



Improving the Efficiency of the Indoor Air Purification from Formaldehyde by Plants Colonized by Endophytic Bacteria *Ochrobactrum* sp.

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Abstract The endophytic bacteria can be in symbiosis with host plants, owing to the natural stability advantages in degrading pollutants. To explore the technological feasibility of this method for indoor formaldehyde removal, a system combining endophytic bacteria and plants was established. In the present study, highly efficient formaldehyde-degrading bacteria *Ochrobactrum intermedium*, named strain ZH-1, was successfully induced with antibiotics (rifampicin) to an antibiotic-labeled strain ZH-1^R without microbial variation. The strain ZH-1^R was then used for colonization in the *Epipremnum aureum* and *Chlorophytum comosum* f. *variegata* plants by three inoculation methods: root irrigation (RI), acupuncture injury to stem (AS), and acupuncture injury to leaves (AL). The results demonstrated that the acupuncture injury to stem (AS) method was the most effective

for inoculating ZH-1^R strain in *Epipremnum aureum* plants. Conversely, acupuncture injury to stem (RI) method yielded the best results for the *Chlorophytum comosum* f. *variegata* plants, highlighting the importance of usage of optimal plant specific inoculation method ensuring the highest possible performance characteristics of the biological system. The results of 8-day formaldehyde dynamic fumigation experiment demonstrated that the removal efficiency of the formaldehyde by *Chlorophytum comosum* f. *variegata* inoculated with ZH-1^R was significantly higher than the one demonstrated by non-inoculated plants. The average increase of 20.17% was observed during daytime, while much more significant improvement by 62.88% was achieved at night. This implied that endophytic bacteria could not only effectively improve the removal efficiency of formaldehyde, but also increased the resistance of not-native host plants to formaldehyde toxicity, suggesting its potential in an integrated system which provides a new path of an efficient and economical approach to radically improve indoor air quality, especially at nighttime.

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1 Introduction

Formaldehyde is receiving increasing attention due to its health hazards and ease of release from building materials including chemical fiber carpets, plastic floor tiles, paints, and other coatings (Salthammer, 2019; Wang et al., 2023a; Wang et al., 2019). Excessive exposure to formaldehyde could cause adverse health effects, including eyes and upper respiratory tract irritation, and even become a carcinogen (Chen et al., 2010; Protano et al., 2022). Based on its toxicity, formaldehyde has been classified by the International Agency for Research on Cancer (IARC) as a human carcinogen, closely associated with nasopharyngeal cancer and possibly leukemia (de Falco et al., 2018; Wild, 2014). Effective removal of formaldehyde from persistent and complex sources has always been a hotspot and challenge of the research (Huang et al., 2022; Yue et al., 2021).

Photodegradation is an important way to remove the formaldehyde (H-CHO) in the atmosphere, in which the H-CHO bond decomposes into $\text{H}\bullet$ and $\text{HCO}\bullet$. However, photodegradation of formaldehyde requires a significant expenditure of energy, since H-CHO bond is 356.5 kJ/mol and the light absorption occurs in the range of 240–360 nm (Manahan, 2022). Therefore, it is difficult to break the H-CHO bond by a photochemical reaction in indoor environments, especially at nights when the amount of the UV light is limited. Currently, indoor formaldehyde removal methods can generally be divided into three categories: physical, chemical, and biological removal (Raj et al., 2019; Wu et al., 2022). Physical and chemical technologies including adsorption, photocatalytic oxidation, and ionization have been used for indoor formaldehyde purification; however, they could not be considered as satisfactory for the task due to excessive energy consumption, high costs, and secondary production of waste streams containing toxic substances (Guieysse et al., 2008; Khaksar et al., 2016a; Sriprapat et al., 2014; Vellingiri et al., 2019).

In recent decades, phytoremediation has received increasing attention from researchers due to its cost-effectiveness, sustainability, and aesthetics, as well as the social benefits associated with zero-energy consumption (Prum et al., 2018). Although plants have a natural ability to remove pollutants, they do not have a complete system for degrading pollutants on their own (Abhilash et al., 2009; Fismes et al., 2002;

Maurya et al., 2023). Moreover, due to the influence of light, temperature, and physiological activities such as photosynthesis, respiration, and stomatal closure, the ability of plants to remove pollutants during daytime is much higher than that at nights (Liang et al., 2018; Xu et al., 2011). This implied that the ability of plants to decompose indoor pollutants seems to be very unstable limiting the efficiency of their removal from the ambient air. As a result, significant numbers of potted plants are required in practice to achieve noticeable results in indoor air purification procedures (Khalifa et al., 2023). This conclusion dictates the need to increase the degree of purification of plants from formaldehyde by supplementing phytoremediation with other technologies.

Microorganisms with formaldehyde removal capacity are very diverse in nature (Husárová et al., 2011; Yang et al., 2020). Compared with adsorption and chemical oxidation, the microbial degradation has the advantages of being environmentally friendly, cost-effective, and pollution free, so the search of efficient formaldehyde-degrading bacteria has become a research focus of numerous investigations (Gao et al., 2022; Wang et al., 2019). An increasing number of formaldehyde-degrading microorganisms are being isolated and identified, including bacteria, yeast, fungi, and marine algae (Shao et al., 2020). Although the microbial methods have many advantages, the growth of microorganisms is strongly influenced by environmental factors, so the efficiency of removing formaldehyde is also unstable and still has limitations in practical application (Vergara-Fernández et al., 2018).

Both the plant purification method and the microbial degradation method have their drawbacks. However, microorganisms and plants can effectively complement each other to create an environmentally friendly and efficient pollution abatement system (Ahsan et al., 2017). Current research of the cooperation between plants and microbes for removing air pollutants has mainly focused on the rhizosphere and phyllosphere (Bashir et al., 2022; Urana et al., 2020). Chen et al. (2010) reported that most plants have a limited ability to remove formaldehyde in the absence of rhizospheric microorganisms, which means that the root zone of a plant and its rhizospheric microorganisms are both required for efficient formaldehyde removal through phytoremediation. The phyllosphere is usually rich in microbial communities with an individual number of $10^7 \sim 10^8$ cells

per gram of leaf (Sandhu et al., 2007). Orwell et al. (2004) reported that microbial inoculation on leaf surfaces could improve the removal rate of volatile toluene in the atmosphere.

However, compared to rhizospheric and phyllospheric bacteria, endophytic bacteria have much closer symbiotic relationships with plants (Sharma et al., 2019), where the latter can serve as a stable nutrient medium for these microbes (Afzal et al., 2014). Also, endophytes can promote the growth of host plants in various ways and, at the same time, some functional endophytic bacteria can directly degrade pollutants or reduce the toxicity of pollutants to enhance the host's tolerance to the hazard (Eevers et al., 2015; Suyamud et al., 2018). In addition, endophytic bacteria could also help plants to transfer pollutants, so that pollutants can be enriched, transformed, and utilized in plants (Li et al., 2019; Su et al., 2018).

Traditionally, a large number of studies have been devoted to the growth-stimulating properties of endophytes, such as nitrogen fixation (Defez et al., 2017), siderophores (Cui et al., 2022), and IAA (the auxin indole-3-acetic acid) and ACC (the enzyme 1-aminocyclopropane-1-carboxylate) deaminases (Chaudhary et al., 2021), as well as the properties of endophytic bacteria to enhance the rate of pollutants' removal (Khaksar et al., 2017). Currently, the combination of endophytic bacteria and plants is mainly used for the removal of heavy metals. Wang et al. (2023b) reported that the endophytic bacterium *Serratia marcescens* PRE01 could be successfully colonized at the root of *Pteris vittata* and increase its total vanadium yield by 25.4%. The experimental results of Li et al. (2020) showed that, compared with the Individual Chlorella, the microalgae endophyte Symbiotic system (MESS) reduced the removal time of COD (chemical oxygen demand) and Cd (II) by 6 days. Khaksar et al. (2016b) used plants, which grown from seeds inoculated with endophytic bacteria, for the removal of formaldehyde, and shed light on the fact that endophyte-inoculated sterile seeds showed a significantly higher percentage of germination compared to non-inoculated sterile seeds with an increased concentration of formaldehyde. At the same time, plants inoculated with endophyte improved the formaldehyde removal rate by almost 49% compared to non-inoculated plants at a formaldehyde concentration of 24 mg/m³ (Khaksar et al., 2016a). It is important to note that different inoculation methods have a great influence on the colonization, localization, and spread of endophytic

bacteria (Afzal et al., 2012). Unfortunately, the systematic study of the dynamics of colonization and development of endophytes in plants, as well as the influence of an environment on the colonization of endophytic bacteria, remains without significant attention.

In this study, formaldehyde-degrading bacteria were labeled and colonized on two common houseplants: *Epipremnum aureum* and *Chlorophytum comosum* f. *variegata*, and the effect of different colonization methods and conditions on colonization dynamics, as well as formaldehyde degradation characteristics, has been investigated.

The main goal of this study was to improve the efficiency of formaldehyde removal, especially during nighttime, through the implementation of a "biological air quality control system." The findings of this study could enable significant enhancement of the system's capability on indoor formaldehyde removal for following implementation at residential and office environments.

2 Materials and Methods

2.1 Reagents and Mediums

The reagents used in this study have been purchased from the National Medicines Corporation Ltd. (Shanghai, China). They include HCHO (40%), CaCl₂·2H₂O (96%), FeSO₄·7H₂O (99.0%), NH₄NO₃ (99.0%), KH₂PO₄ (99.5%), K₂HPO₄ (99.0%), MgSO₄ (98.0%), MnSO₄·H₂O (99.0%), NaCl (99.5%), NaH₂PO₄·2H₂O (99.0%), Na₂HPO₄·12H₂O (99.0%), beef paste (99.5%), peptone (99.5%), agar (ash≤5.0%), C₂H₅OH (99.7%), NaClO (8%), C₅H₈O₂ (99.0%), kanamycin (100 mg/mL), streptomycin sulfate (50 mg/mL), and rifampicin (10 mg/mL). All reagents and calibration standards were based on analytical grade chemicals.

Nutrient Broth (NB) medium contains (per liter of deionized water) beef paste 5.0 g, peptone 10.0 g, and NaCl 5.0 g. The Nutrient Agar (NA) was produced by adding 2 g of agar powder into 1 L of the NB medium. The inorganic salt medium (per liter of deionized water) contains 0.1 g×MgSO₄, 0.02 g×CaCl₂·2H₂O, 0.68 g×KH₂PO₄, 0.001 g×MnSO₄·H₂O, 1.73 g×K₂HPO₄, 0.03 g×FeSO₄·7H₂O, and 1.0 g×NH₄NO₃. The phosphate-buffered saline (PBS) solution contains (per liter of deionized water) 31.24 g×NaH₂PO₄·2H₂O and 71.64 g×Na₂HPO₄·12H₂O. All the above medium and

solutions were sterilized in an autoclave (Hirayama HVE-50, Shanghai Huyue Ming Scientific Instruments Co., Ltd., China) at 1×10^5 Pa and 121 °C for 30 min.

2.2 Preparation of Plants and Microbial Strains

All plants involved in this investigation (*Chlorophytum comosum* f. *variegata* and *Epipremnum aureum*) were purchased from Nanchang flower shops and are shown in Fig. 1. They were supplied in porcelain pots with the inner diameter of 10 cm and height of 7 cm. Each pot contained 300 g of sterilized soil. To retain the soil moisture, 50 mL of deionized water was added to the pots every 2 days during the entire 40 days of planting.

Strain ZH-1, employed in this investigation, was isolated from the rhizosphere microorganism of *Epipremnum aureum* and identified by 16S rRNA gene technology as *Ochrobactrum intermedium* strain. The gene sequencing results of this strain are provided in the Supplementary Material S1. There are many reports available on endophytes of the *Ochrobactrum intermedium* strain, including the oxalate-degrading

endophytic bacteria *Ochrobactrum intermedium* CL6 (isolated from *Colocasia esculenta* tubers (Kumar & Belur, 2018)), and endophytic bacteria *Ochrobactrum intermedium* AcRz3 (obtained from ethnomedicinal plant *Acorus calamus* rhizome), which exhibited growth inhibition of five fungal pathogens (Singh et al., 2018). On this basis, strain ZH-1 looked as a very good candidate for successful colonization into the plants and survival as the endophytic bacteria.

2.3 Antibiotic Labeling of Strain ZH-1 (Antibiotic-Resistant Strains)

Strain labeling is the key common method for checking whether strains can successfully colonize in plants. One of the objectives of this project was to find a suitable antibiotic that could effectively inactivate all of the original endophytes in the plant with the exception of the ZH-1 strain. For this purpose, three commonly used antibiotics (kanamycin, streptomycin sulfate, and rifampicin) were selected to test the efficacy. Each antibiotic was adjusted to three concentrations (100 µg/mL, 200 µg/mL, and 400 µg/mL for kanamycin and

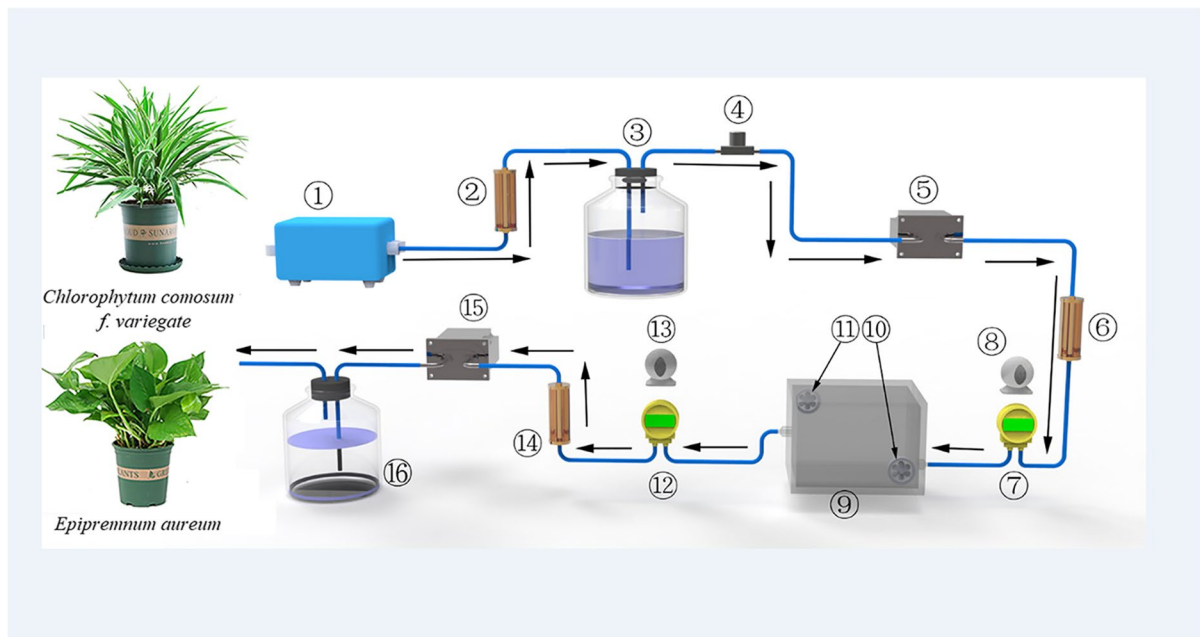


Fig. 1 Schematic diagram of the experimental apparatus. 1—Main air supply pump; 2, 6, 14—Gas flowmeters; 3—Formaldehyde solution; 4—Gas flow valve; 5, 15—Air pumps; 7, 12—On-line formaldehyde detectors; 8, 13—Web cameras;

9—Fumigation container; 10, 11—Fans; 16—Discharge handling vessel. Both plants involved in this study are shown on the left

streptomycin sulfate, and 10 µg/mL, 20 µg/mL, and 40 µg/mL for rifampicin) and added to 100 mL of NB medium. Then, the plant tissue abrasive solution was added after surface disinfection and placed in a constant temperature generator for enrichment and cultivation at 30 °C for 7 days. The growth of colonies in the medium was observed daily. The most effective antibiotics capable of effectively inhibiting the growth of plant endophytic bacteria were selected and added to the ZH-1 culture medium for enrichment in a constant temperature generator (35 °C, 150 rpm, SHA-C, Rongcheng, Shandong, China) for 24 h. In cases of any observed bacterial growth, the colonies were reinoculated to NB medium containing progressively higher concentrations of antibiotics and culturing was repeated for following 24 h. The stability of the antibiotic resistance was confirmed by subculturing strains on Nutrient Agar (NA) medium without addition of the antibiotic. However, if no colonies were observed, the antibiotic was further diluted or replaced.

2.4 Identification of Labeled Strains

Identification of the labeled strain was performed by the 16S rRNA gene method. The 16 s rDNA sequence of the strain was amplified with the bacterial universal primer 27F (5'-AGTTTGATCMTGGCTCAG-3') and the reverse primer 1492R (5'-GGTTACCTTGTACGACT T-3'). The PCR cycling was as follows: denaturation at 94 °C for 30 s, annealing at 55~60 °C for 25~30 s, and extension at 72 °C for 30~50 s. The establishment of the phylogenetic tree and analysis of the phylogeny were completed by using the software MEGA 4.1 and BLAST (Basic Local Alignment Search Tool) to compare 16 s rDNA base sequence with the formaldehyde-degrading bacteria in the NCBI database. PCR products were submitted for DNA sequencing and the result were compared against previously available DNA sequences in the NCBI GenBank (<http://www.ncbi.nlm.nih.gov.blast>) to characterize the bacteria. The BLAST software was also used to compare the genes of the ZH-1 strain before and after antibiotic labeling (Per. Ident).

2.5 Formaldehyde Degradation Before and After Strain Labeling

The antibiotic-resistant strains and the parent strain were inoculated into 100 mL MS liquid medium at 1% (v/v) assuming that formaldehyde was the only carbon source.

The liquid MS medium initially containing 50 mg/L of formaldehyde was used. Then, the media were cultured in a thermostatic oscillator at 150 rpm at 30 °C. Samples of all groups were taken every hour to measure the formaldehyde concentration in the MS liquid medium. Formaldehyde concentration in the medium was measured by acetylacetone spectrophotometric method at 414 nm by an UV-visible spectrophotometer (UV-1800, SHIMADZU, Kyoto, Japan) (Liang et al., 2012).

2.6 Effects of Colonization Dynamics for Different Inoculation Methods

To study the dynamics of colonization with labeled bacteria in test plants by various inoculation methods, the labeled strain was inoculated into test plants by three inoculation methods:

1. Root irrigation (RI) — plants were irrigated around the rhizosphere with 10 mL of a labeled strain culture solution at a concentration of 10^8 CFU/mL. Plants irrigated with 10 mL of sterile medium were used as blank controls.
2. Acupuncture injury to stem (AS) — the culture medium of the labeled strain with a concentration of 10^8 CFU/mL was instilled into the middle part of the stem with a seed needle and pierced three times. Inoculation with a needle soaked in a sterilized medium was used as a control.
3. Acupuncture injury to leaves (AL) — leaves of plants were pierced with an inoculation needle after immersion in the culture medium of labeled strains at a concentration of 10^8 CFU/mL; each leaf was punctured only once. Leaves of inoculated plants dipped in sterilized medium were used as controls.

All above methods were used for colonization of *Epipremnum aureum*, while only RI and AL methods were tested for *Chlorophytum comosum* f. *variegata* as this plant has very short and hardly accessible stem, hidden under leaves. On completion of inoculation, all labeled strains of inoculated plants as well as blank control groups were kept under natural controlled laboratory conditions. The dynamics of colonization of labeled strains in different plant species and tissues was studied 2, 4, 6, and 8 days after inoculation. Each group of experiments was repeated at least 3 times.

2.7 Fumigation Experiment

The experimental apparatus is shown in Fig. 1. Firstly, formaldehyde gas was generated by bubbling a slip stream of air into the formaldehyde solution vessel using an air pump. The formaldehyde concentration was controlled by adjusting the air flow with the gas inlet valve. Inlet and outlet formaldehyde concentrations were monitored with an online formaldehyde detector (ADL-600B-HCHO, ANDEIL, Shenzhen, China). The flow rate was set to 90 L/h at both inlet and outlet points. Two web cameras (YI, 1080P, Shanghai, China) were employed for recording inlet and outlet concentrations in real-time throughout the experiments. Formaldehyde exhaust gas in the system was captured with 2, 4-dinitrophenylhydrazine (DNPH) in aqueous hydrochloric acid in a cleaning vessel.

Cubic fumigation container with 500-mm sides and a wall thickness of 10 mm was made out of clear acrylic plates. Teflon film is affixed to the inner wall to reduce wall adsorption and improve sealing performance. The entire fumigation system was placed close to windows so natural light could be used instead of artificial lighting.

2.8 Formaldehyde Removal by Plants Inoculated with Endophytes

Plants with and without inoculated endophytes were used to investigate the possibility of removing formaldehyde gas with the inlet concentration set at 5 ppm. The inoculated plants along with non-colonized ones used as a black control group were exposed to 8 days of continuous fumigation. To study the effect of removing formaldehyde from the stem-leaf system of a plant, the roots and soil of each plant (*Chlorophytum comosum* f. *variegata*) were covered with sterilized aluminum foil to prevent absorption of formaldehyde by soil and plant roots.

The formaldehyde removal efficiency was calculated as:

$$\eta_{HCHO}(\%) = \frac{C_1 - C_2}{C_1} \times 100\% \quad (1)$$

where C_1 and C_2 are the concentrations of formaldehyde in the inlet and outlet monitoring points.

2.9 Colony-Forming Units (CFUs) of Labeled Strain in Inoculated Plant

To identify the total number of CFU of antibiotic-labeled strains, root and leaf samples of both inoculated and not inoculated plants were washed with distilled water to remove some residue of the soil particles and dust, then dried and finally weighed to ensure that all samples are approximately 1 g. Leaves were sterilized by soaking in 70% C_2H_5OH for 30 s, then transferred to 2% NaClO for 10 s, and washed several times with sterile deionized water. A 100- μ L sample of the final sterile deionized water from the last wash was collected and cultured on an NA plate to ensure surface sterilization accuracy (Ho et al., 2012).

Leaf and root samples after surface sterilization were macerated in 10 mL of sterile phosphate buffer saline (PBS) and grounded with a pre-sterilized mortar and pestle. Serial dilutions were spread on the NA plates containing 50 μ g/mL of rifampicin and cultured at 35 °C for 3 days. Then, the colonies were counted, and the colonization amount was calculated as (Visioli et al., 2014):

$$CA = \frac{CFU}{m}, \quad (2)$$

where CA is the colonization amount, CFU is the colony-forming units, and m is the fresh weight of the plant tissue (g). Three replicates were used for each set of experimental conditions.

Statistical analysis was performed by the Statistical Product Service Solutions (SPSS) software using analysis of variance (ANOVA) test followed by a post hoc least significant difference test.

3 Results and Discussion

3.1 Antibiotic Labeling of Strain ZH-1 (Antibiotic-Resistant Strains)

The plant tissue grinding solution after treatment by surface sterilization was added to NB medium containing the culture of antibiotics. After 7 days of cultivation, different antibiotics showed the different inhibitory effects on microorganisms. In the experimental group with added kanamycin, no significant inhibitory effects on the native endophytic bacteria of *Chlorophytum comosum* f. *variegata* were observed. Regardless of the change in

kanamycin concentration, the culture medium showed clear turbidity after 48 h. However, the addition of streptomycin sulfate had a certain inhibitory effect on the growth of native endophytic bacteria. Turbidity appeared after 96 h in medium containing 100 µg/mL and 200 µg/mL of streptomycin sulfate, and after 144 h in the medium containing 400 µg/mL of streptomycin sulfate. These results indicated that kanamycin and streptomycin sulfate could not completely inhibit the growth of plant endophytic bacteria at the concentrations tested.

In all experimental groups, the medium supplemented with rifampicin showed the best inhibitory effect on the growth of endophytic bacteria, and no obvious turbidity appeared even after 7 days at all concentrations. Spreading of 100 µL aliquot of the medium containing 10 µg/mL rifampicin on agar plates with following incubation at the temperature of 30 °C for 3 days did not show any colony growth on the plates. These results showed that even at the low concentration of 10 µg/mL, rifampicin could effectively inhibit the growth of the native endophytic bacteria of the tested plants. Therefore, rifampicin was selected as the optimal labeling antibiotic for the formaldehyde-degrading bacteria strain ZH-1 and the rifampicin labeled strain has been named ZH-1^R.

3.2 Identification of Rifampicin-Labeled Strain ZH-1^R and Comparison with the Strain ZH-1

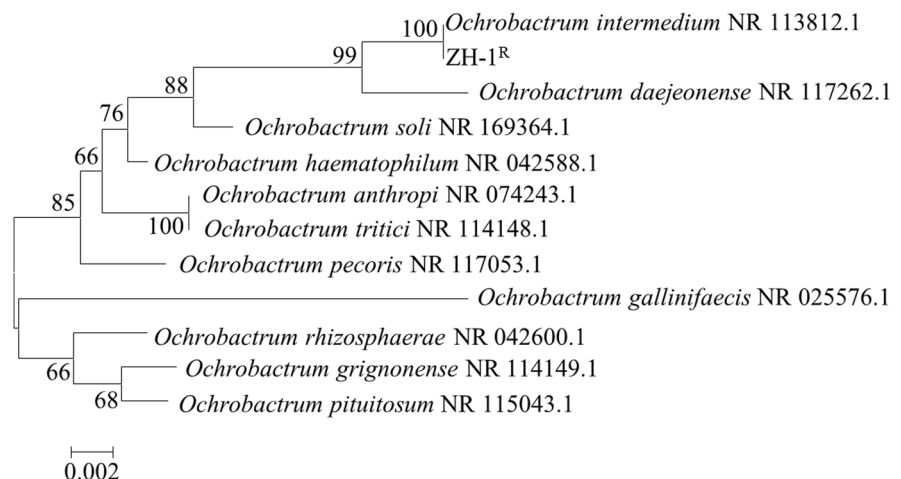
Visually, the strain ZH-1^R colonies are round, opaque, convex, and milky white, and are not filamentous and moldy. Some essential biochemical tests indicated

that ZH-1^R is gram-negative facultative aerobic bacteria. Using sequencing of the 16S rRNA gene of the banded ZH-1^R and BLAST analysis of DNA fragments, the existing gene sequences in the GenBank database and phylogenetic relationships between the ZH-1^R strain and other similar strains were constructed (Fig. 2). Figure 2 shows that strain ZH-1^R has 99% similarity with *Ochrobactrum daejeonense* NR 117262 and 100% similarity with *Ochrobactrum intermedium* NR 113812.1. According to homology analysis results, the strain ZH-1^R was classified as *Ochrobactrum* sp., and identified as *Ochrobactrum intermedium*. The 16S rDNA of strain ZH-1^R was amplified by PCR and the 1266-bp gene fragment was obtained. The entire gene fragment of the strain ZH-1^R was uploaded to the NCBI GenBank and obtained the number of ON013585.

The BLAST software was used to compare the gene sequences of the ZH-1 strain before and after labeling with rifampicin. The results showed that the similarity between ZH-1^R and ZH-1 strains was 95.52% (Per. Ident). This indicated that the antibiotic labeling used in this study did not change the species of the original bacteria strain. The detailed gene sequences of the ZH-1^R strain and the original ZH-1 strain, along with the comparison between them using the BLAST software, are presented in Supplementary Material S2.

Figure 3 shows the results of comparison of formaldehyde degrading capacity between strains ZH-1^R and ZH-1. As is seen, both strains degrade formaldehyde at about the same rate — 50% of available formaldehyde in about 4 h. Then, the entire degradation of the 50 mg/L

Fig. 2 Phylogeny of strain ZH-1^R



formaldehyde solution was achieved in 7 h of run. Such outcome indicated that rifampicin labeling has negligible effect on the ability to degrade formaldehyde.

3.3 Colonization Dynamics of Strain ZH-1^R

After colonizing of the ZH-1^R strain in the test *Epipremnum aureum* plants by RI, AS, and AL methods, the labeled strain ZH-1^R in stem, leaf, and root tissues was recovered after surface sterilization at

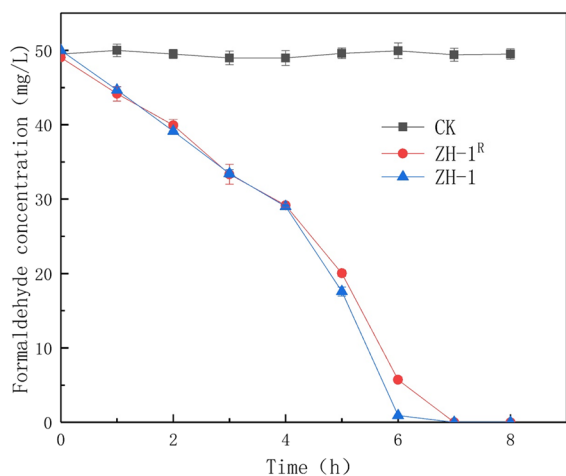


Fig. 3 Removal of formaldehyde by ZH-1 and ZH-1^R strains. CK, control group. The error bars represent mean $\pm$ SD, $n = 3$

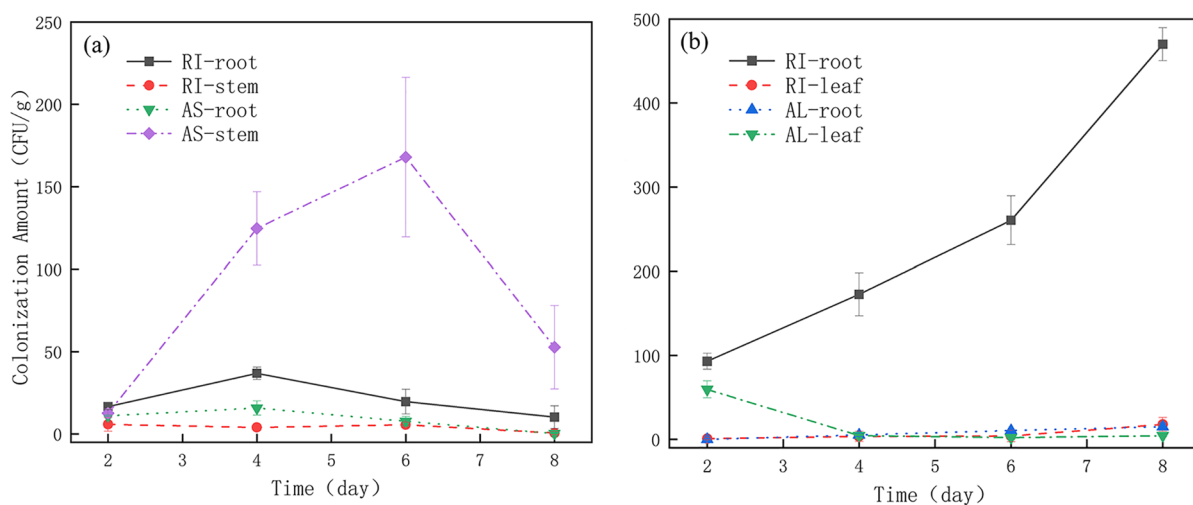


Fig. 4 Colonization amounts of *Ochrobactrum intermedium* in (a) *Epipremnum aureum* and (b) *Chlorophytum comosum f. variegata* obtained by two inoculation methods in the clean atmosphere. The error bars represent mean $\pm$ SD, $n = 3$

different time periods. The results showed that endophytic ZH-1^R strain could be recycled from roots and stems of *Epipremnum aureum* by both RI and AS methods, while nothing could be recovered from leaves, even subjected to AL methods.

As is seen in Fig. 4a, strain ZH-1^R mainly colonized the root tissues of *Epipremnum aureum* inoculated by RI method, but its colonizing effect was not stable, showing a tendency first to increase and then to decrease. Colonization of ZH-1^R in the roots reached the maximum value of 36.84 ± 3.80 CFU/g on the 4th day, and then began to decrease to 10.19 ± 6.85 CFU/g on the 8th day. After RI inoculation, a small amount of ZH-1^R could be recovered from the stem; however, no presence of the ZH-1^R was detected in the leaves. For plants inoculated by AS method, ZH-1^R was mainly colonized in the stem tissue showing similar trend — initial increase reaching maximum at day 6, with following decrease. A small amount of ZH-1^R was also recovered from the roots of the inoculated plants, but nothing was detected in the leaves. Finally, microbes were not detected in any parts of the plans inoculated by AL method. These results indicate that ZH-1^R could be colonized in *Epipremnum aureum* tissues as endophytes by RI and AS methods, and a small amount of ZH-1^R strain can be transferred from the colonization site to other parts of the tissue. However, its colonization was not stable, showing a trend of first increasing

and then decreasing, which was similar to the results of studies by Coy et al. (2019).

Compared with the RI and AL methods, inoculation of ZH-1^R by AS method achieved better colonization effect for *Epipremnum aureum*. Inoculation of ZH-1^R by the AS method not only resulted in a higher amount of plant colonization than that by the RI method, but also increased the duration of colonization. This coincides with the results reported by Bamisile et al. (2018), who concluded that different inoculation methods have a great impact on endophyte colonization in plants. Similarly, researchers have found that when bacteria infect certain plants, they tend to prefer to colonize particular parts of the plant, leaving the rest of the plant bacteria free (Compant et al., 2010).

Figure 4b shows the dynamics of colonization with labeled bacteria of the tested *Chlorophytum comosum f. variegata*. As is seen, the ZH-1^R strain mainly colonized the root tissues of plants inoculated by RI method, and the colonization trend continued to increase with time. For the plants inoculated by AS method, the number of colonies remained at a low level throughout the subsequent period of the experiment, but still recovered a small amount of the ZH-1^R strain in the root tissue on the 2nd day. None of the ZH-1^R strain could be recovered from the blank control groups.

The rhizosphere zone is the primary site for the entry of endophytic bacteria into plants. It supports a large and diverse microbial community with abundant activity (Khaksar et al., 2016a, b, c; Vacheron et al., 2013). As was reported by Afzal and colleagues (2014), the most contaminant-degrading bacteria are more abundant in the roots of host plants than in the stems and leaves.

On this basis, it can be concluded that *Ochrobactrum intermedium* has a preferential colonization location in the root of *Chlorophytum comosum f. variegata* justifying selection of the root inoculation method for subsequent experiments.

3.4 Effects of Gaseous Formaldehyde Stress on Colonization Dynamics of Strain ZH-1^R

The strain ZH-1^R was inoculated into the root of *Chlorophytum comosum f. variegata* for following 8-day experimental run in both clean environment and in the atmosphere containing 5 ppm of gaseous formaldehyde. The results showed that the colonization efficiency under the formaldehyde stress was higher than that in the clean environment, with the highest efficiency

demonstrated on the root tissues. As is shown in Fig. 5, the colonization of the roots had a sharp tendency to increase in formaldehyde presence (FP) rising to 2049.55 ± 291.23 CFU/g during 8 days of the experimental run, while in the clean atmosphere (CA) this number could only reach 469.94 ± 19.63 CFU/g over the same time period. Nevertheless, the increase rate in FP environment was slowed down over time, achieving the daily ratio of the colony number increase of 1.85, 1.56, and 0.26 at 2–4 days, 4–6 days, and 6–8 days, respectively. It must be noticed that the rate of increase under CA colonization conditions was highest at 6–8 days. Significantly, the FP colonization was consistently higher than that of CA reaching 4 times difference at later stages of the experiment.

In contrast, the colonization of leaves under FP demonstrated some decay at 4–6 days and 6–8 days of the experiment reaching the corresponding ratios of -0.46 and -0.19 , respectively. In addition, the highest colonization of leaves was achieved at day 4 (114.98 ± 10.41 CFU/g), with following decay down to 50.02 ± 10.87 CFU/g at the end of the experiment (day 8). On this basis, it could be concluded that the ZH-1^R strain is not capable of efficient colonization on the leaves under CA conditions.

The results showed that exposure to formaldehyde gas at a concentration of 5 ppm promoted the colonization of highly efficient formaldehyde-degrading bacteria, *Ochrobactrum intermedium* ZH-1^R, in

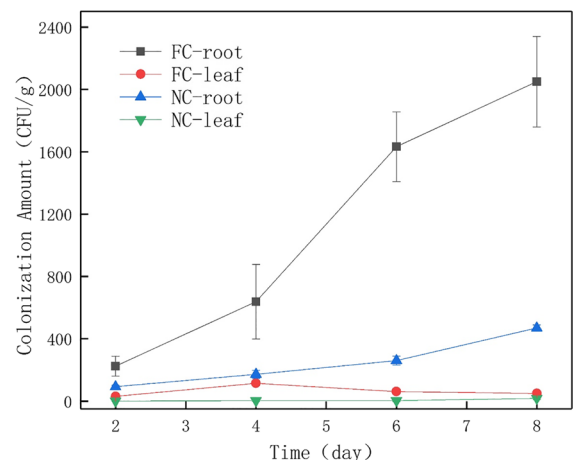


Fig. 5 Colonization amounts of strain ZH-1^R in *Chlorophytum comosum f. variegata* root and leaf tissues in formaldehyde presence (FP) and in the clean atmosphere (CA). The error bars represent mean $\pm$ SD, $n = 3$

Chlorophytum comosum f. variegata. This may be due to the fact that the plants absorbed formaldehyde gas from the atmosphere, which led to an increase in the concentration of formaldehyde in the internal organs of the plant, could provide sufficient nutrients for ZH-1^R endophytes. Also, formaldehyde gas stress had a positive effect on the number of endophytic bacteria inoculated into plants, but a negative effect on natural shoot of epiphytic bacteria (Khaksar et al., 2016b).

Positively, previous studies have shown that endophytic bacteria can improve host tolerance to biotic and abiotic stress and reduce plant damage under formaldehyde stress (Nandy et al., 2020). Thus, successful colonization of the ZH-1^R strain under FP conditions is beneficial in improving the resistance, tolerance, and formaldehyde removal efficiency of the host plant.

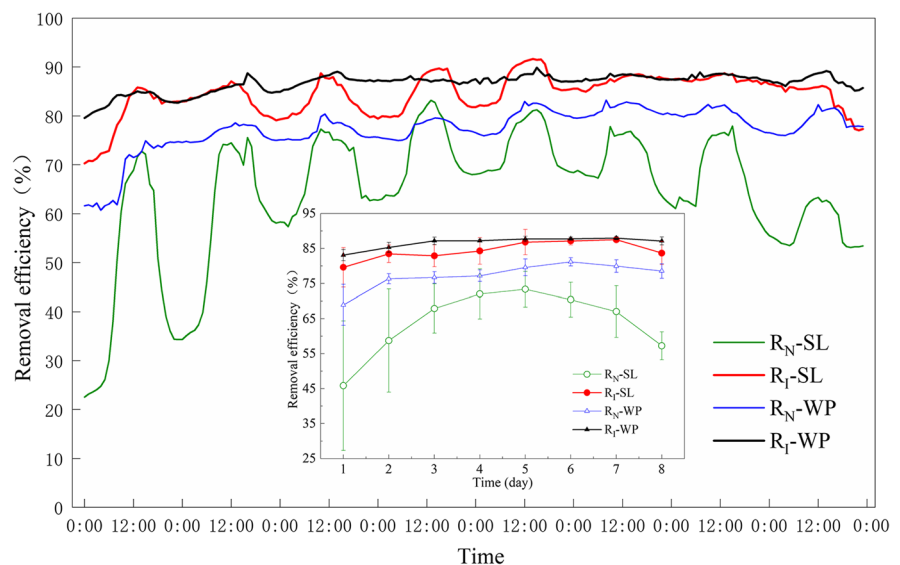
3.5 Continuous Fumigation Experiment

The *Chlorophytum comosum f. variegata* inoculated with the ZH-1^R strain by root irrigation method was fumigated for 8 days in the atmosphere containing 5 ppm of gaseous formaldehyde. The formaldehyde removal efficiency of the plant stem-leaf system (wrap the soil in tinfoil) and the efficiency of the whole plant were tested in the experiments. All plants inoculated with the ZH-1^R strain showed excellent formaldehyde removal capacity regardless of the plant system, with the stem-leaf part having the best results, especially at night time.

The removal efficiency was calculated from Eq. (1) and the results are presented in Fig. 6 (the actual raw data of measurements are presented in S3) confirming that the removal efficiencies of the R_N-SL (stem-leaf system) were much lower than those of the R_N-WP (whole plant), especially during nights. The R_I-SL's removal efficiencies at nights were generally lower than those of the R_I-WP, but the two curves start to converge after day 5. At the same time, the removal efficiency of R_N-SL was decreased significantly reaching 53.38% at day 8, while efficiencies obtained for three remaining scenarios were above 77%. Such outcome could be explained by the results of our previous study where physiological indexes of long-term formaldehyde fumigated plants were suffered varying degrees of damage, which reduced the resistance and tolerance to formaldehyde, as well as the removal efficiency (Li et al., 2019). Finally, it should be highlighted that all groups had lower removal efficiencies during the first day of the experiment. It could be explained by the fact that the test plants were still at the adaptation stage just after entering the formaldehyde containing environment, with following improvement achieved on completion of this stage.

The other important outcome evidenced in Fig. 6 is related to the fact that the formaldehyde removal efficiencies of the plant parts were improved effectively because of the endophyte ZH-1^R colonization. In addition, the efficiency gap between SL (plant's

Fig. 6 Formaldehyde removal efficiency by *Chlorophytum comosum f. variegata* during fumigation. R_I-SL and R_N-SL: plant's stem-leaf systems' removal efficiency of inoculated or non-inoculated; R_I-WP and R_N-WP: whole plant's removal efficiency of inoculated or non-inoculated (inset: removal efficiency during fumigation on daily basis)



stem-leaf system) and WP (whole plants system) also narrowed significantly from an average of 12.83 to 2.04%. The removal efficiency of R_I groups was almost stable during the whole fumigation period, which was different from R_N which declined sharply at later stages of the experiment. Interestingly, the fluctuation of the results was significantly larger for R_N group of plants, as compared to the results obtained for the R_I group. This difference was especially significant between day and night results and is presented by error bars in the inset of Fig. 6. Therefore, it could be concluded that the inoculation of the ZH-1^R strain into *Chlorophytum comosum* f. *variegata* not only increases the formaldehyde removal efficiency of the plants, but also improves their tolerance to the formaldehyde containing environment.

A well-known drawback reported by several researchers is related to significant time related decrease in formaldehyde removal efficiency by non-inoculated plants, which is especially observed during night time (Li et al., 2019; Teiri et al., 2018; Xu et al., 2011). The results demonstrated in Fig. 6 prove that the problem could be solved, providing comparably high results even at night time, if the plants will be inoculated by the ZH-1^R strain.

Figure 7 shows that the formaldehyde removal efficiency achieved by the plants inoculated with the ZH-1^R strain varied from approximately 110 to 290% proving that the ZH-1^R strain is capable of successful colonization on the tested plants significantly contributing to a stable and efficient formaldehyde degradation.

The highest removal efficiency ratio obtained at the earliest stages of the experiment (Fig. 7) could be explained by the fact that the fresh ZH-1^R strain was just placed into the stressful formaldehyde environment and was in hyperactive state. Then, the experiment entered a “flat” adaptation and domestication stage and finally achieved the strengthening phase associated with rapid increase in the removal efficiency illustrated by a “V” shape of the corresponding graphs in Fig. 7.

Furthermore, plant root exudates and autolysis products can be used as nutrients for rhizospheric microorganisms to stimulate microbial activity in the soil, thus enhancing the ability of the soil to absorb gaseous formaldehyde with the help of rhizospheric microorganisms (Kim et al., 2008). Therefore, with the increase of the whole plant removal rate, rhizosphere exudates

released by the plant can also contribute to an increase in the adsorption effect of the soil and the degradation effect of the soil microbiota.

In addition, for the SL group, the inflection point in the daytime occurred 1 day earlier than that in the night group, which fell on the 4th day. The reason for this is thought to be that the colonization strains also improve the resistance of *Chlorophytum comosum* f. *variegata* to a certain extent. The formaldehyde stress and the physiological and biochemical indexes (such as chlorophyll, MDA (malondialdehyde), SOD (superoxide dismutase)) in the leaves decreased the degree of damage, so stable or even improved photosynthesis of *Chlorophytum comosum* f. *variegata* during the day, therefore, also warrants more effective removal of formaldehyde.

Although soil adsorption contributes greatly to the removal of formaldehyde at night by uninoculated *Chlorophytum comosum* f. *variegata*, however, if the formaldehyde adsorbed on the soil is not decomposed in a timely manner by the plant rhizosphere and soil microorganisms, the risk of re-emission of formaldehyde into the air remains. Inoculation of the ZH-1^R strain allows not only to improve the removal of gaseous formaldehyde from the aerial parts of plants, but also to improve the ability

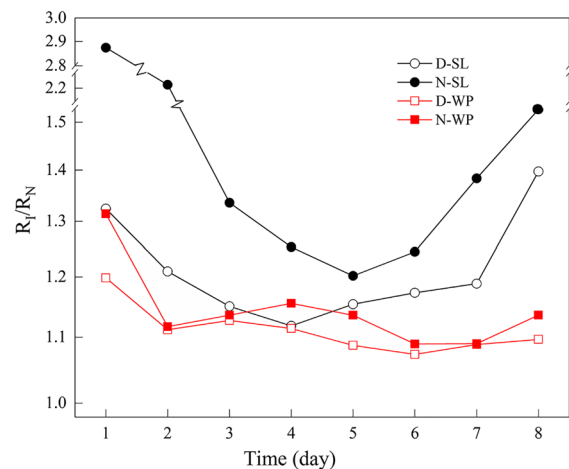


Fig. 7 Comparison of *Chlorophytum comosum* f. *variegata*'s removal efficiency during daytime and night between inoculated and non-inoculated strains ZH-1^R. R_I , removal efficiency of inoculated; R_N , removal efficiency of noninoculated; D-SL and N-SL, plant's stem-leaf systems during the daytime or night; D-WP and N-WP, whole plant during the daytime or night

of the soil and the underground part to completely remove gaseous formaldehyde.

Surprisingly, the whole plant showed two points of inflection both during the day and at night (Fig. 7). It is assumed that the inoculation of the strain has an important effect on the rhizosphere biosphere of the plant, since ZH-1^R gets the maximum recovery rate in the root, so it inevitably has a certain effect on the surrounding native flora. And the release of endophytic secretions and metabolites can also change the original environment of the rhizosphere, thereby causing a complex reaction leading to such a trend of change. However, the detailed mechanism of the reaction required some further studies.

In general, the formaldehyde removal efficiency of *Chlorophytum comosum* f. *variegata* has been greatly improved for the following reasons. First, the effective formaldehyde-degrading bacteria ZH-1^R can effectively decompose formaldehyde. Secondly, formaldehyde resistance of plants was improved after ZH-1^R successfully colonized them, which contributed to higher removal efficiency. Finally, ZH-1^R colonization altered the original rhizosphere microbiota, which would also contribute to formaldehyde removal to a certain extent.

4 Conclusions

Ochrobactrum intermedium ZH-1 was successfully labeled as strain ZH-1^R by using rifampicin antibiotics without changing the nature of the original strain. The ZH-1^R strain was then successfully inoculated into *Epipremnum aureum* and *Chlorophytum comosum* f. *variegata* via acupuncture injury to stem and root irrigation. The endophytic bacterium ZH-1^R better colonized and stabilized in the root of *Chlorophytum comosum* f. *variegata*, even during the 8-day period of fumigation with formaldehyde. In addition, the number of colonies of the ZH-1^R strain under the formaldehyde stress was higher than that in the clean environment, especially those recovered from the roots. Notably, endophyte-inoculated ZH-1^R harbored a significantly higher formaldehyde removal efficiency as compared to a non-inoculated ones, especially for stem-leaf system at nights.

It ought to be finally noticed that an applicability of the proposed approach to other plants and endophytic bacteria requires some additional studies. Also, this

project investigated formaldehyde removal leaving potential effects of endophytic colonization on other indoor pollutants for future investigations.

Author Contribution **JL**: conceptualization (lead); writing—original draft (lead); writing—review and editing (equal); visualization (lead); investigation (lead). **JZ**: software (lead); writing—review and editing (equal); resources (lead). **SC**: methodology (lead); writing—original draft (supporting); resources (supporting). **YJ**: writing—original draft (equal); resources (equal); visualization (supporting); **WZ**: conceptualization (supporting); writing—review and editing (supporting); **IA**: writing—review and editing (lead); supervisor (lead); formal analysis (lead).

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Data Availability The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code Availability Non applicable

Declarations

Ethics Approval and Consent to Participate N/A

Consent for Publication N/A

Conflict of Interest The authors declare no competing interests.

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