

Article

Effects of Root Exudates on Seed Germination and Seedling Growth of Wolfberry (*Lycium barbarum* L.) and the Development of Root Rot Diseases

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Abstract

Root exudates play a critical role in enabling plants to respond to environmental stresses and mediate information exchange within the rhizosphere. These compounds regulate plant–rhizosphere interactions and significantly influence the structural and functional properties of the rhizosphere micro-ecosystem. Under continuous cropping systems, allelochemicals derived from root exudates progressively accumulate in the root zone, thereby contributing to the development of continuous cropping obstacles. In this study, root exudates were collected from wolfberry (*Lycium barbarum* L.) and four forages under controlled conditions to test their effects on seed germination and seedling growth in mangold (*Beta vulgaris* L.) and wolfberry, as well as on the root rot pathogen. Our research shows that forage root exudates could promote wolfberry seedling growth. White clover (*Trifolium repens* L.) and alfalfa (*Medicago sativa* L.), especially, could have their growth increased by up to 61% and 90% ($p < 0.05$). Wolfberry root exudates could promote the seed germination and seedling growth of white clover and mangold, the seed germination of Ryegrass (*Lolium perenne* L.), and the seedling growth of alfalfa. In addition, mangold root rots were identified as Molds, *Aspergillus niger*, and *Fusarium solani* and wolfberry root rots were *Mucor cirrus*, *Rhizopus*, *Fusarium oxysporum*, and *Fusarium solani*. What is more, wolfberry root exudates could promote *Fusarium* plaque expansion and mycelial growth. Ryegrass inhibited the growth of *Mucor*, *Fusarium putrum*, and *oxysporum*, and alfalfa and white clover promoted the plaque expansion of *Rhizopus*, *Aspergillus niger*, and *Fusarium fulcrum*, but inhibited the mycelial growth of related pathogens; mangold root exudates could inhibit wolfberry root rot, which affects interspecific relationships. This study provides robust technical support for elucidating interspecific relationships and promoting the development and application of the wolfberry-forage intercropping system.

Keywords: root exudates; soil-borne diseases; root rot; wolfberry-forage intercropping



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1. Introduction

Root exportation is an important way for plants to respond to external stress, an important carrier material for transmitting and exchanging rhizosphere soil information,

which can regulate rhizosphere dialog, and is also an important factor in forming rhizosphere microecological characteristics [1,2]. Root exudates play an important role in the plant biogeochemical cycle, rhizosphere ecological process regulation, plant growth and development, etc. [3]. Fenugreek root exudates significantly stimulate *Panax ginseng* seed germination [4]. Yan et al. identified two important coumarins in the root exudates of *Stellera chamaejasme* L., which could inhibit the mitosis process of the *Lactuca sativa* root tip, affecting growth [5]. Intercropping can both reduce the occurrence of plant leaf diseases and effectively inhibit the spread and expansion of soil-borne diseases [6–8]. The control of soil-borne plant diseases is one of the key factors to ensure the sustainable development of agricultural production. With the development of ecology, soil-borne plant diseases have been studied from a new perspective. The accumulation of autotoxins and pathogens in soil is the main driving factor of soil-borne diseases [9,10]. Some water-soluble substances detected in the root secretions of alfalfa (*Leguminous*) can cause serious autotoxicity, and different concentrations have different promoting or inhibiting effects on the growth of surrounding plants [11]. Allelopathic effects of root exudates from different alfalfa cultivars exhibit significant variation in terms of seed germination inhibition and seedling growth suppression, with more pronounced phytotoxicity observed under long-term continuous monoculture practices [12].

Root-secreted organic acids, phenolic acids, and terpenoids serve as vital energy sources for soil microorganisms. The diverse components of root exudates differentially influence the composition and abundance of rhizosphere microbial communities [13]. For example, in salicylic acid and jasmonic acid, found in *Arabidopsis thaliana* root, exudates can selectively recruit specific microbial taxa, thereby shaping both rhizosphere and endosphere microbiomes and enhancing plant resistance to diseases [14,15]. Zhang et al. showed that, in rice–watermelon intercropping systems, watermelon roots increase the secretion of phenolic acids, amino acids, and organic acids, which helps reduce the incidence of *Fusarium wilt* in watermelon [16]. Likewise, in maize–pepper intercropping, maize root exudates have been found to inhibit the growth and spread of *Phytophthora capsici*, thus alleviating pepper blight [17]. These results highlight the strong link between root exudates and soil-borne pathogens. Plants may suppress pathogen proliferation either through the release of specific allelochemicals [18] or by modifying their root exudate profiles to indirectly alter pathogen behavior [19]. Gao et al. reported that cinnamic acid released in soybean–maize intercropping significantly decreases the occurrence of soybean red crown rot [20]. Dong et al. further demonstrated that tomato–chrysanthemum intercropping induces chrysanthemum roots to secrete lauric acid, which disrupts gene expression in root-knot nematodes and prevents nematode infection in tomatoes [21]. Moreover, in wheat–watermelon intercropping systems, wheat root exudates effectively control *Fusarium wilt* in watermelon by strongly inhibiting spore germination and the mycelial growth of the causal pathogen [22].

Root rot is recognized as one of the most prevalent and destructive soil-borne diseases globally [23]. Among these pathogens, *Fusarium* spp. are the primary causal agents of root rot in more than 20 economically significant crops, such as wolfberry, tobacco, and tomato [24,25]. Ningxia wolfberry (*Lycium barbarum* L.), a perennial deciduous shrub within the genus *Lycium* of the Solanaceae family, is a traditional Chinese medicinal and edible plant that plays a vital role in regional agriculture. As a key economic crop in northwestern China, it significantly enhances agricultural productivity and supports rural livelihoods. However, prolonged monoculture practices have led to a progressive increase in the incidence of root rot, with infection rates reaching up to 50% in affected areas. This escalating disease pressure has given rise to severe agroecological challenges, including continuous cropping obstacles, marked reductions in yield and product quality, and considerable

economic losses across the production chain [26], ultimately posing a critical threat to the long-term sustainability of the wolfberry industry [27].

Root rot-related and harmful pathogens, as one of the most serious soil-borne diseases in the production of mangold and wolfberry [28], accumulate yearly, along with repeated cropping time, leading to the biggest obstacle to the cultivation of wolfberry. Numerous domestic and international studies have investigated the factors contributing to root rot disease, revealing that its occurrence is significantly associated with planting year, geographical region, duration of continuous monoculture, preceding crop types, soil quality, cultivar selection, and weed presence [29]. The root rot is closely related to phenolic acids in root secretions, and, as the cropping years continue, these compounds accumulate in the wolfberry root, restricting the continuous cropping [30]. By conducting the indoor extraction of root exudates from wolfberry and herbage species, this study systematically investigated their effects on seed germination and seedling growth of mangold and wolfberry, while simultaneously evaluating their inhibitory potential against root rot pathogens. The findings are expected to provide robust technical support for elucidating interspecific interactions within the wolfberry–herbage intercropping systems, thereby providing technical references for optimizing cultivation models and scaling up agricultural applications.

2. Materials and Methods

2.1. Materials and Experimental Design

The research design encompasses five species, including wolfberry and four forage varieties. Wolfberry (*Lycium barbarum* L. cv. 401, Lb) was provided by the Institute of Wolfberry Science, Ningxia Academy of Agriculture and Forestry Sciences (Yinchuan, Ningxia, China.) and the forage seeds were purchased from the Ningxia Yuan sheng Lv yang Forest and Grass Ecological Engineering Co., Ltd. (Yinchuan, Ningxia, China.). Moreover, the forage species were classified into three families: Gramineae: ryegrass (*Lolium perenne* L., Lp), Leguminosae: alfalfa (*Medicago sativa* L., Ms) and white clover (*Trifolium repens* L., Tr), and Chenopodiaceae: mangold (*Betu vulgaris* L., Bv).

Sampling types and methods: forage material was nutrient matrix seedling for 30 days of growth, and wolfberry was 3-leaf tissue culture seedling. When sampling, gently shake off the root matrix and obtain the whole plant. After cleaning and disinfection, first culture the plants in the nutrient solution. The nutrient solution should be changed twice a week. After 7 days, repeatedly clean the roots of the well-growing plants with deionized water 2–3 times, and then transfer them to a 25-well hydroponics box containing 1 L of sterilized deionized water for culture (25 plants in monoculture; in intercropping, 15 grasses + 10 wolfberries). During the culture period, regularly replenish water to maintain the volume at 1 L, and sample the root exudates on the 21st day of culture.

2.2. Acquisition of Root Exudates

The well-grown monocroponic material cultured in the 25-well hydroponics box was selected, and the roots were repeatedly cleaned with sterilized deionized water for 2 to 3 times. The 5 plants in 1 group were placed in a beaker, cultured with 100 mL sterilized deionized water for 24 h, then the water was poured out for repeated operations, and the root exudates were collected after 48 h of re-culture. The enriched liquid was filtered and dried, then methanol was added, and the residue on the bottle wall was eluted by an ultrasonic oscillator (Jintan District Huacheng Runhua Experimental Instrument Factory, Changzhou, Jiangsu, China). After the methanol was completely volatilized, the root exudates were obtained by repeated washing 2 to 3 times and dissolved in 100 mL sterilized deionized water.

2.3. Seed Germination Test

After being disinfected with 75% alcohol for 3 min, disinfected with 3% NaClO for 12 min, washed with distilled water, transferred to Petri dishes (10 cm diameter) covered with filter paper, each dish containing 30 seeds, 2 mL root exudates and 2 mL distilled water (blank control) were dark treated at 28 °C. Three replicates were set for each treatment. The seeded Petri dishes were cultured in a light/dark cycle at temperature (28 °C), 16/8 h, and the germination of the seeds was observed and recorded daily.

The germination rate of the seeds of the 5 plants was calculated according to the description of germination in the International Code of Seed Inspection. Germination rate (%) = (the number of germinated seeds in each Petri dish/the number of seeds sown) × 100%, starting from the 5th day. The germination rate of 2–10 days was calculated, and statistical records were made. Germination potential (%) = (the number of germinated seeds on the day with the highest number of germinations/the number of seeds sown) × 100%. Vigor index (VI) = $(a/1 + b/2 + c/3 + d/4 + \dots + x/n) \times [100/S]$, where a, b, c, d, ... 1,2,3,4, respectively. n indicates the amount of seeds germinated on day 1, x indicates the amount of seeds germinated on day n, and S denotes the number of seeds tested. A total of 10 plants were randomly selected from each Petri dish on day 4 and day 7 to measure the plant height and root length, respectively.

2.4. Root Rot Identification Experiment

2.4.1. Root Rot Sampling

The experimental materials for wolfberry root rot were collected from the experimental field at the orchard farm of Ningxia Academy of Agriculture and Forestry Sciences (38°20' N, 106°16' E), where severe root rot symptoms have been consistently observed over six consecutive growing seasons. The samples for mangold root rot were obtained from a commercial mangold cultivation site in Ma'erzhuang Village, Yanchi County (37°60' N, 107°20' E).

2.4.2. Morphological Identification

The taxonomic identification of the fungal isolates was conducted in accordance with established methodologies from prior studies [31], with modifications to enhance precision and reproducibility. Potato Dextrose Agar (PDA) served as the basal culture medium for initial isolation and morphological characterization. Colony diameter and growth patterns were systematically recorded after 96 h of incubation at 22 °C under a 12 h light–dark cycle to ensure standardized developmental conditions. Microscopic examination was performed using a BX51 fluorescence microscope equipped with differential interference contrast (DIC) optics, enabling high-resolution visualization of cellular structures. Upon detection of mycelial growth, cultures were immediately transferred to fresh PDA plates. This subculturing procedure was repeated three times to eliminate contaminants and achieve axenic cultures. Following purification, colony morphology was thoroughly documented, including overall shape, diameter, pigmentation, surface topography (concave, convex, or flat), and mycelial texture (e.g., cottony, granular, or floccose). Representative colonies of each pathogenic isolate were selected for slide preparation, stained with carmine, and examined under 10×, 20×, and 40× objectives, as well as a 100× oil immersion lens, to evaluate hyphal architecture and conidial morphology. All observations were systematically recorded, and photomicrographs were taken at consistent magnifications to support comparative analysis. Diagnostic morphological traits—such as the presence, size, shape, and arrangement of macroconidia and microconidia, the formation of chlamydospores, and the structural characteristics and dimensions of conidiophores—were carefully assessed.

These phenotypic features were integrated to determine the taxonomic identity of the isolates with greater confidence and scientific rigor.

2.4.3. Molecular Biological Identification

Fungal strains isolated from wolfberry and decayed mangold roots were cultivated in PDB medium for 7–10 days to ensure robust and stable mycelial growth. Cultures were subsequently transferred into 50 mL centrifuge tubes and centrifuged at 4500 r/min for 10 min. The resulting mycelial pellets were homogenized and immediately frozen at -80°C for 2 h to preserve nucleic acid integrity prior to genomic DNA extraction. Total genomic DNA was extracted using the OMEGA Fungal DNA Extraction Kit following the manufacturer's protocol. DNA concentration and purity were determined spectrophotometrically using a UV spectrophotometer, and only samples meeting predefined quality thresholds (e.g., A260/A280 ratio between 1.8 and 2.0) were retained for downstream molecular identification. Sequence analysis was performed, targeting the ribosomal internal transcribed spacer (ITS) region, which is widely recognized as a reliable fungal barcode. PCR amplification was carried out using the universal primers ITS1 (5'-TCCGTAGGTGAACCTGCGG-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3') in a 40 μL reaction system containing 20 μL PCR Mix, 2 μL template DNA, 2 μL forward primer, 2 μL reverse primer, and 14 μL ddH₂O. Thermal cycling conditions included an initial denaturation at 95°C for 5 min, followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 55°C for 30 s, and extension at 72°C for 50 s, with a final extension at 72°C for 10 min, after which reactions were held at 4°C . Molecular identification of the RPB2 gene fragment was conducted using the primer pair 5f2 (5'-GGGGWGAYCAGAAGAAGGC-3') and 7cr (5'-CCCATRGTCTGYT TRCCCATPCR-3'), which target conserved regions of the RNA polymerase II second largest subunit, a widely used phylogenetic marker in fungal systematics. The PCR amplification was performed in a 20 μL reaction mixture consisting of a 10 μL PCR Mix, 1 μL template DNA, 1 μL forward primer, 1 μL reverse primer, and 7 μL ddH₂O. Amplification was carried out under the following thermal cycling conditions: an initial pre-denaturation at 95°C for 5 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 52.1°C for 30 s, and extension at 72°C for 60 s, with a final extension at 72°C for 10 min, and subsequent holding at 4°C .

The rDNA sequences of each related species were selected from GenBank database, and the phylogenetic tree was constructed with the tested strains. DNA sequence was analyzed using an NCBI sequence comparison tool BLAST (<https://blast.ncbi.nlm.nih.gov/>, accessed on 26 November 2025) program, which compares and analyzes the sequence obtained by cloning. Clustal X compares and analyzes multiple sequences. MEGA X neighbor-joining method builds the evolutionary tree, where the number of repetition is set to 1000.

2.4.4. Identification of Pathogenic Fungi

Fungal strains isolated and purified from the roots of wolfberry and mangold displaying root rot symptoms were re-inoculated onto healthy, tissue-cultured seedlings of both host species. After 14 days, characteristic disease symptoms developed in wolfberry seedlings inoculated with *Mucor cirrus*, *Rhizopus*, *Fusarium oxysporum*, and *Fusarium solani*, as well as in mangold seedlings challenged with *Molds*, *Aspergillus niger*, and *Fusarium solani*. Notably, when the strains are co-inoculated in a 1:1 ratio, the resulting disease symptoms closely resemble those observed under field conditions. Notably, co-inoculation of these strains at a 1:1 ratio resulted in disease symptoms that were highly consistent with those observed under natural field conditions, strongly suggesting that the interaction between the strains recapitulates the typical disease phenotype, and significant differ-

ences in disease severity were observed when the strains were inoculated individually, highlighting distinct pathogenic capabilities among the isolates. Moreover, the observed symptoms closely mirrored those of naturally occurring root rot, exhibiting typical necrotic lesions, root browning, and stunted growth, consistent with field-collected diseased plants. Pathogens were successfully re-isolated and purified from symptomatic tissues, and the resulting fungal isolates displayed morphological and biological characteristics identical to the original inocula. Fulfilling all criteria of Koch's postulates, this study confirms that *Fusarium oxysporum* and *Fusarium solani* are the primary causal pathogens of root rot in this wolfberry variety, while *Fusarium solani* is the dominant pathogen associated with root rot in mangold.

2.5. Root Exudate Re-Inoculation Experiment

A fungal plug was aseptically excised from the center of colonies formed by activated strains on PDA medium (cultured at 28 °C) using a sterilized cork borer with an inner diameter of 5 mm. The plug was transferred to fresh PDA medium supplemented with 1 mm root exudates and subsequently inoculated with root rot pathogen strains. Cultures were incubated at a constant temperature of 25 °C under continuous illumination for 3 days. Colony diameters were measured daily on days 1, 2, and 3 using the cross-measurement method; subtracting 5 mm from each measurement accounted for the initial inoculum size and allowed for the accurate quantification of net mycelial growth per strain. All treatments were performed in triplicate to ensure experimental reliability. Morphological analyses were conducted using a BX51 fluorescence microscope (BX51 Microscope, Olympus Investment Co., Ltd., Beijing, China) equipped with DIC (differential interference contrast) optics. Upon hyphal emergence, intact and morphologically representative hyphae were selected, and optimal focus and magnification settings were applied prior to image capture. Hyphal length was calculated based on the calibrated magnification of the acquired images. Three distinct regions were analyzed per sample, and mean hyphal length was computed to improve measurement robustness. Each treatment group consisted of three biological replicates, with 10 microscopic fields randomly selected from each replicate for mean calculation. This design established three independent experimental units and enhanced statistical validity and reproducibility.

2.6. Data Processing and Analysis

All experimental data were analyzed using Excel v2010 (Microsoft Corp., Redmond, WA, USA) and SPSS v17.0 Statistics (SPSS Inc., Chicago, IL, USA). Before statistical analyses, the Chi-square test for normality of the data was conducted. Mean comparisons among treatments were performed using Fisher's protected least significant difference test when the analysis of variance (ANOVA) indicated a significant effect (Fisher's LSD, $p < 0.05$).

3. Results

3.1. Root Exudates' Influence on Seed Germination and Seedling Growth

Germination experiments conducted on four forage species treated with root exudates of wolfberry and ddH₂O demonstrated that these exudates promoted the germination of white clover, mangold, and ryegrass seeds. Notably, the germination rate of mangold seeds increased by 36.11% ($p < 0.05$), a result of particular significance given the species' typically low germination capacity and uneven field emergence. Consequently, wolfberry–mangold intercropping may substantially improve both the emergence rate and uniformity of mangold. In contrast, the root exudates exerted a moderate inhibitory effect on alfalfa seed germination, with an inhibition rate of 6.91% ($p < 0.05$). Further analysis of seedling growth responses showed that *Lycium barbarum* root exudates suppressed ryegrass seedling

growth by 53.66% ($p < 0.05$), while significantly promoting the growth of alfalfa, white clover, and mangold seedlings by 75.24%, 46.74%, and 6.94% ($p < 0.05$), respectively. Overall, wolfberry root exudates exhibit a stimulatory effect on both seed germination and early seedling development in white clover and mangold (Table 1).

Table 1. Effects of root exudates of wolfberry on seed germination and seedling growth.

Treatment	Germination Rate (%)		Inhibition Rate (%)	Length (cm)		Inhibition Rate (%)
	Wolfberry Solution Treatment	Distilled Water Control		Wolfberry Solution Treatment	Distilled Water Control	
Ryegrass	61.90 ± 2.21 c	59.33 ± 1.45 c	−4.33 n.s	5.17 ± 0.08 e	11.16 ± 0.56 c	53.66 ***
Alfalfa	88.74 ± 2.21 b	95.33 ± 4.37 a	6.91 *	7.69 ± 0.56 d	4.39 ± 0.10 ef	−75.24 ***
Clover	92.47 ± 1.77 ab	88.67 ± 3.12 b	−4.29 n.s	4.27 ± 0.07 f	2.91 ± 0.22 g	−46.74 ***
Mangold	12.10 ± 0.89 d	8.89 ± 0.06 e	−36.11 ***	13.43 ± 0.14 a	12.56 ± 0.27 b	−6.94 *
LSD (5%)						

Notes: Mean values ($\bar{x} \pm SE$) followed by the same lowercase letters were not significantly different among treatments based on ANOVA LSD test ($p < 0.05$) of square-root transformed data ($n = 10$). n.s, not significant; *, $p < 0.05$ and ***, $p < 0.001$ (by *t*-test).

Germination tests of wolfberry seeds treated with root exudates from four forage grass species revealed that these exudates exerted varying degrees of inhibitory effects on seed germination; however, the inhibition was not statistically significant ($p > 0.05$). The high germination rate observed in the control group indicates that the root exudates from the tested forage grasses do not impair wolfberry seed germination. Further analysis of seedling growth responses demonstrated that the root exudates significantly promoted the growth of wolfberry seedlings ($p < 0.05$), with enhancement rates of 89.67%, 60.96%, 55.75%, and 35.60% for white clover, alfalfa, ryegrass, and mangold, respectively. Overall, the net effect of forage grass root exudates on both seed germination and early seedling development in wolfberry is positive. This promotive influence, as summarized in Table 2, supports the potential for beneficial interactions in intercropping systems involving wolfberry and forage grasses, providing a scientific foundation for their integrated cultivation.

Table 2. Effects of root exudates of herbage on seed germination and seedling growth of wolfberry.

Root Exudates	Germination Rate (%)	Inhibition Rate (%)	Bud Length (cm)	Inhibition Rate (%)
CK	91.00 ± 1.44 a	0.00	3.97 ± 0.12 d	0.00
Ryegrass	86.99 ± 4.87 a	4.41 n	6.18 ± 0.09 bc	−55.75 ***
Alfalfa	89.16 ± 0.23 a	1.75 n	6.39 ± 0.23 b	−60.96 ***
Clover	87.69 ± 1.89 a	3.22 n	7.53 ± 0.20 a	−89.67 ***
Fodder beet	88.07 ± 1.11 a	2.84 n	5.38 ± 0.07 c	−35.60 ***
LSD (5%)				

Notes: Mean values ($\bar{x} \pm SE$) followed by the same lowercase letters were not significantly different among treatments based on ANOVA LSD test ($p < 0.05$) of square-root transformed data ($n = 10$). ns, not significant; ***, $p < 0.001$ (by *t*-test).

3.2. Pathogens of Wolfberry Root Rot Identification

3.2.1. Morphological Identification of Pathogens to Wolfberry Root Rot Disease

Root systems showing symptoms of root rot were collected from the wolfberry planting base at the garden farm and cultured for fungal pathogen isolation. Four dominant fungal strains were isolated and designated as Lb-A, Lb-B, Lb-C, and Lb-E, respectively. Morphological identification was conducted based on the presence or absence of macroconidia and microconidia, chlamydospores, as well as the size, shape, and mode of conidial production, and the morphology and dimensions of conidiophores, which can be seen in

Figure 1. Lb-A mycelium was white, transparent, branched, and without transverse septum in the early stage, which was divided into latent trophic mycelium and gaseous creeping mycelium, and cyan and black in the late stage. Spore peduncle grew from stolon mycelium, unbunched, solitary, without rhizomes; Sporangium terminal, globular, colorless at first, grayish brown later. The spores of the pathogen Lb-B have no septum, and the apical branches are broom-like, asymmetrical or symmetrical. The sporangium stems are single from the mycelium, branched or unbranched. The colony is white at the beginning, evenly distributed, and the mycelium is long and dense, and the whole becomes black at the latter stage. Lb-A and Lb-B were preliminarily identified as *Mucor* or *Rhizopus*. Small conidium and chlamyospore were observed in the colony of strain Lb-C, which were white and flocculant, mycelium was septate, and the air mycelium was slightly higher arachnoid, and light red pigment was produced in the later stage, which was most obvious at the bottom of the Petri dish. The airborne mycelia formed by strain LP-E on the PDA medium were fluffy, white or powdery white. With the growth of mycelia, bluish gray mycelia clusters could be seen on the front side. The large conidia were sickle-shaped and slightly curved, the small conidia were oval, and the interhyphal or apical chlamydia spores were observed. Lb-C and Lb-E were preliminarily identified as one kind of *Fusarium*. Preliminary morphological analysis indicated that Lb-A and Lb-B, the primary pathogens associated with wolfberry root rot, were tentatively classified as belonging to the genera *Mucor* or *Rhizopus*, whereas Lb-C and Lb-E were tentatively identified within the genus *Fusarium*.

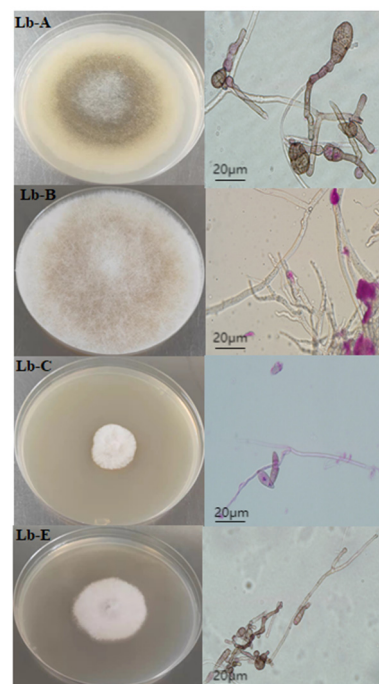


Figure 1. Culture characters and morphological characteristics of pathogen of wolfberry root rot. Notes: Lb-A, B, C, and E represent the colony morphology of the predominant pathogenic fungi isolated from wolfberry root rot, along with the corresponding morphological characteristics of their conidia and hyphae.

3.2.2. Molecular Biological Identification

The second major subgene (RPB2) of root rot pathogen RNA polymerase II was amplified by 5f2/7cr primer. The amplification products were resolved by electrophoresis on a 0.8% agarose gel, yielding fragments of approximately 500–700 bp in size. The purified PCR products were submitted for Sanger sequencing, and the resulting sequences were analyzed using the BLAST algorithm against the GenBank database. Sequences exhibiting

high similarity were retrieved, and a phylogenetic tree was constructed using the neighbor-joining method in MEGA X software (MEGA X 10.1.8 version). The results showed that the Lb-A1 sequence of the wolfberry root rot isolate exhibited 99.67% sequence similarity to *Mucor circinelloides* (MT603942.1). The Lb-B1 sequence shared 100% similarity with *Rhizopus arrhizus* (MN525244.1), while the Lb-C1 sequence showed 100% similarity to *Fusarium solani* (GU170639.1). Additionally, the Lb-E1 sequence demonstrated 100% similarity to *Fusarium oxysporum* (KF913725.1) (Tables 3 and S1–S4, Figure 2).

Table 3. Comparison and description of wolfberry LB-A strain and its related species.

Strain Designation	Scientific Name Abbreviations	Max Score	Total Score	Query Cover	E value	Per. Ident	Acc. Len	Accession
Lb-A	<i>Mucor circinelloides</i>	1107	1107	97%	0	99.67%	618	KF435037.1
	<i>Mucor circinelloides</i>	1103	1103	98%	0	99.51%	1105	MT603942.1
	<i>Mucor circinelloides</i>	1103	1103	98%	0	99.51%	1106	MT603901.1
	<i>Mucor circinelloides</i>	1103	1103	98%	0	99.51%	1065	MT603900.1
	<i>Mucor circinelloides</i>	1103	1103	98%	0	99.51%	642	KX349456.1
Lb-B	<i>Rhizopus arrhizus</i>	1088	1088	95%	0	100.00%	593	MN525244.1
	<i>Rhizopus arrhizus</i>	1088	1088	95%	0	100.00%	592	MN525242.1
	<i>Rhizopus arrhizus</i>	1088	1088	96%	0	99.83%	621	MK174986.1
	<i>Rhizopus arrhizus</i>	1085	1085	97%	0	99.17%	633	MN010553.1
	<i>Rhizopus arrhizus</i>	1085	1085	97%	0	99.50%	629	MN006654.1
Lb-D	<i>Rhizopus arrhizus</i>	1085	1085	96%	0	99.66%	619	MK174988.1
	<i>Fusarium solani</i>	1986	1986	0.99	0	1	1075	GU170639.1
	<i>Fusarium solani</i>	1984	1984	0.99	0	1	1434	LT746274.1
	<i>Fusarium solani</i>	1984	1984	0.99	0	1	1103	KY484955.2
	<i>Fusarium solani</i>	1984	1984	0.99	0	1	1103	KY484946.1
Lb-E	<i>Fusarium solani</i>	1984	1984	0.99	0	1	1168	KT313637.1
	<i>Fusarium oxysporum</i>	1319	1319	0.99	0	1	714	KF913725.1
	<i>Fusarium oxysporum</i>	1317	1317	0.99	0	1	714	KF574854.1
	<i>Fusarium oxysporum</i>	1317	1317	0.99	0	1	713	DQ837657.1
	<i>Fusarium oxysporum</i>	1314	1314	1	0	0.9986	1015	MK059958.1
	<i>Fusarium oxysporum</i>	1314	1314	1	0	0.9986	1067	KX822794.1

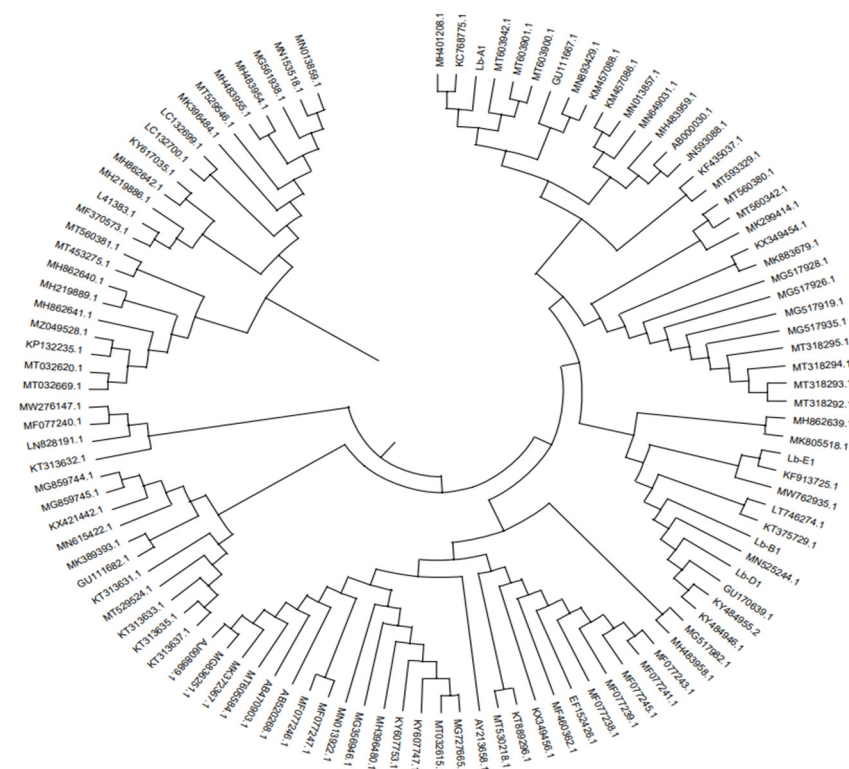


Figure 2. Phylogenetic tree of wolfberry root rot strain based on rDNA-5F2/7Cr sequence.

The genomic DNA of the pathogen was amplified via PCR using primers ITS1/ITS4. The amplification products were resolved by electrophoresis on a 0.8% agarose gel, yielding fragments of approximately 500–700 bp in size. The purified PCR products were submitted for Sanger sequencing, and the resulting sequences were analyzed using the BLAST algorithm against the GenBank database. Sequences exhibiting high similarity were retrieved, and a phylogenetic tree was constructed using the neighbor-joining method in MEGA X software. The results showed that the similarity between Lb-A2 and *Rhizopus arrhizus* (MK174988.1) was 77%. The similarity between Lb-B2 and *Fusarium oxysporum* (MT560342.1) was 91%. The similarity between Lb-C2 sequence and *Fusarium solani* (MN013859.1) was 100%, and the Lb-E2 sequence was 100% similar to *Fusarium oxysporum* (KF574854.1). The pathogens related to the root rot disease of wolfberry were identified as *Mucor circlocladus* (Lb-A), *Rhizopus* (Lb-B), *Fusarium solani* (Lb-C), and *Fusarium oxysporum* (Lb-E) (Tables 3 and S1–S4, Figure 3).

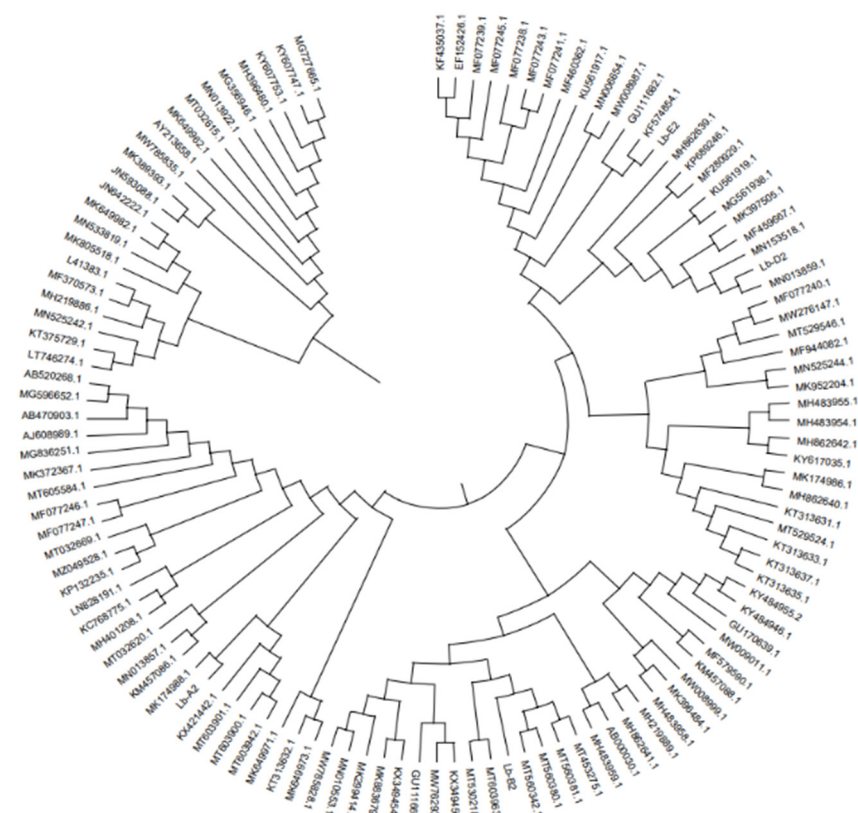


Figure 3. Phylogenetic tree of *wolfberry* root rot strain based on rDNA-ITS sequence.

3.3. Pathogenic Fungi of Mangold Root Rot Identification

3.3.1. Morphological Identification of Pathogens Related to Mangold Root Rot

Following the isolation, purification, and in vitro cultivation of infected mangold roots intended for animal feed, five predominant fungal strains were isolated and designated as Bv-A, Bv-B, Bv-C, Bv-E, and Bv-F for subsequent taxonomic characterization. Morphological identification was conducted through the systematic examination of key diagnostic traits, including the presence or absence of macroconidia and microconidia, conidial size, shape, and mode of formation, conidiophore morphology and dimensions, as well as the development of chlamydospores features that collectively provide critical taxonomic resolution within the genus. These results are presented in Figure 4. The mycelia of Bv-A had no rhizomes, unbunched sporangium, solitary, dense stratified, erect, uniaxial, or pseudouniaxial branching, and all apical sporangium. Sporangium is large, spherical,

oval, or irregular. Preliminary identification as *Mildew*. Bv-B colony 1–2 cm or smaller in diameter, slow growth in the later period, gray-green colony, with obvious shape in the middle, dense short villi, dry appearance, the apex of conidial pedicle expanded into an apical sac, generally spherical, preliminary identification as *Aspergillus*. Bv-C colony was white at the early stage, with short villi erect and uninterleaved. The colony was thin and its thickness increased from inside to outside. Most of the small conidia were single cells with septa, and most of the shapes were ovate or fusiform. The Bv-E colony was white in the early stage, and turned yellow in the later stage, with deepened color. The villi were long and interlaced like cotton wool, and the colonies were thick, and the middle was higher than the edge. Conidium scattered on air mycelium or conidium seat, sickle-shaped and fusiform, with obvious separation, and more separation number. The Bv-F colony was thick and light yellow, and the spreading rate of colony diameter was low. Air mycelium, conidium mostly single cell, or very few microspores. Preliminary identification suggests that Bv-C, Bv-E, and Bv-F are pathogenic fungi belonging to the *Fusarium* genus. Preliminary morphological analysis indicated that Bv-A and Bv-B, the primary pathogens associated with mangold root rot, were tentatively classified as belonging to the genera *Mildew* or *Aspergillus*, whereas Bv-C, Bv-E, and Bv-F were tentatively identified within the genus *Fusarium*.

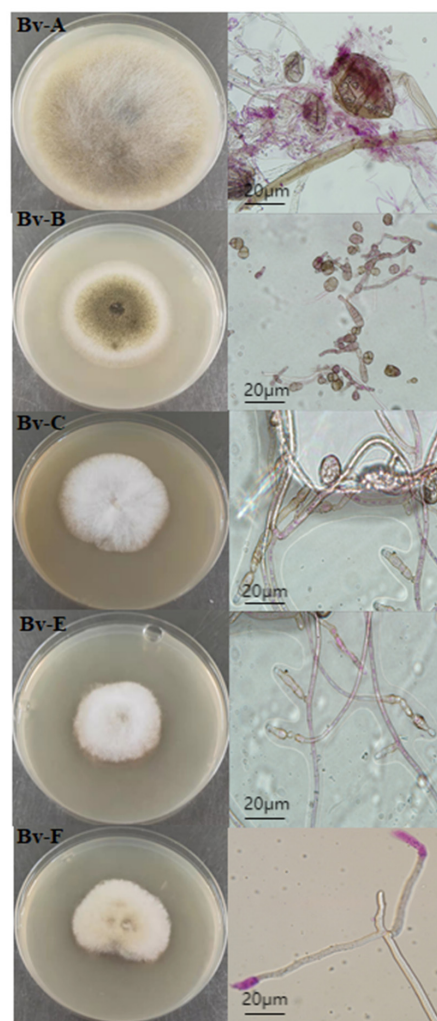


Figure 4. Culture characteristics and morphological characteristics of pathogen of mangold root rot. Notes: Bv-A, B, C, E, and F represent the colony morphology of the predominant pathogenic fungi isolated from mangold root rot, along with the corresponding morphological characteristics of their conidia and hyphae.

3.3.2. Molecular Biological Identification

The second major subgene (RPB2) of root rot pathogen RNA polymerase II was amplified by 5f2/7cr primer. The amplification products were resolved by electrophoresis on a 0.8% agarose gel, yielding fragments of approximately 500–700 bp in size. The purified PCR products were submitted for Sanger sequencing, and the resulting sequences were analyzed using the BLAST algorithm against the GenBank database. Sequences exhibiting high similarity were retrieved, and a phylogenetic tree was constructed using the neighbor-joining method in MEGA X software. The Bv-A1 sequence of the mangold root rot isolate showed high homology to *Mucor circinelloides* (MW578449.1) and clustered with it. Bv-B1 was highly homologous to *Aspergillus niger* (LC577101.1) and formed a cluster. Bv-C1, Bv-E1, and Bv-F1 each shared high homology with *Fusarium solani* and clustered with the reference strains KX421442.1, KM457086.1, and MF460362.1, respectively (Tables 4 and S5–S9, Figure 5).

Table 4. Comparison and description of mangold Bv-F strain and its related species.

Strain Designation	Scientific Name Abbreviations	Max Score	Total Score	Query Cover	E Value	Per. Ident	Acc. Len	Accession
Bv-A	<i>Mucor lusitanicus</i>	1011	1011	0.98	0	0.8759	2796	JN993501.1
	<i>Mucor hiemalis</i>	883	883	0.97	0	0.8511	2652	EF014398.1
	<i>Mucor irregularis</i>	880	880	0.9	0	0.864	1003	JX976270.1
	<i>Mucor irregularis</i>	869	869	0.9	0	0.8616	1003	JX976276.1
	<i>Mucor irregularis</i>	869	869	0.9	0	0.8616	1003	JX976287.1
Bv-B	<i>Aspergillus</i> sp. IFM 64240	1454	1454	0.97	0	0.9987	1050	LC179908.1
	<i>Aspergillus tubingensis</i>	1454	1454	0.97	0	0.9987	1052	LC000573.1
	<i>Aspergillus tubingensis</i>	1454	1454	0.97	0	0.9987	997	KC796436.1
	<i>Aspergillus pulverulentus</i>	1454	1454	0.97	0	0.9987	1040	HE984368.1
	<i>Aspergillus tubingensis</i>	1454	1454	0.97	0	0.9987	3771	XM035498810.1
Bv-C	<i>Fusarium solani</i>	1042	1042	1	0	1	566	MT605584.1
	<i>Fusarium solani</i>	1042	1042	1	0	1	566	MK372367.1
	<i>Fusarium solani</i>	1042	1042	1	0	1	566	MG836251.1
	<i>Fusarium solani</i>	1042	1042	1	0	1	570	MG561938.1
	<i>Fusarium solani</i>	1042	1150	1	0	1	623	KY617035.1
Bv-E	<i>Fusarium solani</i>	1986	1986	0.99	0	1	1075	GU170639.1
	<i>Fusarium solani</i>	1984	1984	0.99	0	1	1434	LT746274.1
	<i>Fusarium solani</i>	1984	1984	0.99	0	1	1103	KY484955.2
	<i>Fusarium solani</i>	1984	1984	0.99	0	1	1103	KY484946.1
	<i>Fusarium solani</i>	1984	1984	0.99	0	1	1168	KT313637.1
Bv-F	<i>Fusarium solani</i>	1048	1048	1	0	1	567	AB470903.1
	<i>Fusarium solani</i>	1048	1048	1	0	1	570	MG561938.1
	<i>Fusarium solani</i>	1048	1048	1	0	1	567	AB470903.1
	<i>Fusarium solani</i>	1046	1046	0.99	0	1	566	MT605584.1
	<i>Fusarium solani</i>	1046	1046	0.99	0	1	566	MK372367.1

The genomic DNA of the pathogen was amplified via PCR using primers ITS1/ITS4. The amplification products were resolved by electrophoresis on a 0.8% agarose gel, yielding fragments of approximately 500–700 bp in size. The purified PCR products were submitted for Sanger sequencing, and the resulting sequences were analyzed using the BLAST algorithm against the GenBank database. Sequences exhibiting high similarity were retrieved, and a phylogenetic tree was constructed using the neighbor-joining method in MEGA X software. The results showed that the Bv-A2 sequence of the mangold root putrid disease strain had high homology with *Penicillium solitum* (JN642222.1). Bv-B2 had high homology with *Aspergillus niger* (LC577101.1) and clustered together. Bv-C2 had high homology with *Fusarium solani* (KP132235.1) and clustered together. Bv-E2 had higher homology with *Fusarium solani* (KY484946.1) and clustered together, and Bv-F2 sequences have higher homology with *Fusarium solani* (KT313632.1), clustered together. Based on the comprehensive

3.4. Root Exudates' Effect on Pathogenic Fungi of Root Rot Disease

3.4.1. Effects of Different Root Secretions on the Plaque Size of Pathogenic Fungi Related to Wolfberry Root Rot Disease

In the medium containing CK, Lb-A had the maximum values in both plaque diameter and mycelial growth rate. It also showed significant differences when compared with the root exudates of the three herbage species. This indicates that the root exudates of alfalfa, white clover, ryegrass, and mangold can effectively inhibit the growth of these fungi. Moreover, ryegrass and mangold have significant effects on inhibiting the spread of the strain and mycelial growth. In the medium containing CK, Lb-B had the smallest plaque diameter, and showed significant difference from the root exudates of the three forage species. There was no significant difference in mycelial growth rate between CK and Lp and Bv. The root exudates of Ms and Tr were significantly higher than those of CK. In the medium treated with Ms and Tr root secretions, Lb-C had the largest plaque diameter, which was significantly different from other treatments, while the mycelial growth rate was the smallest. Ryegrass root exudates-treated medium had significant differences with the control in both plaque diameter and mycelia growth rate, and significantly inhibited the growth of this strain. The root secretion of mangold inhibited the growth of these strains to a certain extent, and ryegrass showed a more significant inhibitory effect on Lb-C fungi. In the medium containing CK, both the plaque diameter and mycelial growth rate of the Lb-E strain reached their maximum values. When compared with the root secretions of the three herbage species, significant differences were observed. This indicates that the root secretions of alfalfa, white clover, ryegrass, and mangold can effectively inhibit the growth of this bacterium. Moreover, mangold and white clover have more significant inhibitory effects on the Lb-E strain. The root exudates of wolfberry promoted the expansion of plaque and mycelia growth of *Fusarium oxysporum* in the root rot of wolfberry (Tables 5 and 6).

Table 5. Effects of different root exudates on the diameter of wolfberry root rot-related fungus colony.

Treatment	Diameter of Pathogenic Fungi (mm)			
	Lb-A	Lb-B	Lb-C	Lb-E
CK	60.52 ± 0.57 a	65.22 ± 1.09 d	17.79 ± 1.82 c	16.88 ± 0.20 a
Ms	57.58 ± 0.38 b	73.89 ± 0.50 b	19.96 ± 1.72 a	16.23 ± 0.11 ab
Tr	56.87 ± 0.66 b	76.42 ± 0.78 a	19.74 ± 0.96 a	16.07 ± 0.11 ab
Lp	53.88 ± 1.50 c	72.93 ± 0.37 bc	14.98 ± 0.17 e	16.16 ± 0.17 ab
Bv	58.11 ± 0.31 b	71.17 ± 0.10 c	16.87 ± 0.35 d	15.43 ± 0.37 b
Lb	53.88 ± 1.50 c	72.93 ± 0.37 bc	18.98 ± 0.17 b	17.16 ± 0.17 a
LSD (5%)				

Notes: Mean values ($\bar{x} \pm SE$) followed by the same letter were not significantly different using LSD ($p < 0.05$) on diameter of pathogenic fungi data ($n = 10$). Ms, Tr, Lp, Bv, and Lb stand for alfalfa, white clover, ryegrass, mangold, and wolfberry.

Based on a comprehensive analysis, the effects of forage root exudates on wolfberry root rot can be summarized as follows: root exudates from mangold and ryegrass exhibit strong inhibitory activity against the pathogens responsible for wolfberry root rot. In contrast, those derived from alfalfa and white clover promote the colony expansion of *Rhizopus*, *Aspergillus niger*, and *Fusarium solani*, while simultaneously suppressing mycelial growth in other root rot-associated pathogens. These findings suggest that such exudates may contain specific bioactive compounds that selectively facilitate the proliferation of the former group of pathogenic fungi. Furthermore, the presence of autotoxic substances in wolfberry root exudates has been shown to exacerbate the progression and severity of its own root rot disease.

Table 6. Effects of different root exudates on mycelial growth rate of wolfberry root rot-related pathogens.

Treatment	Growth Rate of Mycelia (mm·d ^{−1})			
	Lb-A	Lb-B	Lb-C	Lb-E
CK	11.92 ± 1.05 a	13.96 ± 1.72 b	6.85 ± 0.17 a	4.73 ± 0.02 a
Ms	11.28 ± 0.33 b	15.32 ± 2.43 a	4.31 ± 0.05 c	4.53 ± 0.14 ab
Tr	11.32 ± 0.54 b	16.01 ± 0.66 a	3.07 ± 0.03 d	4.27 ± 0.14 ab
Lp	11.40 ± 1.05 ab	13.68 ± 0.22 b	5.70 ± 0.98 b	4.56 ± 0.21 a
Bv	9.46 ± 1.50 c	13.72 ± 0.89 b	5.69 ± 0.43 b	4.07 ± 0.05 b
Lb	11.34 ± 1.00 ab	13.66 ± 0.22 b	6.99 ± 0.98 a	4.76 ± 0.21 a
LSD (5%)				

Notes: Mean values ($\bar{x} \pm SE$) followed by the same letter were not significantly different using LSD ($p < 0.05$) on diameter of pathogenic fungi data ($n = 10$). Ms, Tr, Lp, Bv, and Lb stand for alfalfa, white clover, ryegrass, mangold, and wolfberry.

3.4.2. Effects of Different Root Exudates on the Plaque Size of Pathogenic Fungi Related to Root Rot Disease of Mangold

Both the plaque diameter and mycelial growth rate of Bv-A in the CK medium were the maximum values, and there were significant differences in plaque diameter between BV-A and the three kinds of grass root exudes. The mycelial growth rate of ryegrass showed significant differences. It indicated that the root exudates of ryegrass could effectively inhibit the growth of Bv-A fungi, and the root exudates of wolfberry also had a certain inhibitory effect, but the effect was not significant. The plaque diameter of Bv-B was the largest in the medium containing CK, and it was significantly different from that of alfalfa and ryegrass root exudates. In addition, the growth rate of mycelium was the maximum after treatment of alfalfa and white clover root exudates, and there was no significant difference compared with control and ryegrass treatment, but there was a significant difference compared with wolfberry root exudates. The plaque diameter of Bv-C and Bv-E on Ms-, Tr-, and Lb-treated media was significantly increased over that of the control. In terms of mycelial growth rate, ryegrass, alfalfa, and white clover showed an inhibitory effect, and white clover showed the most significant inhibitory effect, while Lb root exude treatment showed a promotion effect ($p < 0.05$). The plaque diameter of the BV-F strain was the largest on the medium treated with Bv, which had no significant difference compared with Lb treatment, but showed a significant difference compared with Ms, Tr, Lp, and CK ($p < 0.05$). Mycelial growth rate decreased significantly under Tr and Lp root secretion treatment, but there was no significant difference in other strains (Tables 7 and 8).

Table 7. Effects of different root exudates on the diameter of pathogens associated with mangold root rot.

Treatment	Diameter of Pathogenic Fungi (mm)				
	Bv-A	Bv-B	Bv-C	Bv-E	Bv-F
CK	25.83 ± 0.36 a	70.81 ± 2.00 a	17.79 ± 1.82 b	16.25 ± 0.68 d	21.29 ± 2.71 b
Ms	20.18 ± 2.77 b	62.76 ± 0.48 b	18.96 ± 1.72 a	18.80 ± 0.85 b	21.80 ± 1.99 b
Tr	20.06 ± 2.15 b	61.45 ± 0.45 b	18.74 ± 0.96 a	19.86 ± 0.37 a	21.46 ± 1.44 b
Lp	19.45 ± 1.95 b	62.72 ± 1.56 b	14.98 ± 0.17 c	10.06 ± 0.10 e	18.22 ± 2.98 c
Lb	20.61 ± 1.45 b	69.07 ± 1.07 a	18.87 ± 0.35 a	17.55 ± 0.63 c	22.18 ± 3.16 a
Bv	19.45 ± 1.95 b	62.72 ± 1.56 b	17.98 ± 0.17 b	16.76 ± 0.10 d	22.22 ± 1.98 a
LSD (5%)					

Notes: Mean values ($\bar{x} \pm SE$) followed by the same letter were not significantly different using LSD ($p < 0.05$) on diameter of pathogenic fungi data ($n = 10$). Ms, Tr, Lp, Bv, and Lb stand for alfalfa, white clover, ryegrass, mangold, and wolfberry.

Table 8. Effects of different root exudates on mycelial growth rate of pathogens associated with mangold root rot.

Treatment	Growth Rate of Mycelia (mm·d ^{−1})				
	Bv-A	Bv-B	Bv-C	Bv-E	Bv-F
CK	14.21 ± 0.42 a	3.03 ± 0.15 a	5.46 ± 0.32 a	5.40 ± 0.89 ab	4.17 ± 0.01 a
Ms	13.44 ± 0.37 ab	3.13 ± 0.07 a	4.88 ± 0.05 b	4.06 ± 1.02 c	4.07 ± 0.43 a
Tr	14.22 ± 0.19 a	3.13 ± 0.11 a	4.01 ± 0.69 c	4.81 ± 1.02 bc	2.96 ± 0.17 b
Lp	12.66 ± 0.54 b	2.97 ± 0.22 ab	4.44 ± 0.41 c	5.04 ± 0.77 b	3.43 ± 0.09 b
Lb	13.80 ± 0.17 a	2.37 ± 0.19 b	5.56 ± 0.46 a	5.80 ± 0.12 a	4.13 ± 0.11 a
Bv	12.97 ± 0.51 b	2.99 ± 0.27 ab	5.44 ± 0.41 a	5.44 ± 0.77 ab	4.03 ± 0.09 a
LSD (5%)					

Notes: Mean values ($\bar{x} \pm \text{SE}$) followed by the same letter were not significantly different using LSD ($p < 0.05$) on diameter of pathogenic fungi data ($n = 10$). Ms, Tr, Lp, Bv, and Lb stand for alfalfa, white clover, ryegrass, mangold, and wolfberry.

A comprehensive analysis of the aforementioned research findings demonstrates that the five types of root exudates exert distinct and differential effects on the five pathogenic fungi associated with root rot in mangold. Notably, wolfberry root exudates promote both the lesion expansion and mycelial growth of *Fusarium solani*, indicating a potential role in enhancing pathogen aggressiveness. Root exudates from alfalfa and white clover enhance lesion expansion of *Fusarium solani* while suppressing mycelial growth, a pattern consistent with observations in wolfberry root rot, suggesting shared allelopathic mechanisms among these species. Ryegrass root exudates exhibit a significant suppressive effect on the incidence of mangold root rot, highlighting their potential as biocontrol agents. In contrast, mangold root exudates appear to facilitate the development of autotoxic feedback loops, thereby promoting disease progression in conspecifics, although this effect remains statistically non-significant ($p > 0.05$).

4. Discussion

4.1. Effects of Allelopathic Compounds in Root Exudates on Seed Germination and Seedling Growth

Plants can detect and respond to neighboring plants, playing an essential role in plant coexistence and community assembly [32]. Compared with the independent germination and growth of herbage, the treatment of wolfberry root exude could promote the germination of clover, mangold, ryegrass and oat seeds, and the germination and growth of clover, mangold, sweet sorghum, alopecas, and alfalfa seeds, while other herbage demonstrated inhibitory effects, consistent with the results reported by Liu et al. that root exudates and exogenous allelopathic compounds ferulic acid significantly inhibited the emergence rate of ginseng seeds and the higher morphological indices of seedlings [4]. Distinct grass root exudates did not significantly inhibit the germination of Lycium berry seeds, but significantly promoted the growth of seedlings, especially clover and alfalfa of legumes. This is in line with the study of Sun et al. [33]: extracts from different parts of wheat and alfalfa all inhibited cotton seed germination, and wheat extracts showed low concentration promotion on the growth of cotton seedlings [34].

4.2. *Fusarium* Genus as a Causative Agent of Root Rot Disease Threat to Plant Growth and Development

Root rot is a widespread soil-borne plant disease characterized by root decay and foliar chlorosis, leading to significant reductions in crop productivity and, under severe infection, plant wilting or mortality [23]. It is primarily caused by fungal pathogens, with key causal agents including *Rhizoctonia solani* [35], *Fusarium oxysporum*, *Fusarium solani*, *Fusarium concolor*, and *Fusarium moniliforme* [23], as well as *Sclerotinia sclerotiorum* [36].

Among these, *Fusarium oxysporum* is a globally distributed soil-borne pathogen with a broad host range and high pathogenicity, followed by *Fusarium solani* in terms of virulence; in contrast, *Fusarium concolor* and *Fusarium moniliforme* are recognized as low-virulence species [37]. Owing to regional variations in environmental and edaphic conditions, the predominant pathogens associated with root rot in wolfberry exhibit distinct geographic patterns. The disease is typically driven by a complex of pathogenic fungi that colonize the root system and basal stem, inducing extensive tissue damage and systemic physiological decline, which underpins its characterization as “plant cancer” due to the severe impact on plant viability and agricultural output. In the major wolfberry-producing regions of Ningxia and Qinghai, *Fusarium* spp., particularly *Fusarium oxysporum* and *Fusarium solani*, are the dominant pathogens, whereas, in Xinjiang, *Molds* and *Rhizoctonia solani* prevail as the primary causative agents [38]. These established patterns align closely with our experimental findings, which identify *F. oxysporum* and *F. solani* as the principal pathogens responsible for wolfberry root rot in Ningxia. Moreover, this observation is fully consistent with our experimental confirmation that *Fusarium solani* is the primary causal agent of root rot in mangold. Consequently, our future research on soil-borne diseases, particularly root rot, will focus on conducting comprehensive studies on major pathogenic fungi such as *Fusarium* genus.

4.3. Effects of Root Exudates on Soil-Borne Diseases

Controlling plant root rot is essential for sustainable agricultural production. Intercropping reduces leaf disease incidence and suppresses soil-borne pathogens [6–8]. Although wolfberry and mangold root exudates slightly promoted their own root rot, they enhanced *Fusarium* colony expansion and mycelial growth, consistent with findings from Shusheng Zhu’s team [39], thereby increasing fungal pathogenicity and worsening panax notoginseng root rot. Our results show that alfalfa and white clover root exudates selectively promote specific pathogens—*Rhizopus arrhizus* in wolfberry root rot, and *A. niger* and *F. solani* in mangold root rot—while inhibiting other root rot fungi. This dual effect aligns with Yang et al., who found corn root exudates attract *Phytophthora capsici* zoospores but also inhibit their development, potentially enhancing pepper blight resistance [17]. Similar interactions between non-host plants and *Phytophthora* spp. support the role of allelopathic modulation in suppressing soil-borne diseases in intercropping systems [40,41].

Wolfberry production in traditional regions is increasingly constrained by land scarcity and continuous cropping [26], with underlying mechanisms still unclear. Root exudates and plant residues exacerbate these issues by enriching the rhizosphere and creating favorable conditions—such as optimal temperature and humidity—for pathogen growth. Over time, pathogens dominate the soil microbiome, increasing the incidence and severity of soil-borne diseases [42]. Our findings support this: four dominant fungal taxa, *Fusarium*, *Molds*, and *Alternaria* were consistently isolated from the decayed roots of long-term monocultured wolfberry, aligning with reports by Uwaremwe et al. [43]. Notably, root exudates from different forage species selectively influence the growth of fungi causing wolfberry root rot. Specifically, ryegrass and mangold exudates strongly inhibit key pathogens such as *M. circinelloides*, *F. solani*, and *F. oxysporum*. Although direct studies on these exudates are limited, graminaceous plants are known to release benzoxazinoids (BX)—secondary metabolites that act as natural defenses against herbivores and pathogens. Hu et al. showed that wheat and corn constitutively release BX compounds, which reshape fungal and bacterial communities in subsequent crops and enhance systemic resistance in grasses [44]. Further evidence comes from Gao et al., who found that intercropping legumes with grasses suppresses red crown rot in legumes [20], and Xu et al., who demonstrated that wheat root exudates inhibit mycelial growth and the spore spread of *F. oxysporum* in

watermelon, reducing *F. wilt* incidence [22]. Similarly, mangold root rot severely limits the sustainable development of the mangold industry. Our results show that wolfberry root exudates significantly inhibit *F. solani*, the causal agent of this disease. This contrasts with continuous potato systems, where root exudates promote *F. oxysporum* and worsen wilt [45]. Nonetheless, this comparison highlights that prolonged cultivation may lead to the accumulation of specific compounds in root exudates, potentially providing nutrients and favorable conditions that facilitate pathogen establishment.

4.4. Root Exudates Play a Significant Role in Modulating Interspecific Plant Interactions

Root exudates are diverse organic compounds secreted by plant roots into the rhizosphere, including sugars, amino acids, organic acids, phenolics, and enzymes [32]. They play a key role in plant disease resistance by directly inhibiting pathogens, shaping the rhizosphere microbiome, and inducing systemic immunity [46,47]. Exudate composition varies significantly among species and genotypes, leading to different effects on pathogenic microbes. Our results show that root exudates from several plants, including wolfberry, promote mycelial growth and the conidial germination of *Fusarium oxysporum*. In contrast, Ma et al. [24] found that exudates from resistant plant varieties often suppress soil-borne pathogens, while those from susceptible varieties lack inhibition or even enhance pathogen growth. These differences suggest a link between root exudate-mediated allelopathic effects and disease resistance, underscoring the need for comparative studies across varieties with differing resistance levels. Such effects have been observed in solanaceous crops like tobacco [24], but research on root exudates in wolfberry and related species remains limited and largely based on preliminary data from our group. Furthermore, intercropping with wolfberry alters the rhizosphere microenvironment—mainly through changes in root exudate composition—improving crop yield and quality [48–50]. Our studies further confirm that root exudates exert significant influence on the development of soil-borne diseases. Identifying the specific bioactive compounds underlying these effects will be a key focus of future research.

Therefore, we propose that under well-designed intercropping systems, specific root-secreted compounds may serve as key mediators of plant–plant interactions, modulating the susceptibility of neighboring species to pathogen infection. This regulatory role underscores the potential for rhizosphere-mediated disease suppression through biochemical signaling. While the precise mechanisms remain to be fully elucidated, it is evident that the net effect of root exudates, either promoting or inhibiting pathogenic organisms, is not attributable to a single compound but rather emerges from the synergistic or antagonistic interactions among multiple exudate components. Consequently, determining the identity and functional contribution of the most influential compounds requires the systematic characterization of root exudate profiles combined with targeted bioassays to establish causal relationships.

5. Conclusions

This study highlights the role of root exudates in sustainable wolfberry production, focusing on seed germination, seedling growth, and root rot resistance. Key findings are as follows: (1) Root exudates from different forage species differentially affect wolfberry seed germination and seedling growth. Conversely, wolfberry root exudates promote the germination of ryegrass, white clover, and mangold, as well as the germination and growth of alfalfa, white clover, and mangold. Overall, intercropping wolfberry with mangold or alfalfa shows superior performance. (2) Morphological and molecular analyses identified *Mucor circinatus*, *Rhizopus*, *Fusarium solani*, and *Fusarium oxysporum* as primary pathogens of wolfberry root rot; *Molds*, *Aspergillus niger*, and *Fusarium solani* cause mangold root

rot. Alfalfa and white clover root exudates exert differential effects on these pathogens, while ryegrass exudates inhibit *Mucor circladus*, *Fusarium solani*, and *Fusarium oxysporum*, thereby reducing root rot in wolfberry. (3) Wolfberry and mangold root exudates may contain autotoxic compounds that promote pathogen growth or impair root function, increasing susceptibility to root rot. Thus, replacing long-term wolfberry monoculture by disrupting pathogen buildup and improving soil health is an effective strategy to reduce disease incidence.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy15122821/s1>, Table S1: Comparison and description of Wolfberry LB-A strain and its related species; Table S2: Comparison and description of Wolfberry Lb-B strain and its related species; Table S3: Comparison and description of Wolfberry Lb-D strain and its related species; Table S4: Comparison and description of Wolfberry Lb-E strain and its related species; Table S5: Comparison and description of mangel Bv-A strain and its related species; Table S6: Comparison and description of mangel Bv-B strain and its related species; Table S7: Comparison and description of mangel Bv-C strain and its related species; Table S8: Comparison and description of mangel Bv-E strain and its related species; Table S9: Comparison and description of mangel Bv-F strain and its related species.

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