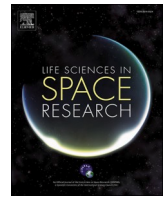




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## Review article

# Recycling nutrients from organic waste for growing higher plants in the Micro Ecological Life Support System Alternative (MELiSSA) loop during long-term space missions

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## ABSTRACT

Space agencies are developing Bioregenerative Life Support Systems (BLSS) in view of upcoming long-term crewed space missions. Most of these BLSS plan to include various crops to produce different types of foods, clean water, and O<sub>2</sub> while capturing CO<sub>2</sub> from the atmosphere. However, growing these plants will require the appropriate addition of nutrients in forms that are available. As shipping fertilizers from Earth would be too costly, it will be necessary to use waste-derived nutrients. Using the example of the MELiSSA (Micro-Ecological Life Support System Alternative) loop of the European Space Agency, this paper reviews what should be considered so that nutrients recycled from waste streams could be used by plants grown in a hydroponic system. Whereas substantial research has been conducted on nitrogen and phosphorus recovery from human urine, much work remains to be done on recovering nutrients from other liquid and solid organic waste. It is essential to continue to study ways to efficiently remove sodium and chloride from urine and other organic waste to prevent the spread of these elements to the rest of the MELiSSA loop. A full nitrogen balance at habitat level will have to be achieved; on one hand, sufficient N<sub>2</sub> will be needed to maintain atmospheric pressure at a proper level and on the other, enough mineral nitrogen will have to be provided to the plants to ensure biomass production. From a plant nutrition point of view, we will need to evaluate whether the flux of nutrients reaching the hydroponic system will enable the production of nutrient solutions able to sustain a wide variety of crops. We will also have to assess the nutrient use efficiency of these crops and how that efficiency might be increased. Techniques and sensors will have to be developed to grow the plants, considering low levels or the total absence of gravity, the limited volume available to plant growth systems, variations in plant needs, the recycling of nutrient solutions, and eventually the ultimate disposal of waste that can no longer be used.

## 1. Introduction

Many space agencies have been and are still working on Bioregenerative Life Support Systems (BLSS) for long-term crewed space missions (Guo et al., 2017; Wheeler, 2017). The goals of BLSS are to ensure the sustainability of the crew's habitat by recycling waste and providing O<sub>2</sub>, clean water, and diverse kinds of food while removing CO<sub>2</sub> from the atmosphere (Guo et al., 2017). Examples of BLSS developed in the past are the Advanced Life Support program of the U.S. National

Administration Space Aeronautics (NASA), and the BIOS-3 system of the Institute of Biophysics in Russia, while the Micro-Ecological Life Support System Alternative loop (MELiSSA) of the European Space Agency (ESA) and the Lunar Palace of the Beihang University in China are currently being developed (Guo et al., 2017; Lasseur and Mergeay, 2021; Wheeler et al., 2003; Wheeler, 2017). Higher plants are anticipated to be grown in most BLSS either to provide a complement to the crew's diet with fresh vegetables or greens as currently done in the International Space Station (ISS) for short missions (Stromberg, 2015) or to supply the crew

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with food, O<sub>2</sub>, and water while capturing CO<sub>2</sub> from the atmosphere during long-term missions (Ferl et al., 2002). For such missions, nutrient delivery to crops will depend on waste recycling to minimize resupplying from Earth (Poulet et al., 2022). Furthermore, making these nutrients available to plant uptake will require a constant flux of water from the media surrounding the plant roots, which will be challenging because of the effects on water fluxes of the absence of gravity in space and of microgravity on the surface of planets (Hatch et al., 2022).

Crops such as wheat, soybean, lettuce, and potato have all been suggested for BLSS (Cloutier et al., 2001; De Micco et al., 2012; Poughon, 1997; Sheridan et al., 2017; Stasiak et al., 2012; Weihreter, 2010; Wheeler et al., 2003; Zabel et al., 2016). Crop choices were based on specific criteria, such as crew requirements (vitamins, micro-nutrients), crop cultivation methods (inputs, lighting, space, crew work required), amounts of food, water, and O<sub>2</sub> produced, and time needed for preparation (Cloutier et al., 2001; Douglas et al., 2020; Poughon and Dussap, 2001). Romeyn et al. (2019) suggested the use of the Crop Readiness Level to assess how far crop testing is from being implemented during space missions; it ranges from level one (basic crop testing) to levels eight (plant successfully grown in space) and nine (plant successfully consumed in space). Lettuce, for instance, has reached level nine since it has been both grown and consumed on the ISS (Stromberg, 2015); tomato has recently reached level eight because it was grown in the ISS and brought back to Earth for analysis (NASA, 2023), while other crops like soybean and wheat are still at the earlier phase of level two, which is cultivar screening (De Micco et al., 2012; Stasiak et al., 2012).

A plant requires 17 elements to grow (C, H, O, N, P, S, K, Ca, Mg, Fe, Mn, Cu, Zn, Mo, B, Ni, and Cl) (Marschner, 2012). In addition to these, adding Si might be useful to increase the tolerance of plants to stresses, while adding Se might improve the quality of edible products for the crew (Marschner, 2012). Most mineral nutrients are taken up in ionic water-soluble forms from the solution by the root system. The total amounts of nutrients needed by higher plants vary by species and cultivars and depend on plant development stage and environmental conditions (Bamsey et al., 2012). In its Veggie growth chamber, NASA uses a controlled-release fertilizer (Nutricote: 18% N, 6% P<sub>2</sub>O<sub>5</sub>, 8% K<sub>2</sub>O), mixed with arcillite, which is a combination of calcined montmorillonite and illite (Massa et al., 2017; Morsi et al., 2022), as a source of nutrients to grow plants on the ISS. In addition to releasing NPK, Nutricote also provides B, Cl, Cu, Fe, Mg, Mn, and Mo (Arysta LifeScience, 2006). This type of fertilizer is made by aggregating salts containing water-soluble nutrients and coating the aggregates with a polymer (Adams et al., 2013; Arysta LifeScience, 2006). The properties of the polymer control the rate of release of nutrients to the solution (Adams et al., 2013). While this controlled-release fertilizer is proving highly useful for testing plant growth on the ISS, that will not be the case for long-term missions on which nutrients will have to come from waste streams and where the delivery of nutrients will have to be adapted to the needs of different plants.

The nutritional status of plants growing in space has rarely been studied. Wolff et al. (2013) note that space-grown plants might accumulate higher amounts of potassium and lower amounts of nitrogen than plants grown on Earth but do not offer reasons for that suggestion. In three sets of experiments, Khodadad et al. (2020) compared the concentration of nutrients in lettuce leaf tissue grown in the Veggie growth chamber on Earth and on the ISS. They observed only a few differences, with higher concentrations of sodium, phosphorus, sulfur, and zinc in their second experiment and in potassium in their third for plants grown on the ISS, while the iron concentration was lower in their third experiment for plants grown on the ISS. These differences were attributed to stress to the plants caused by flight, as suggested by a higher concentration of phenolic compounds in leaves of plants grown on the ISS. Liu et al. (2018) showed that roots of *Petunia hybrida* were less mycorrhized under simulated microgravity because of inhibited hyphae extension. As a result, the plants took up less phosphorus under simulated microgravity than under Earth gravity. This short review

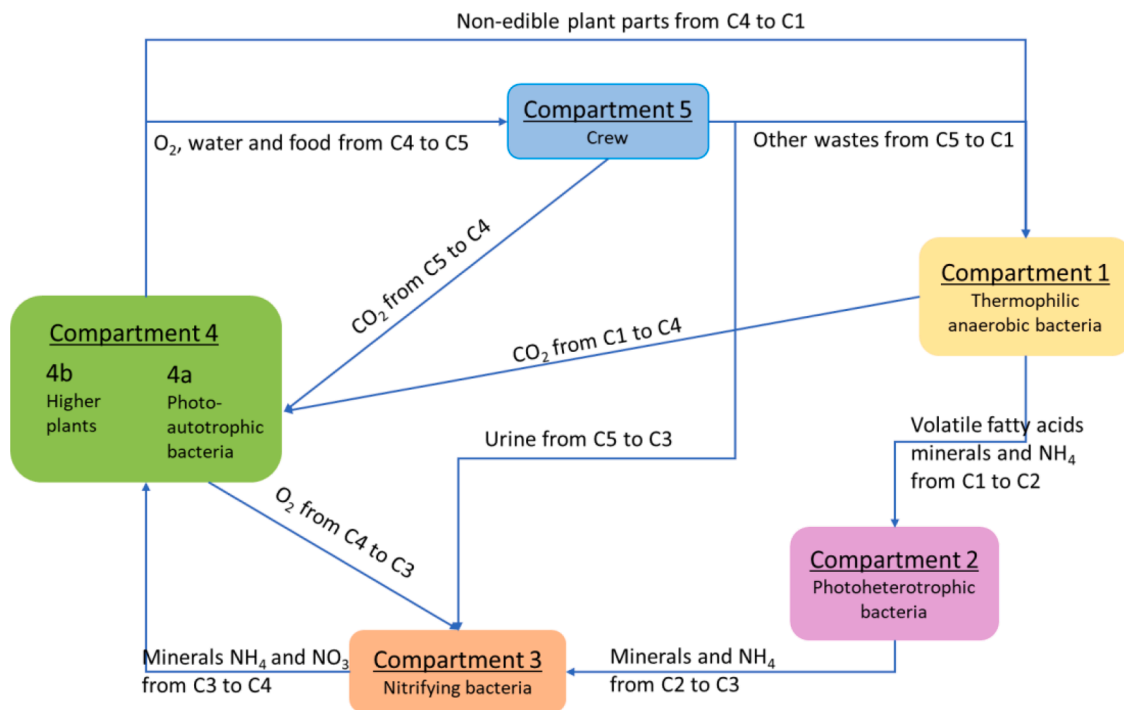
shows that we still do not fully understand the nutrition of plants growing in space.

Plant nutrition requires a continuous flux of water transporting the nutrients from the solution to the root and then to the aerial parts. However, microgravity can lead to a loss of convective transport of gases at the leaf surface, which can lead to an increase in the boundary layer thickness around the leaves, significantly diminishing gas exchange (Poulet et al., 2018). Microgravity can also result in increased boundary layer thickness around roots, leading to a decrease in O<sub>2</sub> transfer to the root and the appearance of anoxia and nutrient deficiencies during plant growth (Poulet et al., 2016). The buildup of boundary layers around leaves can be alleviated by the installation of an efficient ventilation system for the aerial plant parts (Poulet et al., 2018), but ensuring sufficient water uptake and aeration at root level remains problematic (Hatch et al., 2022). Hatch et al. (2022) recently developed the Plant Water Management technology, in which water transfer is controlled by conduit geometry of tubing, surface tension, and wetting. The aptitude of the Plant Water Management technology to ensure proper water transfer to the plant was assessed using synthetic plant models (composed of wicks for the roots and an artificial leaf allowing evapotranspiration to occur) installed either on arcillite or in hydroponic systems. In-flight tests of both systems on the ISS demonstrated the successful transfer of water from a reservoir through the wick to the artificial leaf and atmosphere, and the release of air previously trapped in the water in the vicinity of the “root,” allowing for oxygenation of the “root zone” (Wasserman et al., 2022, 2022). The implementation of such a system in BLSS will require nutrients to be delivered in water-soluble ionic forms either to an arcillite substrate or in a hydroponic system so that they can be transported with water to the roots.

In the present study, we review what needs to be considered so that nutrients recovered from waste streams in the MELiSSA loop could be used to design nutrient solutions appropriate for enabling various crops to efficiently deliver diverse food, O<sub>2</sub>, clean water, and capture CO<sub>2</sub>. We choose the MELiSSA loop as an example among the different BLSS because its compartments are explicitly connected to one another, showing which compartment is delivering what to which other compartment(s), and because a substantial amount of research has been published on it over the years, as shown in the review by Lasseur and Mergeay (2021). In the first part of the present study, we provide a short presentation of the MELiSSA loop (Fig. 1). We then analyze stepwise how the processes implemented in each MELiSSA compartment affect the form and availability of nutrients, and finally we address the challenges of preparing nutrient solutions adapted to the needs of various plants in the context of the MELiSSA loop. Note that, we do not discuss in this review the mineral nutrition of cyanobacteria included in the MELiSSA loop or the use of regolith found on the Moon or on Mars as a growth substrate (Paul et al., 2022).

## 2. Description of the overall MELiSSA loop

The MELiSSA loop was developed from knowledge of the functioning of aquatic ecosystems (Lasseur et al., 2010). Several kinds of organic waste are produced in a space habitat, such as urine, feces, gray water as defined for MELiSSA by Lasseur et al. (2018), kitchen residues, paper, and plant residues. All waste except urine (ESA, 2022) is currently planned to be transferred to the first compartment (C1) of the loop, the solid organic waste degradation compartment (Christophe Lasseur, director of the MELiSSA program, personal information), where anaerobic digestion takes place (Fig. 1). This digestion should allow for the hydrolysis of proteins, saccharides, and celluloses by thermophilic bacteria, leading to the liquefaction of organic matter and the release of volatile fatty acids, minerals, and CO<sub>2</sub>. The CO<sub>2</sub> produced in C1 can be used by plants and cyanobacteria (*Limnospira indica*) in the plant and algae compartment (C4). The volatile fatty acids and liquefied organic matter produced in C1 are transferred to the liquid organic waste degradation compartment (C2). In the current version of the MELiSSA



**Fig. 1.** Fluxes of substances in the current MELiSSA loop, adapted from [ESA \(2022\)](#). C1 is the solid organic waste degradation compartment, C2 the liquid organic waste degradation compartment, C3 the nitrifying compartment, C4a the algae compartment, C4b the plant compartment, and C5 the crew compartment.

loop ([ESA, 2022](#)), these organic compounds are mineralized by *Rhodospirillum rubrum* in the absence of  $\text{O}_2$  in C2. However, in the future this digester could be replaced by a microbial electrochemical cell (MEC) (Christophe Lasseur, director of the MELiSSA program, personal information), as proposed by [Luther \(2018\)](#), [Luther and Rabaey \(2020\)](#), and [Popat \(2020\)](#), to improve  $\text{CO}_2$  recovery from organic matter degradation. MECs are relatively recent systems made of a cathode that produces  $\text{H}_2$  from water electrolysis and of a microbial anode able to oxidize organic compounds to  $\text{CO}_2$  ([Rousseau et al., 2020](#)). In the current set up C2 does not produce  $\text{CO}_2$ , but if a MEC is implemented in C2, the  $\text{CO}_2$  produced will be transferred to C4. In both cases the ammonium and other minerals present in the solution can be further transported to the nitrifying compartment (C3). This compartment, which also receives the urine produced by the crew, contains a mix of *Nitrobacter* sp. and *Nitrosomonas* sp. that can transform ammonium first into nitrite and then into nitrate, using  $\text{O}_2$  derived from C4. The nitrate, what remains of the ammonium, and other mineral nutrients are then transferred from C3 to C4, which includes C4a, in which the cyanobacteria *Limnospira indica* is grown, and C4b, where higher plants grow. While both C4a and C4b remove  $\text{CO}_2$  from the atmosphere and produce  $\text{O}_2$  and food for the crew, the water released by transpiration from the higher plants in C4b provides the crew with clean water ([Fig. 1](#)).

### 3. Nutrient recovery from the solid and liquid organic waste degradation compartments (C1 and C2)

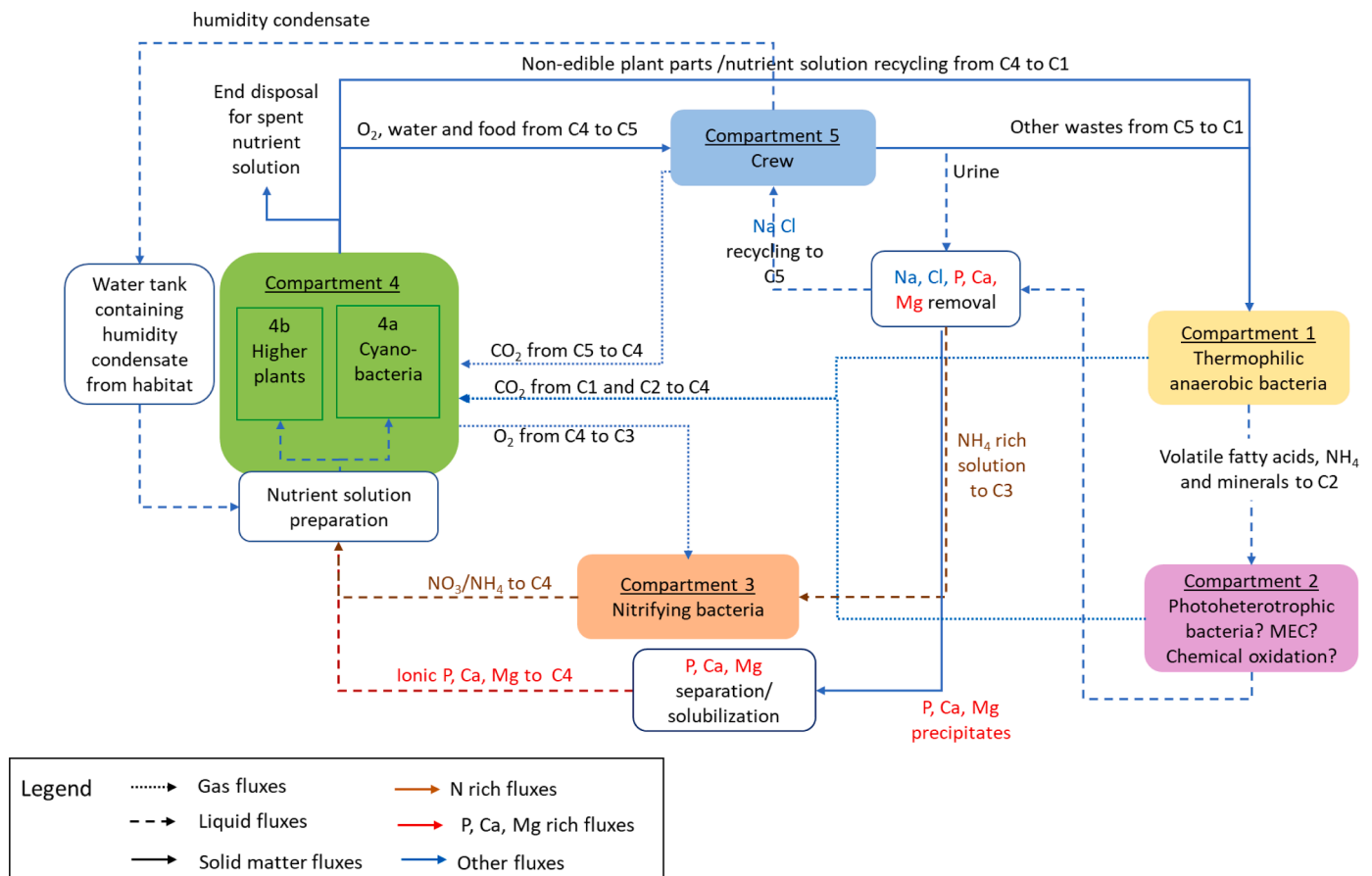
The transformation of carbon present in organic waste in  $\text{CO}_2$  in C1 and C2 is important from a plant nutrition point of view to provide sufficient  $\text{CO}_2$  for photosynthesis and for the release of nutrients bound to these organic matters into the solution in forms available to plants; it is also important for minimizing final total waste volume.

Biochemical equations describing the processes occurring in C1 and C2 appear in [Hendrickx et al. \(2006\)](#) and [Poughon et al. \(2009\)](#). These equations consider the stoichiometries of substrates and products in terms of their C, N, S, O, H, and P contents but do not provide information on other elements. Until now, most of the experimental work done on C1 has focused on organic matter liquefaction—that is, on the

transformation of solid organic matter in liquid—and on  $\text{CO}_2$  production ([Lissens et al., 2004](#); [Poughon et al., 2013](#)). [Lissens et al. \(2004\)](#) reported a maximal rate of C liquefaction of 83%, but they produced mostly  $\text{CH}_4$ , which is not wanted in the MELiSSA loop ([Poughon et al., 2009](#)) and no  $\text{CO}_2$ . [Poughon et al. \(2013\)](#) reached 50% of organic matter degradation and did produce  $\text{CO}_2$ , but only at low rates. [Luther \(2018\)](#) considers that C1 currently allows a recovery of only 15% of C added as waste in the form of  $\text{CO}_2$ , while about 35% of this C and 45% of N added in waste are transferred in dissolved forms to C2. [Lissens et al. \(2004\)](#) note that only a third of phosphorus added to the reactor was recovered as orthophosphate at the reactor outlet. They interpreted this as due to the “adsorption (of phosphate) on particulate matter”. However, this could have three explanations. First, microorganisms have taken up phosphorus because they need it to grow. [Mouginot et al. \(2014\)](#) mention an average molar C:P ratio of 72:1 for bacteria. The second possibility is that phosphorus has precipitated with cations during anaerobic digestion. This has been observed many times in organic waste ([Barat et al., 2009](#); [Carliell and Wheatley, 1997](#); [Frossard et al., 1994, 1997](#)). Such precipitation processes can ultimately decrease phosphate availability for crops, as shown by [Frossard et al. \(1996\)](#). Third, phosphate may have left the reactor in forms other than orthophosphate, perhaps as colloidal phosphorus.

Little information exists on nutrient recovery from C2. [Favier-Teodorescu et al. \(2003\)](#) showed that *Rhodospirillum rubrum* grown in the absence of  $\text{O}_2$  in a photobioreactor under different light conditions was able to remove volatile fatty acids from the solution while producing only a limited amount of  $\text{CO}_2$ . These authors suggest that this bacterium was storing high amounts of phosphorus in polyphosphate when submitted to excessive light conditions. More recently, [Luther et al. \(2018\)](#) and [Luther and Rabaey \(2020\)](#) suggested that installing a MEC in C2 would improve the recovery of organic C added to C1 as  $\text{CO}_2$  up to 40%. Moreover, this MEC would remove 80%–100% of the volatile fatty acids ([Fig. 2](#)).

With the aim of obtaining greater  $\text{CO}_2$  recovery from organic matter degradation but without assigning their research to any MELiSSA compartment, [Zhang et al. \(2019\)](#) used mild temperature hydrothermal oxidation with  $\text{H}_2\text{O}_2$  on anaerobic fermentation filtrates to oxidize



**Fig. 2.** Modifications suggested in the MELiSSA loop to provide higher plants with nutrients. C1 is the solid organic waste degradation compartment, C2 the liquid organic waste degradation compartment, C3 the nitrifying compartment, C4a the algae compartment, C4b the plant compartment, and C5 the crew compartment. A final decision on C2 has not yet been made by ESA. Instead of hosting photoheterotrophic bacteria, it might host a microbial electrochemical cell (MEC) that is more efficient in terms of transforming organic matter in  $\text{CO}_2$ . Furthermore, proposals have been made to couple the MEC with chemical oxidation to achieve even greater efficiency in transforming organic matter into  $\text{CO}_2$ . The transfer of protons and hydroxyls is not shown. They will be generated by water electrolysis in the sodium, phosphate, calcium, and magnesium removal units and transferred to the C4b to stabilize the pH in the nutrient solution, hydroxyls will be transferred to C3 to improve the nitrification rate, and protons will be used to solubilize calcium and magnesium phosphate minerals.

organic C in  $\text{CO}_2$  and transform organic nitrogen into ammonium and nitrate. The highest C recovery as  $\text{CO}_2$  was 68%, and up to 80% of nitrogen was recovered as ammonium or nitrate, but no attention was paid to other elements. In subsequent work, Zhang et al. (2020) used supercritical water oxidation in the presence of  $\text{H}_2\text{O}_2$  to transform a model solid organic waste (a mix of toilet paper, feces, red beet, straw wheat, and lettuce) into  $\text{CO}_2$  and water in the absence of  $\text{O}_2$ . They showed that more than 90% of the C fed to the reactor was transformed into  $\text{CO}_2$ , with the rest found as dissolved organic C. Integrating chemical oxidation with the MEC mentioned above has the potential to transform up to 85% of the C added into  $\text{CO}_2$  (Luther and Rabaey, 2020; Luther et al., 2018) (Fig. 2). However, Zhang et al. (2020) also observed that a large proportion of elements (Na, P, K, Mn, Fe, Ca, Mg, Ni, Cu, and Zn) entering the reactor was not recovered in the liquid phase after organic matter oxidation. Zhang et al. (2020) suggest that these elements had precipitated in the reactor and that strategies should be developed to avoid the precipitation of minerals in the reactor. They also observed higher concentrations of Cr in the outlet compared to the inlet, suggesting that the reactor was releasing this element.

In view of the above-reported points, we recommend that for each process conducted within C1 and C2, an input-output mass balance be established for each chemical element (that is, for both nutrients and toxic elements) to quantify their recovery rate and the release of unwanted elements within the system. We also recommend further developing methods that will increase the mineralization rate of organic

carbon into  $\text{CO}_2$ , as well as methods to capture nutrients released from the mineralized organic matter.

#### 4. Nutrient recovery from the nitrifying compartment (C3)

Substantial information has been gathered on nutrient recovery from human urine (Larsen et al., 2021; Wald, 2022), as fresh human urine contains large concentrations of nitrogen and phosphorus (Rose et al., 2015). However, we do not have yet information on how to recycle nutrients when both urine and substances derived from C2 are transferred to C3. Therefore, we will focus in this section on nutrient recovery from urine as a model. We first review phosphorus recovery from urine and the availability of the recovered phosphorus to plants before turning to nitrogen recovery in nitrate and then discussing the impact of salinity on nitrification.

Very rapidly after its release from the human body, the urea that is present at a high concentration in fresh urine becomes hydrolyzed by urease-producing microorganisms. This leads to an increase in pH (up to 9) and carbonate concentration, causing the precipitation of struvite ( $\text{MgNH}_4\text{PO}_4 \cdot 6\text{H}_2\text{O}$ ) and calcium phosphate minerals such as octacalcium phosphate ( $\text{Ca}_8\text{H}_2(\text{PO}_4)_6 \cdot 5\text{H}_2\text{O}$ ), which over time becomes hydroxyapatite ( $\text{Ca}_5(\text{OH})(\text{PO}_4)_3$ ) (Barat et al., 2009; Udert et al., 2003b). In undiluted stored urine, about 30% of phosphorus precipitates; this percentage increases if urine is mixed with Ca- and Mg-rich solutions (Udert et al., 2003c). Another option to precipitate calcium and



magnesium phosphates and facilitate the separation of these elements from the solution is to use the approach developed by De Paepe et al. (2020), who proposed stabilizing urine at pH 11 to 12 through the production of hydroxyls derived from water electrolysis, which also leads to the precipitation of P minerals. This approach allows for the removal of 40% of phosphate from urine. Phosphate forms produced under these conditions have not yet been analyzed but could present sodium phosphates (such as  $\text{Na}_3\text{PO}_4 \cdot 0.5\text{H}_2\text{O}$ ), newberyite ( $\text{MgHPO}_4 \cdot 3\text{H}_2\text{O}$ ), kovdorskite ( $\text{Mg}_2\text{PO}_4(\text{OH}) \cdot 3\text{H}_2\text{O}$ ), and amorphous P forms and less struvite than when precipitates are formed at pH 9 (Ma et al., 2014). The stabilized urine can then be diverted and nitrified as described by De Paepe et al. (2021).

The availability of phosphate derived from struvite to plants growing in soilless systems appears to be good but variable. Arcas-Pilz et al. (2021) observed a lower phosphate availability from struvite than from water-soluble phosphate for *Phaseolus vulgaris* grown in perlite, while Hauck et al. (2021) showed that *Tagetes patula*  $\times$  *erecta* took up as much phosphate from struvite-amended white peat as from water-soluble phosphate-amended peat for three of the four struvites they studied. These results suggest that the solubility of struvite itself can vary due, for example, to changes in the conditions under which it has been precipitated. For instance, Ma et al. (2014) showed that varying the pH in the initial solution would lead to the formation of struvite crystals of different forms and to the coprecipitation of phosphate minerals other than struvite in low concentrations. But differences in plant responses following struvite addition could also be due to differences in growth conditions. The high efficiency of struvite in Hauck et al. (2021) study might be related to the high cation exchange capacity (CEC) ( $115 \text{ eq m}^{-3}$ ) and the more acidic pH of the white peat they used compared to the lower CEC ( $6 \text{ eq m}^{-3}$ ) and higher pH of perlite, as measured by Lemaire (1999). Indeed, a higher CEC and lower pH will lead to faster dissolution of P minerals (Hedley et al., 1995). Phosphate derived from hydroxyapatite, on the other hand, is known to be very slowly released to plants grown in hydroponics (Louw-Gaume et al., 2010). To circumvent the variable solubility of phosphate precipitates issued from urine treatments, El Nakhel et al. (2021) dissolved them in sulfuric acid before adding them to nutrient solutions used to grow lettuce. This is probably the best option given the nutrient solution delivery systems envisaged for microgravity-grown plants (Hatch et al., 2022). The protons necessary for this dissolution in the MELiSSA loop might be derived from water electrolysis using the above-noted method proposed by De Paepe et al. (2020).

Unless urease is inhibited at pH higher than 11, pH values of 9 typically triggered by urea hydrolysis increase the risk of ammonia volatilization (Udert et al., 2003a, 2003b). Urine can be nitrified to avoid this loss of  $\text{NH}_3$  to the atmosphere and to decrease ammonium concentration in the nutrient solution provided to the plant (Udert et al., 2003a). Nitrification includes two steps, both of which occur under aerobic conditions. Ammonium is first transformed into nitrite by ammonia-oxidizing bacteria. This reaction is associated with proton release. Then, nitrite is converted to nitrate by nitrite-oxidizing bacteria. The accumulation of nitrite has to be prevented, not only because it is highly toxic to many organisms, but also because high nitrite concentrations will prevent the growth of nitrite-oxidizing bacteria (Udert and Wächter, 2012), leading to increased  $\text{N}_2\text{O}$  emissions (Faust et al., 2022). Nitrite-specific electrodes are being developed to prevent nitrite accumulation during urine nitrification (Britschgi et al., 2020). The production of hydroxyls through water electrolysis can also be used to neutralize the protons produced through nitrification and can thus increase the overall rate of ammonium transformation in nitrate, as reported by De Paepe et al. (2021). Ilgrande et al. (2019) showed that nitrifiers that travelled on the ISS for seven days retained their functionality upon return to Earth, suggesting that nitrification could have useful space applications.

Urine also contains high concentrations of sodium and chloride (Rose et al., 2015). Sodium and chloride are essential for humans but

toxic to many plants. If NaCl is not removed from the solutions entering C3, it might also decrease nitrification efficiency and, more specifically, the activity of nitrite-oxidizing bacteria such as *Nitrobacter winogradskyi*, leading to nitrite accumulation (Jeong et al., 2018) and increased  $\text{N}_2\text{O}$  emissions (Faust et al., 2022). Guo et al. (2021) observed that the addition of chloride led to a decrease in nitrification rates in soils. Janiak et al. (2021) observed a strong negative impact of increased salinity on nitrite-oxidizing bacteria, reducing the rate of nitrate production from urine. However, the dilution of urine with water to decrease salinity in their study was sufficient to rapidly restore high rates of nitrate production. Given the difficulties of removing NaCl from urine (see Section 5), partial nitrification/anammox (PN/A) could be implemented to produce  $\text{N}_2$  directly from urine (Lackner et al., 2014; Spiller et al., 2022; Timmer et al., 2022). The  $\text{N}_2$  produced could help replace the slow losses of pressurized gases, including  $\text{N}_2$ , that occur from the habitat into the low-pressure space on the surface of the habitat and to vacuum in outside space (Timmer et al., 2022; Wieland, 1994). However, implementing complete denitrification of nitrogen from urine would lead to a strong reduction of nitrogen forms available to plants and require that most plants grown in the MELiSSA loop be legumes associated with rhizobia, substantially reducing the crew's dietary diversity.

We suggest that phosphate, calcium, and magnesium should be precipitated from the urine produced by the crew and from other processed liquid organic waste leaving C2 before allowing the nitrogen-rich solution to enter the nitrifying compartment (Fig. 2), as previously proposed by De Paepe et al. (2020). As for the organic waste degradation compartments C1 and C2, we suggest creating a full elemental balance between the inputs and outputs to and from C3 and assessing the changes in nitrogen and phosphate forms during their transfer through C3. It will also be important to assess the amounts of nitrogen that should be denitrified as  $\text{N}_2$  and that needed to be recycled to plants. Finally, we suggest further assessing the impact of sodium and chloride on the biological processes taking place in C3.

## 5. Challenges to providing crops in compartment 4b with balanced nutrition based on nutrients recovered from other MELiSSA loop compartments

The preceding sections suggest that two streams of nutrients could be delivered within the MELiSSA loop to higher plants: one containing high concentrations of phosphate, calcium, and magnesium derived from the precipitates obtained from urine and effluent derived from the liquid organic waste degradation compartment (C2), and a nitrogen-rich solution derived from the nitrifying compartment (C3; see Fig. 2). As potassium does not produce insoluble precipitate with phosphate and has chemical properties similar to ammonium, potassium will probably end up in the solution going through the nitrifying compartment. If sodium and chloride are not removed, they will most probably also be transferred to the hydroponic system via the nitrifying compartment, but we see later in this section that options exist to remove sodium. Since the majority of sulfur is probably mostly bound to organic matter, the degradation of organic matter will likely lead to the release of sulfur as sulfate, which will also be transferred to the solution going through the nitrifying compartment. Finally, it is not yet possible to foresee in which of these two streams micronutrients will be present. It will therefore be necessary to measure all elements (including the toxic ones) in these two streams to test the above-mentioned hypotheses.

Using water derived from condensates collected in the habitat rather than water released by plants by transpiration, which is of high quality and should be reserved for the crew, it will be possible to mix the nitrogen-rich solution with the P/Ca/Mg-rich solution to produce a nutrient solution as similar as possible to the one used by Wheeler et al. (2003). Whereas that solution allowed those authors to grow a wide variety of crops, it did not consider the specific needs of each crop and could thus lead to nutrient imbalance or luxurious consumption; that is,

nutrient uptake beyond the level needed by the crop. Nutrient imbalances can have a powerful impact on plant growth and crop quality; for instance, an excess of ammonium can limit potassium uptake, an excess of chloride can limit nitrate and phosphate uptake, and too much calcium and potassium limit magnesium uptake (Bamsey et al., 2012; Geilfus, 2018; Marschner, 2012; Sambo et al., 2019). From an agronomic point of view, excessive nitrogen nutrition can lead to longer vegetative growth in cereal and thus a delay in the harvest, while a lack of potassium or an excess of nitrogen will decrease potato tuber production and tuber quality during storage. Furthermore, given the resource scarcity inherent in BLSS, it is necessary to target the highest possible nutrient use efficiency by crops (defined as the ratio between the amount of nutrient in exported plant part and the amount of nutrient added) and therefore to prevent the luxury consumption of nutrients to the greatest possible extent. Ideally, to reach a maximal nutrient use efficiency, it would be necessary to prepare stock solutions of different nutrients and mix them to deliver precise concentrations of nutrients to the hydroponic systems. However, this would require that nutrients present in these streams be separated from one another. In principle, this goal can be achieved using cation and anion exchange resins, but those will be difficult to use in the MELISSA context because such resins might be rapidly subjected to fouling (saturation of the resin with organic compounds) and lose their efficiency to exchange ions (Wiercik et al., 2020).

In any case, whether crops will be fed only with the two nutrient streams noted above or more precisely using different stock solutions, element concentrations and pH levels in the nutrient solution will have to be constantly monitored and possibly adjusted during plant growth (Son et al., 2016). The pH value of the nutrient solution in which a plant will be growing will need to be adjusted because in soilless systems optimal plant growth occurs at pH values between 5 and 7 (Bamsey et al., 2012), with higher values leading to a loss of nutrient solubility and lower values to element toxicities. The dominant form of nitrogen in a nutrient solution has a powerful impact on the development of its pH during plant growth. Nitrate-based plant nutrition leads to a pH increase in the solution, while ammonium-based nutrition results in solution acidification (Marschner, 2012). The ratio of nitrate to ammonium coming from the nitrifying compartment will therefore have to be fine-tuned so that the pH of the nutrient solution remains constant during plant growth. Another possibility to acidify or alkalize the nutrient solution would involve adding protons or hydroxyls to the solution using the water electrolysis process proposed by De Paepe et al. (2020). Optode sensors are used to measure soil solution pH in situ (Meller et al., 2020) and could be adapted to measure changes in pH in nutrient solutions. A simple measure of the electric conductivity of the solution will not detect nutrient imbalances in the solution because electric conductivity is a proxy for the total ion concentrations in a solution. Online ion-selective sensors are therefore needed to determine the concentrations of single ions (Bamsey et al., 2012; Richa et al., 2021; Son et al., 2016). Bamsey et al. (2012, 2014) developed bulk optodes able featuring low mass, volume, and cost to measure potassium and calcium activities in nutrient solutions. The current lifetimes of these optodes are 50 h for potassium and 30 h for calcium and should be extended to last much longer. Jakobsen et al. (2023b) were able to conduct nearly real-time monitoring of potassium, nitrate, and ammonium using ion-specific electrodes within an accuracy of 2 mg nutrient  $L^{-1}$  during one month of lettuce growth in a closed-loop system, while Jakobsen et al. (2023a) monitored and controlled nitrate concentration in a similar system for one month, with a low-drift, fast-response time electrode and an accuracy of 3%. Finally, Phillips et al. (2007) showed that cation-selective polymeric membrane electrodes could precisely measure sodium concentration in undiluted urine. Such sensors could also be used in nutrient solutions to measure changes in sodium concentration over time. Sensors able to precisely measure the concentration of each nutrient (including phosphate, sulfate, etc.) and toxic elements over the long run still have to be developed.

Nitrogen losses from soilless systems have rarely been measured (Daum and Schenk, 1996; Yang and Kim, 2020). However, they have been measured in the hydroponic compartment of aquaponic systems (i. e., systems combining fish and plant production). Hu et al. (2015) and Yang and Kim (2020) confirmed that ammonia losses were negligible at  $pH < 7$ . However, Zou et al. (2016) showed that around 30% of total N inputs could be lost at pH 6.0 by denitrification from their aquaponic system, with the vast majority being lost as  $N_2$ . As discussed in section four on nitrification,  $N_2$  production can help compensate for leaks of gases from the spacecraft, but this will also lead to a loss of available N for plants. Such  $N_2$  losses can be corrected by  $N_2$  fixation carried out by cyanobacteria (Langenfeld et al., 2021), even at low  $N_2/CO_2$  partial pressure (Verseux et al., 2021) in C4a, and by legumes when grown in the presence of rhizobia in C4b. Given the crucial role of  $N_2$  in the atmosphere of the spaceship and of available nitrogen for plant production, it will be necessary to include a full nitrogen mass balance, including the different compartments of the MELISSA loop, as proposed by Loader et al. (1997). This will enable determining whether  $N_2$ -symbiotic fixation by plants and cyanobacteria should or should not be fostered.

Growing crops in the long term in closed systems will result in the accumulation of toxic compounds in the nutrient solution of C4b. As urine and feces are rich in sodium and chloride, these elements will accumulate in the nutrient solution of C4b over time, causing toxicity symptoms and eventually yield decrease (Kingsbury and Epstein, 1986; Slabu et al., 2009) and ultimately leading to the need to renew the solution (Carmassi et al., 2005). Ideally, sodium and chloride should be removed from the urine of the crew after its excretion (Fig. 2). Aponte and Colón (2001) proposed a six-compartment system to remove sodium with electrodialysis. This system can remove 98% of sodium from urine, but it also removes other ions such as potassium, phosphate, and ammonium and therefore would not be suitable for the MELISSA loop, where those nutrients are required for plant growth. Wang and Wei (2020) proposed using nanofiltration to recycle monovalent mineral salts from urine. Although they were successful in removing sodium and chloride from urine, they also removed a significant amount of potassium, which is essential for plant growth. Recently, building on the work by De Paepe et al. (2020), Demey et al. (2022) developed a method including alkalization, electrodialysis, and ion exchange to remove Na from urine. This approach achieved 98% sodium removal while maintaining other nutrients in fluxes that can be recycled to the plant. However, whether this method is able to sufficiently decrease the chloride concentration in the solution is not yet known, and the authors do not explain how they would deal with the problem of resin fouling. Nevertheless, their method sounds promising and should be further developed, such as for removing sodium and chloride from the effluent coming out of the liquid organic waste degradation compartment (C2). If after having removed sodium and chloride from this effluent and urine, some was left, it should be possible to implement specific crop management options to mitigate the impact of the remaining sodium and chloride on plant growth. One option, as proposed by Bañuelos and Lin (2006), would be to grow crops in a sequential manner, with beans first, as the most salt-sensitive crop; as NaCl accumulates, crops that are more and more tolerant could be grown, such as soybean, onion, potato, and rice, followed by spinach, tomato, wheat, and beet (Galvani, 2007) and finally *Salicornia* sp. (Ushakova et al., 2008). Salt-tolerant cultivars of these crops should of course be systematically preferred to salt-sensitive ones. It should be possible to further increase the salinity tolerance of these crops by inoculating halotolerant bacteria to the nutrient solution, which could limit sodium uptake by crops due to the sodium sorption capacity of the biofilm they produce (Haque et al., 2022).

Growing crops in hydroponics over the long term can also lead to the release of toxic organic substances such as phenols by roots. These need to be eliminated either by activated carbon or by microorganisms (Hosseinzadeh et al., 2017; Lee et al., 2006). Finally, other organic compounds that we do not yet know might also be produced in the

various compartments of the MELiSSA loop and have a toxic effect on plants. Plant pathogens and other pests can also accumulate in hydroponic systems (Nelson, 1987; Schuerger, 2021; Stanghellini and Rasmussen, 1994). This issue can be resolved by disinfecting the nutrient solution with UV, as described in Xie et al. (2017), and the seeds with bleach and HCl or with ethanol, as described by Massa et al. (2017); however, this would kill both the pathogens and beneficial organisms (Son et al., 2016). Another option is to inoculate beneficial organisms in the nutrient solution (Sheridan et al., 2017). Their establishment will avoid the development of pathogens by occupying their ecological niche (Vallance et al., 2011) and might have positive impacts on plant growth and quality (Lee and Lee, 2015; Sambo et al., 2019). Beyond the issue of plant pathogens, human pathogens might also accumulate in different compartments of the MELiSSA loop (Douglas et al., 2020), requiring sterilization using, for example, UV radiation of nutrient-rich solutions coming into the hydroponic system.

Finally, methods will have to be developed for recycling the nutrient solution when it becomes unsuitable for plant growth. The approach reported by Demey et al. (2022) might be an option to remove Na, P, Ca, and Mg, while a MEC coupled with chemical oxidation in C2 could be used to mineralize organic matter (Fig. 2). But once no further use of the spent solution is possible, water will have to be evaporated and recuperated while the solids will have to be deposited, perhaps as construction materials as proposed in the Water Wall Life support system (Gormly et al., 2012; Guo et al., 2017).

## 6. Concluding remarks

In the conclusions of the review paper by Clauwaert et al. (2017) on nitrogen cycling in BLSS, the authors state that most of the work done by the time of their study had focused on carbon, oxygen, and water, with very little work carried out on other nutrients. A substantial amount of effort relevant to BLSS has been since then dedicated to nitrogen and phosphate, and work has also started on potassium, calcium, and magnesium, but many nutrients (such as sulfur) remain to be studied.

Whereas substantial efforts have been made on recovering nutrients (mainly nitrogen and phosphate) from human urine, much work remains to be done to recover the elements present in other liquid and solid organic waste. It is essential to continue research into removing sodium and chloride from urine and other organic waste to prevent the spread of these elements to the rest of the MELiSSA loop. A full nitrogen balance at habitat level will have to be achieved: on one hand, sufficient N<sub>2</sub> will be needed to keep atmospheric pressure at a proper level and on the other, enough mineral nitrogen will have to be provided to the plants for biomass production. Overall, we suggest adapting the current schema of the MELiSSA loop shown in Fig. 1 by adding a module that enables removing sodium, chloride, phosphate, calcium, and magnesium from urine and from the effluent derived from C2 and integrating the two streams of elements going to the hydroponic system to produce the nutrient solution (Fig. 2). Even though the dosing of nutrients derived from these two streams (P, Ca, and Mg on one side and N and likely other elements to be measured on the other) should allow for a broad range of crops to be grown, it will not be possible to design nutrient solutions adapted to each crop. We will need to assess the nutrient use efficiency for these crops and study how it can be increased. We will also have to consider the type of water to be used to produce the nutrient solution and the recycling of the nutrient solution; finally, some substances will have to be definitively removed from the loop at some point in time.

The use of nutrients derived from waste by plants will have to be assessed not only under classical terrestrial conditions but also under sealed conditions, as in the Plant Characterization Unit (Pannico et al., 2022), and under simulated microgravity (e.g., with clinostats as in Liu et al., 2018) before being studied in the Advanced Plant Habitat, hardware that has recently been validated on the ISS (Monje et al., 2020). It will be important to consider model substrates for these experiments

such as synthetic feces, as proposed by Penn et al. (2018), and fresh synthetic urine, as proposed by Sarigul et al. (2019), to obtain results relevant to recycling nutrients from waste.

This information will have to be integrated within the overall MELiSSA plant model (Ciurans et al., 2022; Poulet et al., 2020) to assess how plants will react when growing under suboptimal conditions and how CO<sub>2</sub> capture and O<sub>2</sub>, water, and food production will be affected. Beyond that, the plant model will need to be integrated into the full MELiSSA loop model (Poughon et al., 2009) to assess how the different processes can be synchronized with one another and how the biomass of a sub-optimally grown plant will feedback on the functioning of C1, C2, and C3, on the composition of the newly produced nutrient solution, and on the performance of the subsequent crops.

## Declaration of Competing Interest

None.

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