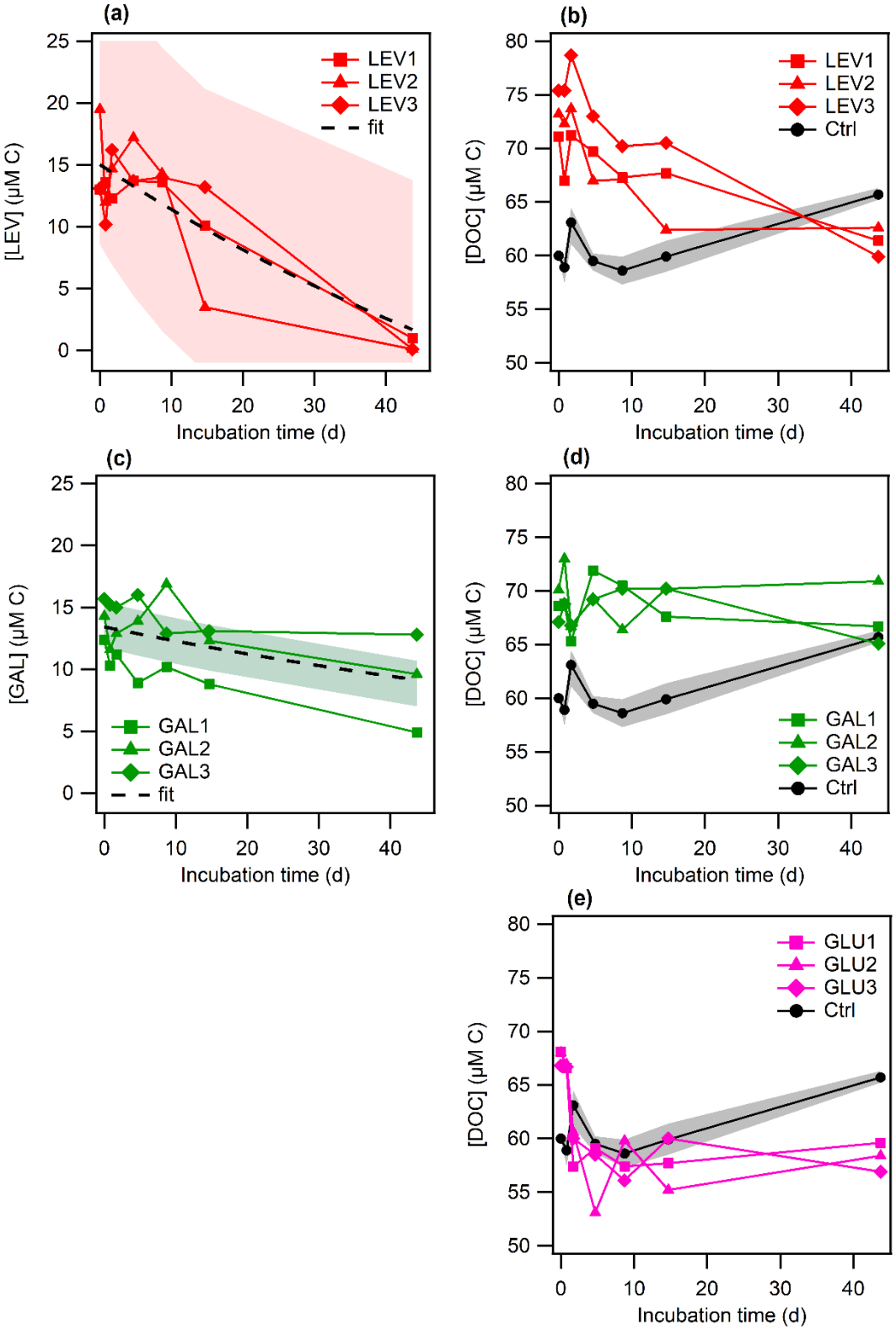

Fig. 1. Time course responses of anhydrosugars (levoglucosan: a and galactosan: c) and DOC concentrations (b, d, e) for all biodegradation experiments. The exponential fit of the average anhydrosugar concentrations is also presented with a dashed line with a 95% confidence interval shaded with a red/green surface (a, c). The time response of the mean DOC concentrations in the control experiments is shown in black (b, d, e), with the maximum and minimum observed values shaded in black. Abbreviations: LEV, levoglucosan; GAL, galactosan; GLU, glucose; Ctrl, control.

In line with the above observations, the decrease in the concentration of anhydrosugars and glucose was accompanied by an increase in heterotrophic prokaryotic production (HPP) and abundance (HPA) (Fig. 2). In the levoglucosan experiments (Fig. 2a and b), both HPP and HPA reached maximum values after at least ~15 d, whereas for the galactosan experiment, significant increases in both parameters (Fig. 2c and d) were observed only at the end of the incubation period (44 days), consistent with the slight decrease in galactosan concentration and DOC. In the glucose experiments (Fig. 2e and f), a rapid increase in both HPP and HPA was observed after ~ 1 d of incubation, with maximum values of 2000 ± 300 ng C L^{-1} h^{-1} and (1.11 ± 0.03) ×10^6 cell mL^{-1}, respectively, representing an increase of at least one order of magnitude from the initial values. As expected, control experiments showed little variation in HPP and HPA, with values relatively stable at ~ 10 ng C L^{-1} h^{-1} and ~ 1.7×10^5 cell mL^{-1}, indicating low prokaryotic activity in the absence of added organic substrate.

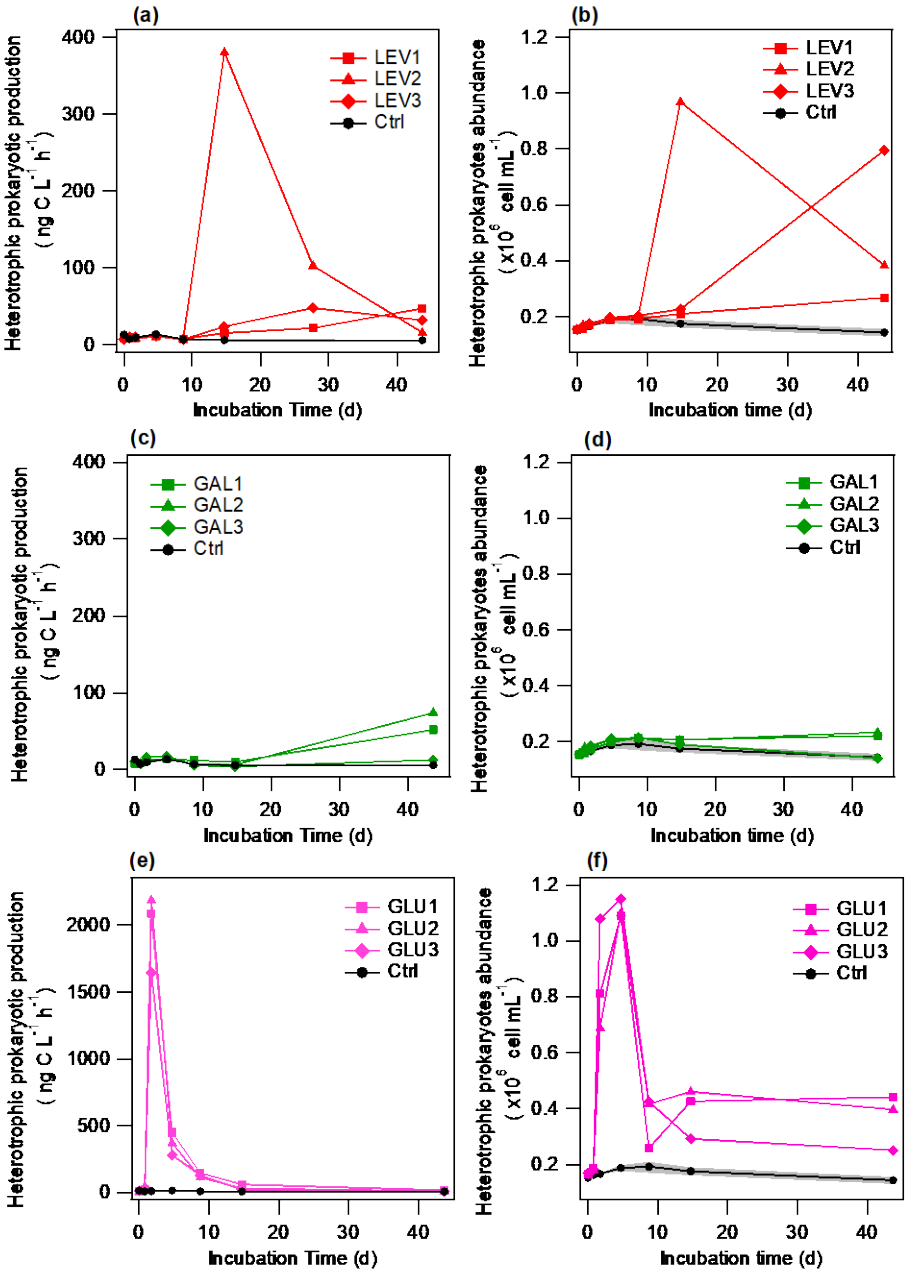

Fig. 2. Time course responses of heterotrophic prokaryotic production (HPP: a, c, e) and abundances (HPA: b,d,f) in anhydrosugars (levoglucosan and galactosan) and glucose biodegradation experiments. The time response of the mean of HPP and HPA values in the control experiments are shown in black dots, with the maximum and minimum observed values shaded in black. Abbreviations: LEV, levoglucosan; GAL, galactosan; GLU, glucose; Ctrl, control.

For the levoglucosan experiment, the measurements of HPP and HPA showed a degree of variability among replicates, which was not a measurement artifact since all investigated parameters were consistent within replicates. Indeed, HPP and HPA increases were observed first in the second replicate of the levoglucosan experiment (LEV2 in Fig. 2a and b), which displayed simultaneous decreases in DOC and levoglucosan concentrations (Fig. 1a and b). This variability may be related to differences in the ignition time at which some species of heterotrophic prokaryotes start to degrade the substrate added within the replicates, the low frequency of sampling during the most intense period of prokaryotic activity (which may miss the real time of peaks in this case) and finally the biological heterogeneity and complexity of biotic interactions within the bottles Such variability among the replicates has already been reported in similar biodegradation experiments carried out with atmospheric aerosols (Djaoudi et al., 2020), phytoplankton culture (Suroy et al., 2015) or fast sinking particles (Panagiotopoulos et al., 2002).

Inorganic nutrient concentrations showed similar patterns with the above observations (Fig. S1). For levoglucosan, nitrate and phosphate concentrations decreased after ~44 d of incubation (initial concentrations: 3.3 ± 0.1 and 0.20 ± 0.1 µM, respectively; final concentrations: 2.6 ± 0.3, and 0.16 ± 0.01 µM, respectively) indicating that the utilization of these nutrients provides the N and P sources necessary to degrade levoglucosan by marine heterotrophic prokaryotes. In contrast, for the galactosan experiment, nitrate and phosphate concentrations remained constant and similar to those of the control experiment. Finally, nitrite and silicate concentrations for all the experiments were similar to the control experiment indicating, low utilization compared to the initial concentration of these nutrients during the experiments and/or equilibrium between uptake and mineralization processes. In contrast, in the glucose experiment, a significant increase in nitrite and phosphate concentrations was observed at the end of the incubation, showing a decoupling between nutrient uptake and regeneration with time.

3.2. Are anhydrosugars labile substrates assimilated by marine prokaryotes?

The results of this study demonstrated that anhydrosugars exhibited different dynamics compared to a labile substrate such as glucose with regard to their utilization by marine heterotrophic prokaryotes. Specifically, levoglucosan and galactosan exhibited a distinct lag time during which their concentration remained unchanged (Fig. 1a and c), in contrast to the immediate degradation of glucose which occurred 1 d after the beginning of the experiment (Fig.1e). In fact, levoglucosan assimilation started between 9 and 15 d, while for galactosan, it was after 15 d. Although the decrease in both anhydrosugars was much slower than that of glucose, galactosan showed a much longer persistence in seawater than levoglucosan. The average half-life times (calculated assuming first-order kinetics (Castro-Jiménez et al., 2022)) were 78 ± 12 and 8 ± 1 d (n = 3) for galactosan and levoglucosan, respectively. Previous field studies in marine and aquatic environments showed a rapid utilization of glucose by bacterioplankon with glucose always exhibiting the shortest turnover time (5-12 h) over other monosaccharides including galactose (Bunte and Simon, 1999; Skoog et al., 1999). Considering that levoglucosan and galactosan are dehydrated forms of glucose and galactose, respectively the differences in assimilation between these two anhydrosugars observed in this experiment may be possibly to the different utilization rates between glucose and galactose as demonstrated for the marine environment.

The time responses of HPP and HPA (Fig.2) confirmed that both levoglucosan and galactosan are bioavailable substrates, although they do not appear to be the first choice for marine heterotrophic prokaryotes compared to a model of labile substrates such as glucose. They can be partially taken up at the scale of a few weeks, suggesting that they may be considered semilabile compounds based on their reactivity (Carlson and Hansell, 2015; Nelson and Wear, 2014). The semilabile nature of these substrates also concurs with the radiocarbon measurements made on levoglucosan ($\Delta = 48.5‰$) and galactosan ($\Delta = 35.4‰$) standards used for this biodegradation experiment highlighting the modern age of these compounds which further points to recent photosynthetic molecules (Nouara et al., 2019).

The low uptake of anhydrosugars by marine heterotrophic prokaryotes, as revealed by biodegradation experiments, is consistent with their detection at low concentrations in marine sediments (Hopmans et al., 2013; Schreuder et al., 2018) or other aquatic ecosystems (Elias et al., 2001). Nevertheless, as the compounds are semilabile, they might potentially be biodegraded and thus reintegrated into the carbon cycle. To better understand the biological fate of C for anhydrosugars, the bacterial growth efficiency (BGE) of levoglucosan was calculated (see details in Supplementary Section S1). Under our experimental conditions, levoglucosan had a BGE of 17 ± 5% (n=3). Compared to the BGE calculated for glucose (70 ± 10%; n=3), and assuming conservative leucine-carbon conversion factors through the 4 experiments and time, this suggests that levoglucosan is primarily used by bacteria for cell maintenance and energetic needs rather than growth, resulting in its mineralization into CO_2. The BGE of galactosan was not calculated due to its very low degradation during the incubation period and possible interference with the biological simultaneous use of bulk marine DOC. However, the fate of this compound will likely be the same as levoglucosan due to the low HPP and HPA observed.

3.3. Which bacteria can process anhydrosugars?

To further explore the prokaryotic populations involved in anhydrosugar degradation we analyzed community structure through 16S rRNA gene sequencing at three different incubation times (0, 4.7 and 43.7 days). The results showed that the initial (T0) prokaryotic community was mostly composed of Alphaproteobacteria (50-68%), with a strong predominance of the SAR11 clade, along with diverse Gammaproteobacteria. Such dominance of SAR11 is common in oligotrophic NW Mediterranean surface waters (Coclet et al., 2019; Navarro et al., 2023; Salter et al., 2014). This pattern remained highly similar throughout the experiment in the control condition (Fig. 3 and S1). Similarly, no significant changes were observed in community richness between the initial community and the control condition during the 43.7 days of incubation (Fig. 3 and 4). In contrast, the prokaryotic community richness significantly decreased after 4.7 days in glucose-amended incubation ($P < 0.002$). The presence of glucose also prompted a significant shift in community structure ($P < 0.01$) linked to the fast development of Gammaproteobacteria from the Vibrionaceae family, representing 68-76% of the entire community after 4.7 days of incubation (Fig. S1). Such opportunistic growth of Gammaproteobacteria, especially Vibrionaceae is consistent with previous work (Eilers et al., 2000; Haider et al., 2023). Depletion of glucose triggered a succession by members of Bacteroidota from the Cryomorphacae and Flavobacteriacea families, together with Crenarchaea from the Nitrosopoluminus genera. Given the ability of *Nitrosopumilus* to perform ammonium oxidation (Walker et al., 2010) and the copiotrophic character of Cryomorphacae or Flavobacteriacea known to contribute to heterotrophic blooms after phytoplanktonic blooms (Ho et al., 2017; Teeling et al., 2016), we propose that the succession of dominant prokaryotes observed with glucose addition reflects niche partitioning between opportunists (Vibrionaceae) and recyclers using organic matter from dead organisms (Bacteroidota) and regenerating nutrients (*Nitrosopumilus*). This hypothesis is consistent with the nutrient dynamics described above.

For levoglucosan and galactosan, the prokaryotic richness did not significantly vary in the short term ($P > 0.05$, Fig. 4), in coherence with the observed delay (> 8.7 days) of the decay of these anhydrosugars. A significant decrease in the prokaryotic diversity was observed at the end of the incubation (43.7 days) for levoglucosan ($P < 0.01$). The observed decrease was less pronounced than that observed for glucose after 4.7 days. Similarly, distance analysis did not reveal any significant change in community structure after 4.7 days of incubation, but it significantly shifted after 43.7 days of incubation with levoglucosan and galactosan compared to the initial community and the previous sampling time ($P < 0.01$). This significant shift corresponded to the development of Alphaproteobacteria from the family Rhodobacteraceae, with a notable development of genera Dinoroseobacter, Jannaschia and HIMB11, with less consistency among replicates for the latter. For two replicates exposed to levoglucosan, Alphaproteobacteria from the Rhizobiales order were particularly enriched (Fig. 3). The SAR11 clade exhibited an important decrease in its proportion with the addition of levoglucosan. The three genera of Rhodobacteraceae selected with anhydrosugars are known to belong to the Roseobacter group (Durham et al., 2014; Wagner-Döbler et al., 2009, 2003). Their delayed selection in our experiments is consistent with the delayed growth and slow growth efficiency mentioned above. This suggests a specific enzymatic capacity of these genera for processing anhydrosugars. Very few studies have reported the bacterial mechanisms and/or metabolic pathways for levoglucosan degradation (Iwasaki et al., 2018; Kuritani et al., 2020), although it appears to be a common function/process distributed across different bacterial phyla (Kaur et al., 2023). However, the demonstration of such potential for marine bacteria including the bacterial degradation of galactosan, remains to our knowledge unknown and warrants further investigation. Nevertheless, our study suggests for the first time the association of widespread marine bacterial genera with the biodegradation of biomass burning tracers. The Roseobacter group is known for its abundance and tremendous diversity in the global ocean (Daniel et al., 2018; Luo and Moran, 2014). By suggesting the importance of specific enzymatic capacities to process semilabile compounds, this work paves the way for further research linking the molecular composition of semilabile organic compounds accumulating in epipelagic/mesopelagic waters and the diversity of the Roseobacter group.

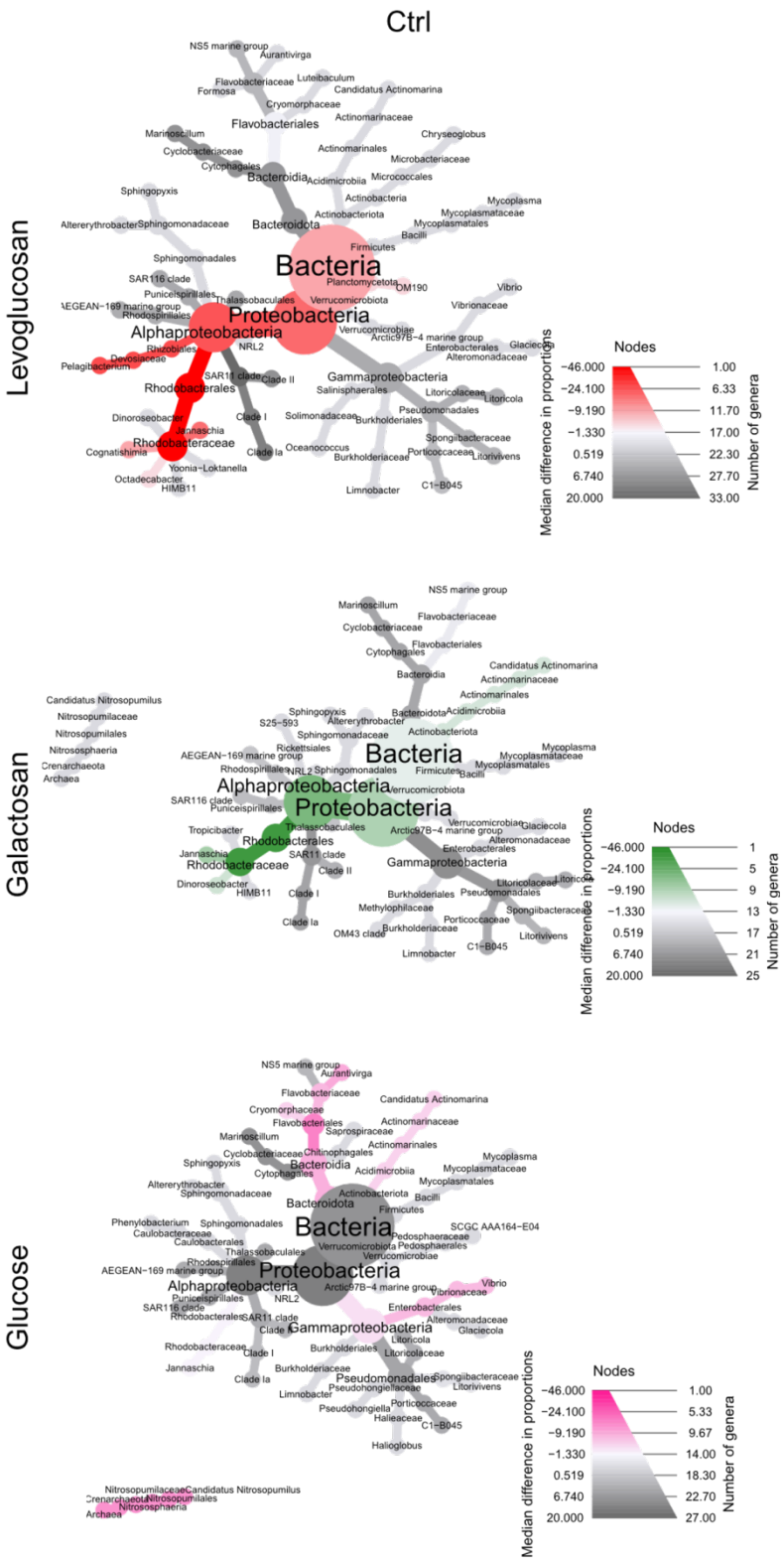

Fig. 3. Heat trees comparing the relative variations in the most abundant (> 2%) prokaryotic taxa between the control condition and different amendments after 43.7 days. Taxa more represented in the control condition appear in dark colors while taxa enriched in levoglucosan, galactosan or glucose-amended conditions appear in red, green, or pink, respectively. Node size is related to the number of genera representing the taxa. The color intensity of edges and nodes is proportional to the enrichment of the taxa in the corresponding condition (median difference based on triplicate experiments). Light gray taxa show similar representation in the compared conditions.

The noteworthy heterogeneity of genera from the Roseobacter group selected among replicates with anhydrosugars addition suggests a functional redundancy that deserves further investigation, the functional ability to process these semilabile compounds appears to be held at the Roseobacter group scale. The demonstrated ability to exchange plasmids between phylogenetically distant members of this group (Petersen and Wagner-Döbler, 2017) could largely contribute to their functional redundancy. Such functional redundancy could even be extended to Rhizobiales, since the possibility of genetic exchange between roseobacters and rhizobia has been demonstrated (Bartling et al., 2017). This could explain the selection of some Rhizobiales in two replicates of the levoglucosan condition observed in our work.

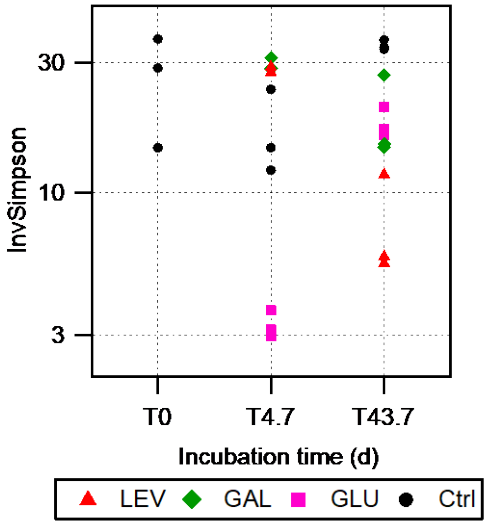

Fig. 4. Inverse Simpson index for prokaryotic richness at three incubation times.

4. Conclusions

Our findings have shown that BB tracers (levoglucosan and galactosan) can be assimilated by marine heterotrophic prokaryotes on a time scale of a few weeks and thus may be considered as semilabile substrates. Although these two anhydrosugars cannot entirely represent the complex biomass burning particles the present study suggests that marine prokaryotes mostly use these substrates for cell maintenance and energetic needs (and thus carbon is mostly mineralized into CO_2). Prokaryotic diversity analyses revealed the predominance of a few bacterial genera from the Roseobacter clade that were specifically selected by the addition of the anhydrosugars. These results suggest that the tremendous diversity of this widespread marine bacterial clade could reflect its ability to process a large diversity of semilabile compounds (here represented by levoglucosan and galactosan) constituting dissolved organic matter pools in surface ocean waters.

5. Acknowledgement

We would like to acknowledge the captain and crew of the RV ANTEDON for their assistance in sample collection. We are grateful to P. Martinot, M. Tedetti and C. Guigue for their valuable laboratory assistance and fruitful discussions; to A. Barani and the PRECYM facility of the MIO for their support in sample preparation for HPA measurements.

6. Financial support

Funding was provided by the French National Recherche Agency (FIRETRAC project No ANR-20-CE01-0012-01) whereas infrastructure support was provided by the European Regional Development Fund (ERDF; project 1166-39417).

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Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

CP conceived and designed the study. LP collected the seawater. JMGS and CP collected all samples. JMGS and CA developed the method to determine anhydrosugars in seawater and performed the analyses. NG, FVW and BM performed the nutrient, bacterial production and bacterial diversity analyses, respectively. JMGS, CP, FVW and BM synthetized the data and write the manuscript with inputs from all authors.