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Urine-derived solids as nutrient sources to enhance microbial wood degradation in a composting environment☆

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ABSTRACT

Human urine and woody biomass are two abundant biological resources that can be co-valorized through biological wood oxidation (BWO), a meso-thermophilic composting process that generates low-temperature heat and nutrient-rich soil amendment. Here, we investigated the potential of three urine-derived solid formulations as nutrient supplements to enhance microbial wood degradation at 40 °C: phosphoric acid-dehydrated urine (PDU), oxalic acid-dehydrated urine (ODU), and struvite. Among these, PDU achieved the highest wood dry mass loss (27.5 % after 42 days) and oxygen consumption, with its effectiveness attributed to greater phosphorus availability, biochemically stabilized urea that gradually hydrolyzed in situ, and a sustained mildly acidic pH, conditions which collectively supported fungal colonization and carbohydrate degradation in wood. In contrast, struvite exhibited low solubility, high alkalinity, and an unfavorable N/P ratio (0.4) that limited nutrient availability and suppressed microbial activity, resulting in minor wood degradation. Complementary experiments with synthetic nutrient solutions showed that N supplied as urea was more effective than its hydrolyzed products (ammonium bicarbonate and ammonium hydroxide) and ammonium sulfate, likely because it released ammonium gradually and buffered pH shifts during composting. These findings highlight the potential of integrating acid urine dehydration with BWO as a means to advance nutrient circularity and energy sustainability.

1. Introduction

The collection and valorization of forestry harvesting residues plays a significant role in reducing wildfire and insect outbreak risks while supporting the development of renewable technologies and bioeconomy [1]. Wood, the primary component of forestry residues, presents a habitat for diverse microorganisms [2] and a crucial raw material for continuously operating biorefineries [3]. Aerobic and meso-thermophilic (20–50 °C) microbial wood decomposition has been harnessed to sustainably convert low-value wood residues into bioenergy [4], biochar [5], and functional materials [6]. Specifically, compost heat recovery system (CHRS) has emerged as a promising approach to valorize low-value wood residue and a sustainable alternative to combustion for prolonged, low-temperature heat generation [7]. An application example of this approach is biological wood oxidation (BWO), a composting process operating at 40 °C that uses wood as the sole solid substrate [8]. Despite its considerable biotechnological potential, microbial wood degradation is inherently constrained by the limited availability of nutrients in wood, which hinders the growth and activity of microbial agents [2,9]. Therefore, nutrient supplementation has been a central factor in optimizing the efficiency of BWO.

Human urine is rich in essential nutrients needed for microbial life, e.g., nitrogen (N), phosphorus (P), and potassium. Previous studies have shown that the addition of untreated human urine can lead to 19.1–31.4 % dry mass (DM) loss of wood during BWO over a period of 42–46 days [8,10]. This suggests that recycling urine-derived nutrients in BWO or similar wood-dominated CHRSs could provide a decentralized solution for wood residue valorization, low-temperature heat generation, and

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source-separated sanitation and nutrient recovery [10]. However, in practice, the direct use of untreated urine in CHRSs faces several potential challenges. First, during the urine collection, storage, and transportation processes, untreated urine is often subjected to microbial contamination and enzymatic urea hydrolysis, resulting in nutrient losses, ammonia volatilization, and odor issues that reduce system acceptability [11]. Additionally, urea hydrolysis can lead to pH increases and trigger unwanted P precipitation within the urine collection and distribution systems, causing P loss and potential pipe clogging [11]. Furthermore, the high water content of untreated urine (>95 %) presents not only logistic difficulties but also the risk of introducing excess moisture into CHRSs, leading to oxygen transfer limitation and slowed wood degradation [12]. These challenges highlight the need for pretreatment to stabilize and concentrate the nutrients in urine before introducing them into large-scale CHRSs.

To date, various technologies have been developed to concentrate urine-derived nutrients in both liquid and solid forms [13]. Compared to liquid urine concentrates, solid urine-derived products demonstrate a further reduced volume and increased nutrient concentrations [14], offering practical benefits to be used in CHRSs. These potential benefits include (i) enhanced nutrient stability during transportation and storage [15,16], (ii) simplified logistical operations due to significantly reduced volumes [17], (iii) lower risk of precipitation in pipelines as the solids can be mixed directly with the composting substrate, and (iv) increased flexibility in terms of application timing and dosage [18].

To concentrate urine into solids, struvite precipitation and urine dehydration are two approaches advancing on the technology readiness level scale and approaching industrialization [14]. Struvite precipitation, as an extractive treatment, selectively recovers N and P from hydrolyzed urine into magnesium ammonium phosphate ($MgNH_4PO_4{\cdot}6H_2O$), which is a crystalline and slow-releasing mineral. This approach is commonly used worldwide to recover P from urine, although the recovery of N and other nutrients is relatively limited [14]. The second approach, acid/alkaline dehydration, involves N stabilization through the addition of acid or alkaline sources, followed by low-temperature evaporation (below 60 °C) [15,19]. In contrast to struvite precipitation, urine dehydration is considered a conservative treatment, as it retains N primarily in the form of urea and preserves most urinary nutrients in the final products [20]. The characteristics of urine-dehydrated products depend on the type and dosage of chemicals used. For instance, compared to alkaline dehydration, acid dehydration requires a lower chemical dose and can prevent calcite formation, yielding products with higher N content and nutrient recovery rates [19]. Another example is that phosphoric acid-based dehydration can generate products with higher P contents than those produced using P-free acids [19].

Urine-derived solids, specifically struvite, have been studied as fertilizers for plants [21] and pH conditioners to improve manure [22] and food waste composting [23]. To the best of our knowledge, their use as the primary nutrient source (particularly, N and P) in lignocellulose-rich composting has not been systematically investigated. We hypothesize that the effect of urine-derived solids on microbial wood degradation during composting is primarily associated with two aspects. The first is their nutritional characteristics, involving the type, form, stoichiometry, solubility, and availability of nutrients crucial for the growth and functioning of microbial wood degraders. These nutritional characteristics can play an important role in regulating the growth, enzyme activity [24], lignocellulose degradation [9], and community composition [25] of microbial wood degraders. The second aspect concerns the fate of urine-derived solids during composting, including but not limited to their supplementation, in situ transformation, and long-term accumulation. These processes can influence both nutrient availability and environmental pH, thereby modulating the composting chemistry as well as microbial enzyme activities [26] and community dymanics [27].

Accordingly, the present study explores the potential of urine-derived solids as nutrient sources for enhancing microbial wood degradation in the BWO environment. Using untreated urine as a control, we investigated three solid products derived from source-separated human urine: phosphoric acid dehydrated urine (PDU), oxalic acid dehydrated urine (ODU), and struvite. BWO performance was evaluated based on oxygen consumption, dry mass loss of wood, lignocellulose degradation, N and P consumption, environmental pH, and development of visible biomass. By identifying promising urine-derived solids to improve BWO, this study contributes to the sustainable valorization of human urine and wood residues for energy and nutrient recovery.

2. Materials and methods

2.1. Wood material

Wood chips of silver birch (*Betula pendula*) were purchased from a local supplier in The Netherlands, ground by a knife mill (SM 2000, Netzsch, Germany), and sieved into particles (mesh size between 1 and 2 mm) with an average length of 5.2 mm and cross-sectional diameters of 0.8–1.0 mm (characterized microscopically by Eclipse 400, Nikon, Tokyo, Japan). All wood particles were oven-dried at 105 °C for 3 days and stored at −20 °C until use.

2.2. Inoculum

BWO microorganisms sampled from a garden waste compost pile were cultivated on fresh wood chips at 40 °C for over six months, with passive aeration and regular supply of nutrient solution (composition specified in Table S1). The liquid inoculum was prepared following the procedure outlined in a previous study [8].

2.3. Nutrient sources and nutrient supplementation

Freshly excreted urine was collected from about 20 volunteers (aged 20–65 years old, male and female) using sterile 500 mL polypropylene flasks. These donations were pooled and thoroughly mixed. Of the collected urine, 1 L was preserved in sealed containers and stored at −20 °C (marked as UU, untreated urine), while 3 L underwent acid urine dehydration at 50 °C with the addition of either phosphoric acid (3 g/L) or oxalic acid (5 g/L) [19]. The mass concentration factor (CF, the ratio of the initial mass to the final mass of urine after dehydration) was around 46.8 for phosphoric acid dehydrated urine (PDU) and 50.2 for oxalic acid dehydrated urine (ODU). Struvite sample was obtained from a pilot-scale struvite reactor treating source-separated hydrolyzed HU in Leeuwarden, The Netherlands, with its characteristics specified by Zamora et al. (Harvest No. 7) [28]. Characteristics of the four urine-derived nutrient sources were detailed in Table S2.

Using UU as a control, the first experiment (Experiment 1) investigated and compared the effectiveness of PDU, ODU, and struvite as BWO nutrient sources. PDU and ODU, being highly soluble in water, were first rehydrated with demineralized water to a CF of 1, then introduced into BWO reactors in liquid form. This approach minimized nutrient variation between replicates and ensured more uniform nutrient distribution among the wood particles. Struvite, which has low water solubility, was ground into powder and added directly to the reactors as solids. To maintain consistent moisture levels across all treatments, an equivalent amount of demineralized water as in the other treatments was added to struvite-supplied BWO reactors. After nutrient supplementation, the substrate matrix was mixed manually with a metal spatula.

The second experiment (Experiment 2) evaluated the impact of N forms on the performance of BWO, as the N forms differed among the tested urine-derived solids and may have contributed to the differences observed in Experiment 1. To this end, three nutrient solutions were prepared, namely artificial unhydrolyzed urine (AUU), artificial hydrolyzed urine (AHU), and bicarbonate-controlled AHU (AHU_B−, replacing NH_4HCO_3 with N-equivalent amount of $(NH_4)_2SO_4$). The composition of three solutions was designed based on Landry et al. [29] with additional supply of trace elements (Table S3).

2.4. Experimental design

Lab-scale BWO, schematically shown in Fig. S1, was performed in air-tight glass bottles (650 mL, Schott, Germany) and incubated at 40 °C in a temperature-controlled incubator (Elbanton, The Netherlands) for 42 days. The experimental duration was set based on prior studies indicating that wood degradation in BWO typically proceeds most efficiently within this time frame [8]. Each reactor contained 5 ± 0.01 g of wood particles and received specified amounts of inoculant, nutrients, and demineralized water, as detailed in Table S4. Since N is one of the most crucial nutrients for wood-degrading microorganisms [30], the addition rates of different nutrient sources were normalized to achieve a consistent N addition rate (0.1 % on the dry matter basis of the wood), as established in previous studies [9,10]. The availability of specific nutrients and the initial pH in each BWO treatment are characterized in Table 1.

The initially dosed N can be depleted within 7–14 days of BWO [10]. Consequently, periodic nutrient supplementation was initiated on days 14 and 28. On these days, one replicate of each treatment was terminated for analyses of DM loss and residual N, P, and pH value, while the remaining replicates received a dosage of nutrient and continued their BWO. Statistical analysis was performed using data from the three replicates that remained at the end of the experiment.

2.5. Measurement of oxygen concentration

The oxygen concentration ($[O_2]$) inside the reactor was measured daily by Fibox 4 trace and Sensor Spot SP-PSt 3 (PreSens, Germany) and used for calculating the cumulative oxygen consumption (COC, in mol/kg DM) and oxygen consumption rate (OCR, in mol/kg DM/d). The procedure of $[O_2]$ measurement and air refreshing were described in previous work [10].

2.6. Characterization of N, P, pH, and biofilm of BWO residue

Analyses of soluble N, soluble P, and pH of BWO residues were conducted with their water extracts, following procedures described in previous study [10]. The pH value was measured using a standard pH meter (PHM210, Radiometer, France). The extracts, after the syringe filtration (0.45 μm pore size), were analyzed spectrophotometrically for total N (TN), N fractions (NH_4^+-N, NO_3^--N, and NO_2^--N), and orthophosphate (PO_4-P), using LATON cuvette tests (Hach, USA). Biofilms detached from wood particles were characterized microscopically under Nikon Eclipse 400 equipped with a CCD camera (Nikon, Tokyo, Japan). The total consumption efficiency of N and P is defined as the ratio of the amount consumed to the amount dosed over the entire experimental period (Eq. 1):

$$\textit{Consumption efficiency}\ (\%) = \frac{\textit{amount dosed} - \textit{residual amount on day 42}}{\textit{amount dosed}} \times 100 \quad (1)$$

2.7. Determination of dry mass loss and lignocellulosic compositions

The solid BWO residue was placed in an aluminum container and dried at 105 °C until a constant weight was achieved. DM loss was calculated from the initial and final weights (Eq. 2):

$$\textit{DM loss}\ (\%) = \frac{\textit{initial dry weight} - \textit{final dry weight}}{\textit{initial dry weight}} \times 100 \quad (2)$$

Table 1
The availability of specific nutrients (per single nutrient supplementation) and the initial pH in BWO treatment receiving UU (unconcentrated urine), PDU (phosphoric acid dehydrated urine), ODU (oxalic acid dehydrated urine), struvite, AUU (artificial unhydrolyzed urine), AHU (artificial hydrolyzed urine), and AHU_B− (artificial hydrolyzed urine without bicarbonate), respectively.

Item (mg/g DM wood per single dosage, otherwise specified)	Experiment 1 - BWO treated with					Experiment 2 - BWO treated with		
	UU	PDU	ODU	Struvite-T[a]	Struvite-I[b]	AUU	AHU	AHU_B−
COD	1.10	1.20	1.20	\	0.22	0.07	0.06	0.07
COD (mol/kg DM wood)	0.03	0.04	0.04	\	0.00	0.00	0.00	0.00
TN	1.00	1.00	1.00	1.00	0.01	0.95	0.95	0.99
NH_4^+-N	0.06	0.06	0.05	1.00	0.01	0.08	0.89	0.90
NO_3^--N	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PO_4-P	0.05	0.29	0.05	2.55	0.03	0.09	0.09	0.09
Ca	0.02	0.02	0.02	0.01	0.01	0.02	0.02	0.02
K	0.36	0.43	0.42	0.02	0.00	0.22	0.22	0.22
Mg	0.01	0.01	0.01	1.80	0.02	0.01	0.01	0.01
Na	0.33	0.39	0.38	0.00	0.02	0.31	0.31	0.31
P	0.05	0.33	0.06	2.55	0.03	0.09	0.09	0.09
N/P ratio	18.5	3.4	19.3	0.4	0.4	10.4	10.5	11.0
Initial pH[c]	5.6	4.0	4.2	\	7.9	5.1	7.7	7.9

[a] Total nutrient availability, calculated from the elemental composition of struvite sample used in this study (Table S1), assuming TN presents solely as NH_4^+-N and total P as PO_4-P.

[b] Initial nutrient availability, e.g. the amount of soluble struvite fractions at the start of the experiment. Values were analyzed with the syringe filtered (0.45 μm pore size) struvite suspension, which has a solid-to-liquid ratio of 0.1 g (the initial struvite dosage per BWO reactor) in 11.3 mL of demineralized water (the initial total moisture content in the reactor).

[c] Measured after the initial nutrient supplementation as described in Section 2.6.

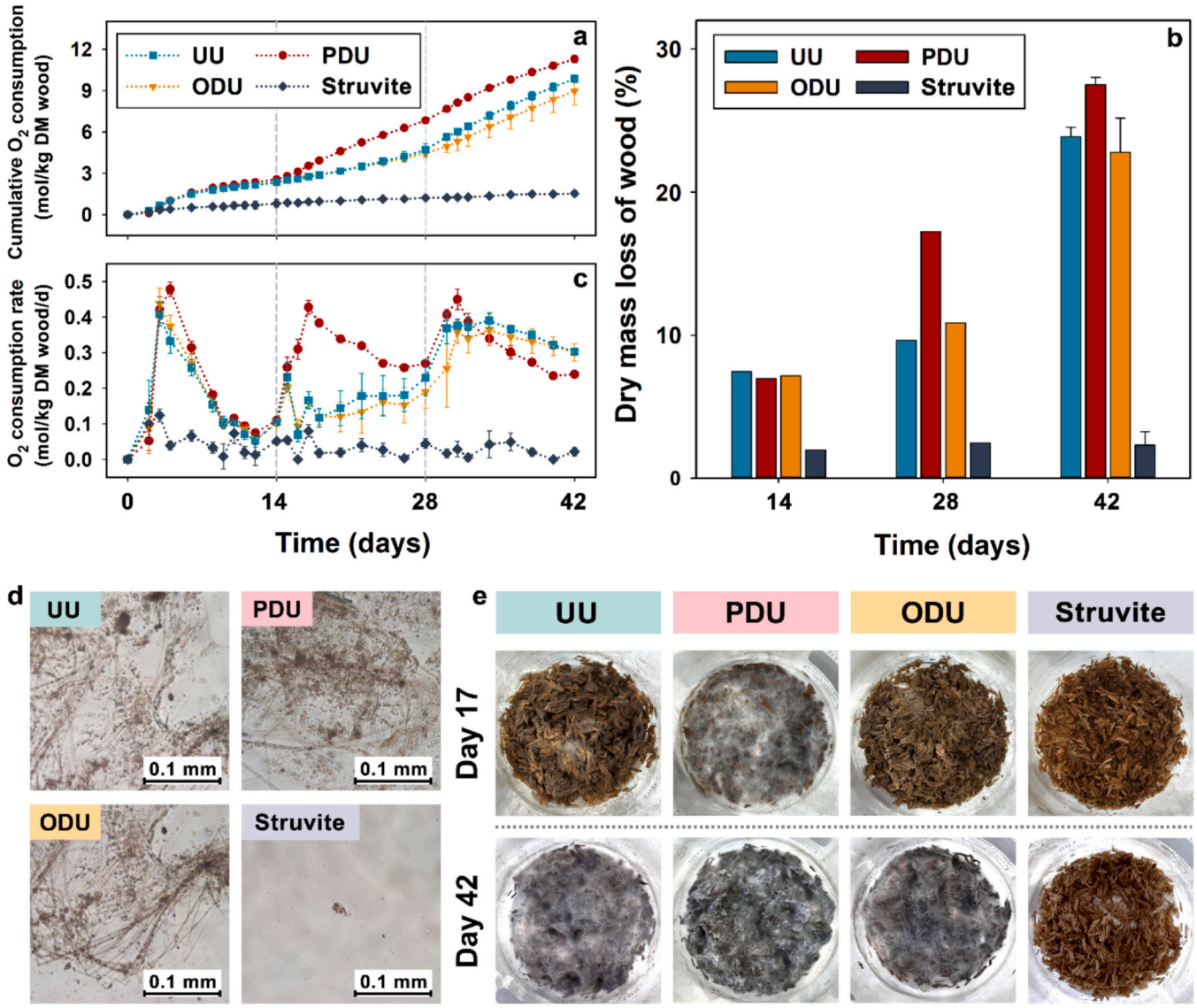

Fig. 1. Performance of biological wood oxidation (BWO) supplied with urine and urine-derived nutrient sources: untreated urine (UU), phosphoric acid dehydrated urine (PDU), oxalic acid dehydrated urine (ODU), and struvite. Indicators: (a) cumulative oxygen consumption, (b) dry mass loss of wood, (c) oxygen consumption rates, (d) microscopic images of biofilm growing on the substrate, and (e) visible biomass within the BWO reactors. The grey dashed lines in Fig. 1a and c mark the dates of periodic nutrient supplementation. The DM losses of BWO-struvite may be slightly underestimated due to the possible presence of undissolved struvite minerals in the system.

Afterwards, the materials were ball milled and subjected to routine analysis of polysaccharide composition and lignin fractions at an accredited laboratory (Eurofins Food Testing Netherlands B.V., Heerenveen, The Netherlands). The sample preparation and analytical procedures were detailed in SI.

2.8. Statistical analysis

Statistical analysis was conducted using standard descriptive procedures and SigmaPlot 14.0 (Systat Inc., United States). For each treatment, standard deviations of oxygen consumption were calculated based on a minimum of three replicates throughout the experiment, while statistical analyses of wood dry matter (DM) losses and residual total N, P, and pH were conducted only for samples collected on day 42 ($n = 3$). One-way ANOVA followed by a Tukey's HSD Post hoc test was performed to assess statistical differences ($p \leq 0.05$).

3. Results and discussion

3.1. Acid dehydrated urine outperformed struvite in enhancing microbial wood degradation during BWO

The first experiment (Experiment 1) compared the effectiveness of PDU, ODU, and struvite as BWO nutrient source to that of UU. By day 42, BWO-PDU demonstrated the highest COC (Fig. 1a) and DM loss of wood (27.5 %, Fig. 1b), followed by UU and ODU treatments, which did not differ significantly ($p > 0.05$). PDU also led to the highest removal rates of glucose (representing cellulose), xylose (major component of birch hemicellulose), and total polysaccharides during BWO (Table S5 & S6). Struvite was the least effective nutrient source and resulted in a minimal DM loss of approximately 3% after 42 days. These results indicate that, under the tested conditions, acid dehydrated urine can promote BWO as effectively as untreated urine, while struvite cannot. Moreover, the phosphoric acid present in PDU appeared to stimulate microbial oxygen consumption, particularly during days 14 and 28 as indicated by OCRs

(Fig. 1c), and promotes the degradation of polysaccharides in wood.

BWO is considered a fungi-dominated process [31], since fungi are widely recognized as the most biochemically active degraders in mixed-culture microbial wood degradation, due to their potent extracellular enzymatic systems and their ability to penetrate within wood with extensive hyphal structures [32]. In this study, a predominant growth of filamentous fungi was observed in UU, PDU, and ODU treatments, but not in BWO-struvite (Fig. 1d and e). Therefore, the substantially lower performance of BWO-struvite compared to the other three treatments may be attributed to its limited development of fungi. The growth, degradation activity, and dominance of BWO microorganisms are likely influenced by both local nutrient conditions and environmental pH. These two factors are examined and discussed in Sections 3.1.1 and 3.1.2, respectively.

3.1.1. *Effect of local nutrient conditions*

N and P, as key macronutrients affecting the growth and cellular metabolism of wood-decaying microbes [9], exhibited different dissolution and consumption dynamics across the four treatments. In UU, PDU, and ODU treatments, these nutrients were readily available in the liquid phase and were clearly consumed within each nutrient-dosing interval (Fig. 2a and b). In contrast, in BWO-struvite, only about 1 % of the initially dosed N and P were readily water soluble (Table 1), and the concentrations of soluble N and P gradually increased over time following each subsequent struvite dosage. This slow release of N and P from struvite might delay the fulfillment of immediate nutrient requirements of BWOmicrobes during their intial growth phase, potentially slowing down their development and metabolic activities.

When the experiment concluded, UU, PDU, and ODU treatments achieved a comparable and efficient total N consumption (over 99.8 % efficiency, Table S7). Notably, the absolute total P consumption was significantly higher in BWO-PDU (0.65 mg/g dry matter wood) compared to those treated with UU and ODU (0.13 and 0.12 mg/g dry matter wood, respectively). In BWO-struvite, noticeable N and P consumption was observed between days 28 and 42, but precise estimation of intermittent nutrient consumption was not possible due to unclear dissolution kinetics of struvite. Nonetheless, BWO-struvite clearly demonstrated the lowest overall N consumption efficiency among all treatments, with at least 29.2 % of the dosed N remaining in the liquid phase and unutilized by day 60. Among the four nutrient sources, two major differences in N and P stand out: the forms of N and the total availability of P. We herein discuss the role of P and its potential effects on BWO in this section, as the impact of N forms is addressed in Section 3.2.

As a critical macronutrient, P plays an indispensable role in cellular processes including energy transfer, nucleic acid synthesis, cell membrane formation, and protein (enzyme) regulation [33]. However, P availability can exert dual effects on microbial wood degradation. In forest ecosystems, low to moderate P additions have been shown to improve the growth, respiration, enzyme production, and wood decomposition of both fungi [34,35] and bacteria [36]. Long-term (>2 months) P fertilization also increased cellulase, β-glucosidase, and xylanase activities in wheat soil, which are key enzymes involved in the degradation of lignocellulosic carbohydrates [37]. As such, we speculate that P availability in the UU and ODU treatments was likely suboptimal for microbial growth and lignocellulose metabolism, whereas elevated P concentrations in the PDU treatment promoted these, leading to increased degradation efficiency of wood (particularly, polysaccharides). Bacterial community structures in UU and PDU treatments, as discussed in SI (Fig. S2), could lend some support for this hypothesis. In contrast, high concentrations of dissolved phosphates can exert antimicrobial effects, particularly against gram-positive bacteria and certain fungi, by mechanisms such as chelation of essential metal ions and pH alteration [38]. Therefore, in BWO-struvite, phosphate availability may have been excessive, potentially creating unfavorable pH conditions and nutrient imbalances that inhibited BWO microbial activity.

Besides the individual effect of P availability, nutrient stoichiometry is another critical factor influencing the physiology of microorganisms. This subject has been extensively studied in soil systems, where the average global N/P ratio of microbial biomass is estimated to be approximately 6–7:1 [39]. Moreover, the N/P supply ratio has been

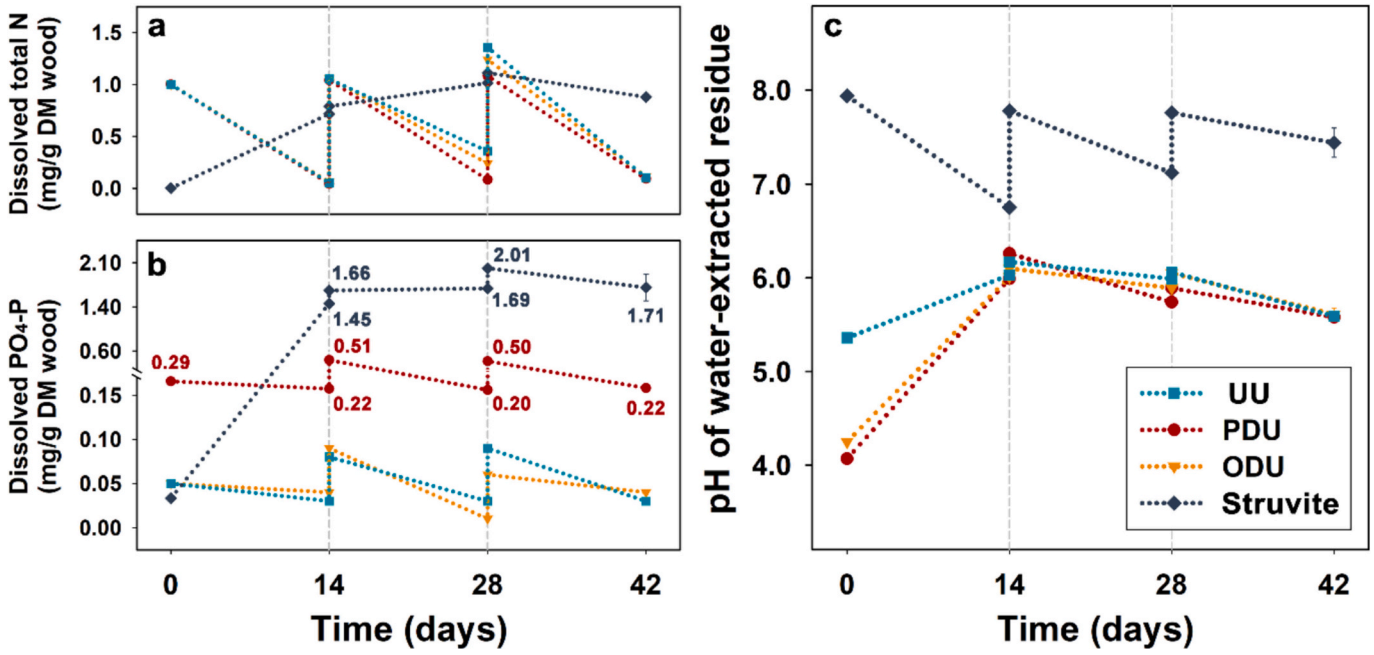

Fig. 2. Process dynamics of biological wood oxidation (BWO) supplemented with four nutrient sources: untreated human urine (UU), urine concentrated by phosphoric acid dehydration (PDU), urine concentrated by oxalic acid dehydration (ODU), and struvite (magnesium ammonium phosphate). Measurements include: (a) dissolved total nitrogen (TN) content in the substrate, (b) dissolved phosphate content (PO4-P) in the substrate, and (c) environmental pH of the substrates. The inherent pH of the wood materials used in this study, measured with water extracts as described in Section 2.6, was approximately 4.7. This caused the initial environmental pH in BWO (values on day 0 in Fig. 2c) to deviate from the intrinsic pH values of the nutrient sources listed in Table S2.

identified as a key factor regulating the relative dominance of fungi and bacteria during mixed-culture lignocellulose degradation: lower N/P ratios (below 5.0) tend to favor bacterial dominance, while higher ratios (15–45) are associated with fungal dominance [40]. If similar dynamics apply to the microbial communities in BWO, the markedly low N/P ratio observed in BWO-struvite (as low as 0.3) may represent a severe nutrient imbalance for fungi, whose contribution is likely crucial to overall wood degradation performance. Taken together, the effect of P on BWO appears to be both concentration- and matrix-dependent. To optimize P condition for improving BWO, further research on BWO could explore (i) concentration thresholds at which P benefits or inhibits wood degradation, (ii) the interactions and combined effects of P addition with other environmental factors (e.g., N level and pH) on the system's performance, and (iii) the response of BWO microbial community (especially, fungi) to these conditions, outcome of which would advise on how to optimal design and control periodic nutrient dose.

Another observation from Fig. 2 is that microbial nutrient consumption differed across different stages of growth and wood degradation during BWO. In the initial phase (typically spanning 7 to 10 days), microbes are expected to target easily accessible, labile wood components (e.g., damaged polysaccharide contents and simple phenolics), resulting in the first OCR peak (day 2, Fig. 1c). The development of microbial biomass is often limited at this stage, possibly due to microbes prioritizing metabolic adaptation over extensive replication [41]. As shown in Fig. 2a, during days 0–14, N consumption in UU, PDU, and ODU treatments were much higher (exceeding 0.94 mg/g DM wood) than those of P consumption (below 0.07 mg/g DM wood), suggesting that N may play a relatively more critical role than P in promoting early-stage microbial growth. This is supported by the general observation that protein and RNA contents in biomass often peak during the initial growth phase of fungi and bacteria [42], as these nitrogenous molecules are essential for enzyme synthesis and metabolic adaptation [41].

Following the depletion of labile carbon sources, microbes likely shifted to degrading structural lignocellulose. Fungi, as potent lignocellulose degraders, can progressively develop a hyphal network around and within wood to access and attack these recalcitrant carbon sources [43]. At this stage, microbial (especially fungal) demand for P may exceed that of earlier phases, due to the critical functions of P in powering energy transfer (via ATP synthesis), supporting rapid cell division (through nucleic acids synthesis), and building cellular structures (particularly, phospholipids in cell membranes) [44]. This hypothesis is supported by two observations: (i) P consumption in UU, PDU, and ODU treatments significantly increased during days 14–28 compared to days 0–14, and (ii) BWO-PDU, which had higher P availability and consumption than UU and ODU treatments, also demonstrated more advanced and extensive fungal biomass development (day 17, Fig. 1e) and significantly higher peak OCR values from days 14 to 28. From days 28 to 42, OCRs in UU and ODU increased to levels comparable to those in PDU, along with substantial biomass development observed (day 42, Fig. 1e). Possibly, the nutrient dosage on day 28 had addressed the nutrient (especially, P) limitation facing by UU and ODU treatments, thereby enhancing their biomass synthesis and wood-degrading efficiency. The above results suggest that P availability may be particularly crucial for BWO after the initial growth phase, when the substrate transition (from easy to recalcitrant carbon) and exponential microbial growth (characterized by rapid, extensive mycelia formation) are occurring. Increasing P availability in appropriate amounts during these phases may shorten microbial adaptation time and promote biomass synthesis, thereby improving the overall wood degradation performance.

Besides N and P, urine also contains many other nutrients that are important for microbial wood degradation, such as metal elements (e.g., sulfur, iron, manganese, and copper) functioning as protein constituents and enzyme cofactors [10,45], as well as degradable organic carbon and vitamin to stimulate microbial growth. Although these components were not directly measured in this study, they were likely less available in BWO-struvite compared to in other BWO treatments, as struvite production is typically optimized for selective precipitation of NH_4^+, PO_4^{3-}, and Mg^{2+}, with limited recovery of trace metal elements [46]. Therefore, the potential deficiency of certain nutrients in BWO-struvite could also have contributed to its lower BWO performance, as micro- and trace elements was found to be crucial for effective BWO [10].

3.1.2. Effect of environmental pH

The environmental pH critically affects the microbial growth, enzymatic functions, and community compositions in decaying wood [27]. In UU, PDU, and ODU treatments (Fig. 2c), the environmental pH was initially acidic (below 5.4) and rose to approximately 6.0 by day 14. This pH increase was likely due to in situ urea hydrolysis as indicated by Table S7. Subsequently, the pH levels in all three treatments gradually decreased, fluctuating within a slightly acidic range of 5.6–6.3. Probably, as wood degradation progressed, the alkalizing effect of buffering anions (e.g., bicarbonate and phosphate) was outweighed by the release of acidic compounds from decomposing wood (e.g., phenolics and organic acids) [47] and from microbial metabolism (e.g., nitrification and oxalate production) [48]. Overall, the slightly acidic environmental pH in UU, PDU and ODU treatments (4.0–6.3) aligned closely with the optimal pH range reported for many wood-decaying fungi [49], which may have favored wood degradation in BWO. Such acidity could also suppress ammonia volatilization and associated nitrogen loss that typically occurs under alkaline conditions [50].

The addition of struvite, in contrast, resulted in significantly higher initial (7.9) and operational pH levels (6.8–7.9) in BWO. In this treatment, the pH decrease during each nutrient-dosing interval was also observed; however, these decreases were insufficient to counterbalance the pH increases that followed each struvite dosage. The dissolution of struvite during BWO may be driven by three major processes: (i) increase in total struvite dosage over time, (ii) pH decrease caused by the acidity of wood, and (iii) pH decrease due to microbial activities. An abiotic dissolution test of struvite was conducted (BWO-struvite-A) to assess the relative contribution of these factors (Table S8). The comparison between BWO-struvite and BWO-struvite-A confirmed that nutrient release from struvite increased with its dosage and was affected by microbial factors. In early-stage BWO (e.g., the first 3–14 days), partial dissolution of struvite (approximately 25 % of total dose by day 14, in BWO-struvite-A) was initiated by pH decline caused by the dissolution of wood-derived acidic substances [47]. Subsequently, microbial activities (e.g., the NH_4^+ consumption and the release of acidic metabolites from wood degradation) contributed to a further decrease in environmental pH and enhanced struvite dissolution in BWO-struvite. By day 42, BWO-struvite demonstrated lower pH (7.4 vs. 7.6) and higher residual soluble PO_4-P (1.71 vs. 1.67 mg/g DM wood) compared to BWO-struvite-A (Tables S7 and S8).

Overall, the environmental pH in BWO-struvite remained near or above 7.0 for most of the experimental duration. This pH range is generally considered tolerable [51] but not ideal for most wood-decaying fungi, as many fungal lignocellulose-degrading enzymes are sensitive to alkaline conditions [52,53] and fungal wood degradation can be significantly reduced at pH above 7.0 [51]. Therefore, BWO-struvite was likely dominated by bacteria, which tend to prevail under neutral and alkaline pH conditions [27] but generally degrade wood at a much slower rate than fungi [54].

3.1.3. Summary and implications of Experiment 1

The results of Experiment 1 suggested that acid urine dehydration is a promising approach to concentrate human urine for subsequent nutrient application in BWO or other wood-dominated CHRS. Specifically, two key factors contributing to efficient wood degradation in BWO were identified: (i) a comprehensive, readily available nutrient supply with an appropriate P level, and (ii) a slightly acidic environmental pH. The highest BWO performance was observed with the addition of PDU, which provided an operational soluble PO_4-P level of

0.20–0.51 mg/g DM wood and a pH range of 4.0–6.3. However, contradictory results were observed in a previous study, where the addition of PO_4-P at levels of 0–0.5 mg/g DM wood did not significantly affect the wood degradation during BWO [9]. We propose two potential explanations for this. First, the previous study used wood blocks, which can degrade around four times more slowly than sawdust-sized wood used in this study [8]. This slow degradation rate of wood blocks may have overshadowed any differences that PO_4-P addition might have caused in the previous investigation. Second, the previous study introduced PO_4-P as potassium dihydrogen phosphate, while this study used phosphoric acid. These two forms of PO_4-P likely had different impacts on environmental conditions such as pH and ionic strength, which could further affect microbial activity during composting [55]. As such, future research should investigate the most effective form and dosage of PO_4-P for BWO.

Experiment 1 also found that struvite, with its high alkalinity and PO_4-P content, was an ineffective BWO nutrient source when added alone on the defined N basis. However, it may still serve as a P source and an alkalizing agent for BWO when combined with ODU or other non-phosphoric acid (e.g., sulfuric acid)-based dehydrated urine. The acidity of acid-dehydrated urine may enhance struvite dissolution, increasing N and P availability in the system and helping buffer the operational pH if it drops below the optimal range. This combined use is practically relevant, as phosphoric acid may not be abundantly available

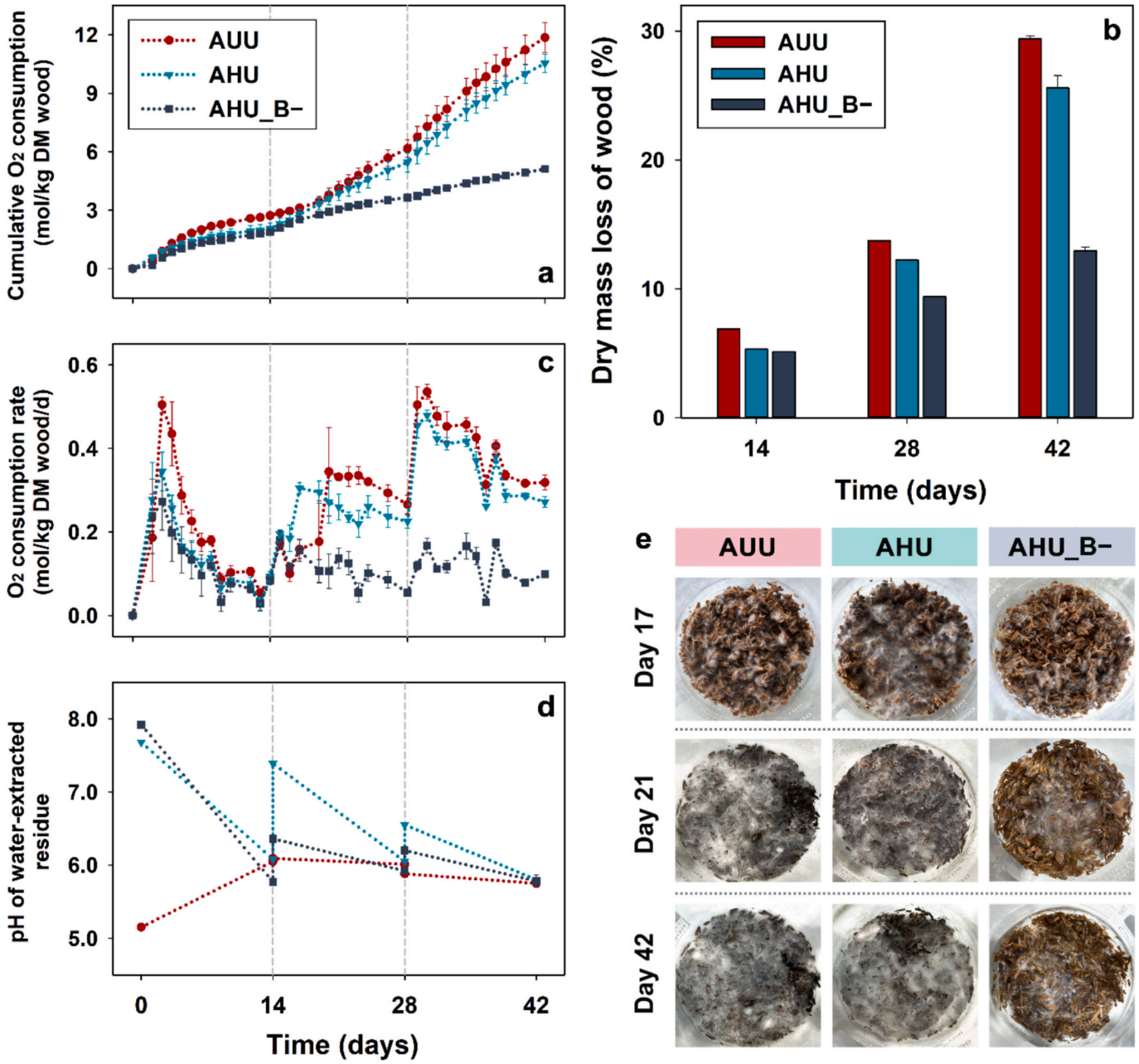

Fig. 3. The effect of three artificial urine solutions on BWO: artificial unhydrolyzed urine (AUU, with N present solely as urea), artificial hydrolyzed urine (AHU, with N present as hydrolyzed urea, i.e., NH_4OH and NH_4HCO_3 in a 1:1 M ratio), and a bicarbonate-controlled AHU (AHU_B−, where NH_4HCO_3 is replaced with an N-equivalent amount of $(NH_4)_2SO_4$). Performance indicators: (a) cumulative oxygen consumption, (b) dry mass loss of wood, (c) oxygen consumption rate, (d) pH of water extracted BWO residue, and (e) visible biomass inside the BWO reactors. The inherent pH of the wood materials used in this study, measured with water extracts as described in Section 2.6, was approximately 4.7. This caused the initial environmental pH in BWO (values on day 0 in panel d) to deviate from the intrinsic pH values of the nutrient sources listed in Table S3.

or the most cost-effective acid source for large-scale urine dehydration operations. In this regard, the mixing ratio of different nutrient sources, the dissolution dynamics of struvite, and their impacts on nutrient transformation and long-term pH stability in BWO may be subjects of interest.

3.2. In situ urea hydrolysis had a positive impact on BWO

In UU, PDU, and ODU treatments, over 94 % of the total N input was urea-N, which likely underwent enzymatic hydrolysis to bioassimilable NH_4^+-N, bicarbonate, and hydroxide ions during BWO (Table S7). This reaction, however, was absent in BWO-struvite, where N mainly existed as slow-release NH_4^+-N. This raises questions regarding the impact of dominant N forms (urea-N vs. NH_4^+-N) and in situ urea hydrolysis on BWO. To elucidate this, the second experiment in this study (Experiment 2) evaluated BWO treated with three artificial solutions: artificial unhydrolyzed urine (AUU, containing solely urea-N), artificial hydrolyzed urine (AHU, containing a 1:1 M ratio of NH_4HCO_3 and NH_4OH), and bicarbonate-controlled AHU (AHU_B−, where NH_4HCO_3 was replaced with N-equivalent molar of $(NH_4)_2SO_4$ to investigate the individual effect of bicarbonate ion as a product of urea hydrolysis).

The results of Experiment 2 confirmed the positive effect of in situ urea hydrolysis on microbial wood degradation during BWO. As shown in Fig. 3a and b, AUU led to the highest total COC and DM loss of wood, 10 % higher than those treated with AHU ($p < 0.05$). The two treatments resulted in similar N consumption dynamics but different pH values (Table S7), suggesting that the positive effect of in situ urea hydrolysis was likely attributed to its regulation of environmental pH. During the first 10 days, BWO-AUU demonstrated higher OCRs compared to BWO-AHU (Fig. 3c), possibly due to its lower starting pH (5.0), which may favor early fungal growth and adaptation [51,56] (Fig. 3d, Table S9). From days 14 to 28, BWO-AUU experienced potentially delayed fungal biomass development (Fig. 3e) and OCR peaking. This might be caused by a temporary limitation in available NH_4^+-N, given that microbial urea hydrolysis in the urine-collection system can take several days to complete [14]. However, such delays were not observed between days 28 and 42. At this stage, increased biomass accumulation may have enhanced ureolytic activity and accelerated in situ urea hydrolysis, so the production of NH_4^+-N could be quite efficient. In general, the pH in BWO-AUU remained relatively stable, ranging from 5.1 to 6.1, while the pH in BWO-AHU started alkaline and experienced transient increases following each nutrient dose (Fig. 3d). The stable, mildly acidic pH conditions in BWO-AUU, facilitated by in situ urea hydrolysis, may have supported pH homeostasis and metabolic efficiency of BWO microbes (especially fungi), thereby leading to higher wood degradation performance. Overall, the findings from Experiment 2 suggest that urine pretreatment should preferably retain N in the form of urea rather than NH_4^+-N to benefit BWO in the long term.

The DM losses, OCRs, and biomass accumulation of BWO-AHU_B− were comparable to those treated with AHU during the first 14 days but were significantly lower thereafter (Fig. 3a–c). Compared to AHU, AHU_B− lacked bicarbonate but had a higher sulfate concentration. To the best of our knowledge, the toxicity of sulfate to wood-decaying microorganisms is rarely reported. Setting aside the interference of sulfate, these results suggest that (i) bicarbonate/carbonate species may be important in supporting long-term BWO, and (ii) the inferior performance of BWO-struvite may be partly attributed to the lack of bicarbonate/carbonate species within the system as a buffer or a single-carbon source [57] (further discussion in SI).

3.3. General discussion

3.3.1. Insights from cross-experiment comparison

In previous BWO studies, COC was found to correlate with DM loss of wood [9,10]. Fig. 4a presents data from the two independent experiments in this study, which together exhibit a strong linear correlation between COC and DM loss. This suggests that aerobic microbial activity in BWO is closely linked to wood degradation, and therefore, oxygen consumption can serve as a reliable indicator of DM loss.

In this study, PO_4-P addition rate and environmental pH represent two crucial interdependent variables, as phosphate, beyond its role as a nutrient, can act as a buffer and influence the environmental pH when present in excess. Fig. 4b depicts the consolidated relationship between PO_4-P addition rates, environmental pH of the BWO residue, and DM loss of wood across two experimental sets. Relatively higher DM losses are noted under slightly acidic environmental pH (approximately 5.5–6.0) combined with low to intermediate phosphate addition rates (0.05–0.29 mg PO_4-P/g DM wood per 14 days). Notably, although AUU and AHU in Experiment 2 received a lower phosphate dose (0.09 mg PO_4-P/g DM wood), they achieved comparable or slightly higher DM loss compared to PDU in Experiment 1 (0.29 mg PO_4-P/g DM wood) under similar pH conditions. Apparently, environmental pH exerts a more direct and pronounced influence on microbial wood degradation than the PO_4-P addition rate; however, this interpretation remains provisional and warrants further systematic investigation under more controlled matrix conditions.

Compared to AUU and AHU in Experiment 2, UU, PDU, and ODU in Experiment 1 exhibited higher COD values (Table 1), likely due to the presence of organic compounds in real urine, such as creatinine, amino acids, and various other metabolites [58]. The functions and effects of these organic compounds on BWO remain unclear. If they were completely oxidized, their theoretical maximum contribution to total

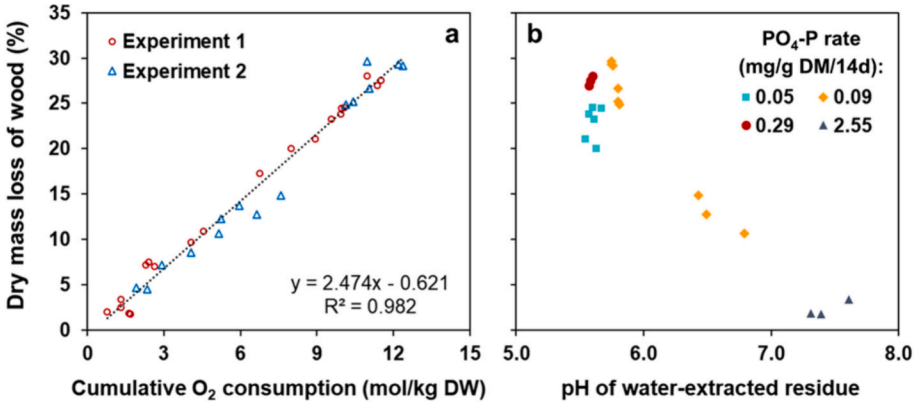

Fig. 4. Relationships between (a) cumulative oxygen consumption and dry mass loss of wood, based on data from all sampling points across two experimental sets in this study; and (b) pH of BWO residue (Y-axis), PO_4-P addition rates (legend, unit: mg PO_4-P/g DM wood per 14 days), and dry mass loss of wood (X-axis), using data from BWO samples at day 42 from both experiments in this study.

COC on day 42 would be only 0.12–0.16 mol/kg DM wood, which is marginal compared to the total COC values achieved in these treatments (11.0–12.4 mol/kg DM wood). Moreover, AUU and AHU, despite having lower COD, achieved similar or even higher COC and DM losses than UU, PDU, and ODU (Tables S6 and S9). This suggests that some organic compounds present in real human urine, such as pharmaceuticals or antibiotics, may exert slight inhibitory effects on BWO, which requires further investigation.

Despite inter-experimental variations, comparisons between Experiment 1 and Experiment 2 may lend additional support for several of the hypotheses proposed in Section 3.1. For example, BWO-AUU, which had a higher P availability (0.09 mg/g DM wood) than BWO-UU (0.05 mg/g DM wood), demonstrated increased total DM losses and absolute P consumption. Similarly, AHU and AHU_B−, with greater nutrient solubility, a higher N/P ratio, and a more comprehensive nutrient composition, resulted in significantly higher COC and overall DM losses than struvite. Initially, the AHU and AHU_B− treatments exhibited alkaline pH values similar to BWO-struvite (7.9 and 7.8); nevertheless, filamentous fungi were able to grow (Fig. 3e) and lower the pH to slightly acidic ranges in both treatments. These findings collectively suggest that an effective nutrient source for BWO should be capable of promoting fungal activity to achieve efficient wood degradation. To this end, a comprehensive nutrient composition, high solubility, appropriate elemental stoichiometry and P availability, and sufficient buffering capacity to maintain a slightly acidic environmental pH appear desirable.

3.3.2. Comparison with previous studies and broader implications

With the addition of UU, this study noted 23.9 % DM loss of wood after 42-day BWO (Table S6), which is lower than reported in a previous study (31.4 % in 46 days) using untreated human urine from a different source [8]. This variation may be related to differences in (i) microbial inoculum, which was sampled at different time points, (ii) urine composition, e.g., the previous study reported a PO_4-P addition rate of ~0.08 mg/g DM wood per 14 days and a pH of 5.90, both differing from UU used in this study, and (iii) the wood substrate, as different batches of wood materials were employed across studies. Nevertheless, the DM losses achieved with UU, PDU, and ODU in this study (22.8–27.5 % in 42 days) remained significantly higher than those reported using synthetic nutrient media (16.8 % in 46 days) in previous study, reaffirming the efficacy of human urine and its acid-dehydrated derivatives as BWO nutrient sources.

Compared to conventional nutrient (N and P) sources such as animal manure, dehydrated urine presents distinct advantages in enhancing wood degradation in composting systems. Biochemically, urinary P is primarily present as readily bioavailable inorganic phosphate, unlike animal manure where a larger fraction exists as organic P and requires microbial solubilization before becoming bioassimilable [59]. Moreover, the easily soluble nature of dehydrate urine allows for more effective and uniform nutrient distribution within the compost matrix, in contrast to the semi-solid formulation of animal manure which often leads to heterogeneous nutrient availability. From a practical perspective, human urine is ubiquitously produced in all anthropogenic settings, and can be more efficiently collected and processed in large quantities than animal manure. Once stabilized into solid forms, dehydrated urine offers advantages in storage and transport, with lower logistical demands, reduced environmental risks (e.g., pathogen contamination and greenhouse gas emissions), and potentially lower carbon-footprint compared to animal manure [60,61]. These attributes position dehydrated urine as a promising nutrient source that not only supports efficient wood degradation in composting processes, but also facilitates localized nutrient recycling in settings with limited access to traditional sources such as animal manure [62].

3.3.3. Research limitations and future perspectives

From a mechanistic perspective, the multifaceted roles of phosphate in microbial systems should not be overlooked. In addition to serving as a nutrient and pH buffer, phosphate can also regulate enzyme synthesis and functioning (e.g., through substrate phosphorylation) [63], as well as influence microbial community structure of both fungi and bacteria [64]. In this study, the higher polysaccharide removal observed in the PDU treatment suggests a positive effect of elevated phosphate addition on the microbial degradation of cellulose and hemicellulose. However, the underlying mechanisms remain unclear, as enzymatic activities were not assessed and microbial community analysis was limited to bacteria due to practical constraints. Follow-up research should explore how phosphate addition, across different rates and pH values, affects microbial enzymatic functions and community dynamics, and how these factors collectively influence wood degradation in BWO.

Another important consideration is that, given the high water solubility of acid-dehydrated urine, they were applied in aqueous form in this small-scale study to ensure uniform nutrient distribution. However, in composting practices, pre-dissolving such solids may not always be feasible, which underscores the need to better understand nutrient release dynamics from solid dehydrated urine, particularly in scaled-up applications. Material characterization, including surface morphology, functional group identification, and analysis of component interactions, could provide mechanistic insights into how physicochemical properties influence the release and transformation of these nutrients under more heterogeneous and dynamic composting conditions.

4. Conclusion and outlook

This research investigated the effectiveness of three human urine-derived solids in enhancing microbial wood degradation during biological wood oxidation (BWO), a composting process designed to efficiently degrade wood for heat production. After 42-day BWO, the addition of phosphoric acid-based dehydrated urine yielded the highest DM loss of wood (27.5 %), followed by oxalic acid dehydrate urine (22.7 %), and finally struvite (2.3 %). The results and further analysis pinpoint the dynamics and interplay of three key factors that may influence the system's performance observed in this study: the forms of N, the concentration of soluble P, and the environmental pH, which can be affected by transformation and accumulation of buffering ions within the system (e.g., NH_4^+, PO_4^{3-}, and HCO_3^-). Optimization of these factors through adjustments to nutrient dosages, application timing, or the mixing of different nutrient sources, may further improve local composting conditions and wood degradation performance.

Integrating BWO with acid urine dehydration offers a novel solution for nutrient recycling with added environmental and energy benefits. First, it facilitates the enrichment and stabilization of urine-derived nutrients within the compost, which may serve as a soil improver with several advantages: (i) the fixation of N and P into organic forms, reducing nutrient leaching and runoff potential [65]; (ii) a high content of humic substances, formed from decomposed wood and microbial biomass [66]; and (iii) a potential reduction in pharmaceutical content and associated environmental risks, as some wood-decaying fungi have demonstrated abilities to oxidize certain pharmaceuticals [67,68]. Several studies have reported that the combined application of urine and compost can lead to higher crop yields compared to using either urine [69] or compost alone [70,71]. Therefore, while acid dehydrated urine can be applied directly as a fertilizer, blending it with BWO compost may offer additional fertilizing benefits [72]. Future research could explore the removal of micropollutants from human urine during BWO and systematically characterize the quality of the blends, including its nutrient profiles, pH, electrical conductivity, maturity, and germination index, to better understand its potential for fertilization and soil improvement.

Another advantage of this integrated system is the possibility to recover heat generated by BWO to power the urine evaporation unit and even serve other energy needs. For every ton of DM wood in BWO, approximately 600 kg of untreated urine (12 kg of its dehydrated equivalent, with a CF of 50) would be processed over a 42-day period.

This could potentially generate 4200–5300 MJ of heat per ton DM wood, as estimated from the COC of UU, ODU, and PDU treatments in this study (calculation specified in SI) [73]. Assuming a heat recovery efficiency of 70 %, each kg of untreated urine (or its dehydrated equivalent) supplied to BWO could produce 4.9–6.2 MJ of reusable heat (Table S10). This amount of heat has the potential to not only cover the energy required for urine evaporation (estimated at 0.8–5.3 MJ per kg urine in a pilot-scale field study) [74] but also leave surplus available for other applications, such as space heating for households, greenhouses, or livestock shelters in rural areas, or integration into district heating systems in urban settings. In this sense, the integration of acid urine dehydration and BWO could be upscaled and implemented across a broad range of contexts, where ecological sanitation, wood residue management, low-temperature heating, and sustainable agriculture present key priorities.

CRediT authorship contribution statement

Anran Li: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Xueyi Mai:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Sijie Huang:** Data curation, Formal analysis, Methodology, Resources, Visualization, Writing – review & editing. **Prithvi Simha:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Cees J.N. Buisman:** Writing – review & editing, Validation, Supervision, Resources, Investigation, Conceptualization. **Wei-Shan Chen:** Writing – review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cej.2025.167178.

Data availability

Data will be made available on request.

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