Research Advances on Plant Endophytes Enhancing Plant Resistance to Biotic Stress (Postprint)

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Abstract

During plant growth and development, plants encounter threats from various adversities, leading to nutrient loss and substantial yield reductions. Traditional regulation of plant stress resistance through chemical pesticides causes severe environmental pollution and even endangers human health; therefore, it is necessary to seek suitable pesticide alternatives from natural components. Endophytes, which inhabit nearly every plant, are natural constituents of the plant microecosystem and may exert more positive and direct effects on plants due to their specialized ecological niches. However, the mechanisms by which endophytes enhance host resistance to biotic stress remain poorly understood. This article addresses the origins, diversity, and resistance to biotic stress of plant endophytes. First, it summarizes the primary transmission modes of plant endophytes as horizontal and vertical transmission; second, it compiles and analyzes the diversity of endophyte species and their distribution patterns within plants; finally, it elaborates in detail on the fundamental characteristics and mechanisms through which plant endophytes enhance plant tolerance to biotic stress (resistance to pathogenic bacterial diseases and pest resistance), namely that plant endophytes can utilize niche competition or nutrient competition and produce induced resistance to curb pathogen infection, or synthesize secondary metabolites such as antibiotics, alkaloids, and chitin-related compounds to inhibit the growth of pathogens or nematodes, thereby preventing and controlling diseases and pests. Furthermore, based on the current research status of endophytes enhancing plant biotic stress resistance, future development directions are prospected to provide references for the development and utilization of more environmentally friendly biological control agents.

Full Text

Preamble

Progress in Research on Plant Endophytes Enhancing Plant Resistance to Biotic Stress

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Abstract: Plants face numerous threats during growth and development, leading to nutrient loss and significant yield reductions. Traditional chemical pesticide approaches for regulating plant stress resistance cause severe environmental pollution and pose risks to human health, necessitating the search for natural alternatives. Endophytes, which inhabit virtually all plants, represent natural components of the plant micro-ecosystem and may exert more positive and direct effects on plants due to their specialized niche. However, the mechanisms by which endophytes enhance host resistance to biotic stress remain poorly understood. This review addresses the origins, diversity, and biotic stress resistance of plant endophytes. We first summarize the primary transmission modes of endophytes as horizontal and vertical transmission, then analyze the diversity of endophyte species and their distribution patterns within plants. Finally, we elaborate on the fundamental characteristics and mechanisms by which endophytes enhance plant tolerance to biotic stress (resistance to pathogenic diseases and pests). Endophytes can inhibit pathogen infection through niche or nutrient competition and induced resistance, or suppress pathogen and nematode growth by synthesizing secondary metabolites such as antibiotics, alkaloids, and chitin-like compounds, thereby controlling diseases and pests. Based on current research, we propose future development directions to provide references for developing more environmentally friendly biocontrol agents.

Keywords: endophytes, colonization, phytohormones, secondary metabolites, plant-microbe interactions, biocontrol

Abstract (English): Plant growth and development can be threatened by a variety of adversities, causing problems such as nutrient loss and significant yield decreases. The majority of the farming community uses agrochemicals as a sole method to control insect pests and plant diseases. Excessive use of these chemicals has resulted in the development of resistance in pests and diseases, not only in traditional plant varieties but also in transgenic plants. Prevalence of these chemicals can cause severe health issues for farmers, livestock, and consumers. Additionally, these agrochemicals cannot be degraded by biological means and cause environmental pollution. Therefore, application of naturally available microbes is a safe alternative and complementary approach to tackle pests and phytopathogens. In this review, we describe the origin, diversity, and resistance to biotic stress of endophytes. Firstly, we provide an overview of the transmission routes that endophytes can take to colonize plants, including vertically via seeds and pollen, and horizontally via soil, atmosphere, and insects. Secondly, we summarize and analyze the diversity of endophyte species and distribution diversity in plants. Finally, the basic characteristics and action mechanisms of endophytes in enhancing plant tolerance to biotic stress (anti-pathogenic bacteria and insect pests) are described in detail, including how endophytes induce salicylic acid- and jasmonic acid-mediated induced systemic resistance (ISR) and protect the host plant by competing for space and nutrition with pathogens. Some secondary metabolites produced by endophytic microbes have antifungal, antibacterial, and insecticidal properties, which strongly inhibit phytopathogens. In addition, based on the research status of endophyte-enhanced plant biotic stress resistance, future development directions are prospected to provide reference for the development and utilization of more environmentally friendly biological control agents.

Keywords: endophytes, colonization, phytohormones, secondary metabolites, plant-microbe interactions, biocontrol

Plant endophytes are bacteria, fungi, and actinomycetes that live within the organs and tissues of healthy plants without causing obvious disease symptoms, representing natural components of the plant micro-ecosystem (Wilson et al., 1995; Jia et al., 2016). Endophytes have been isolated from various plants, and through co-evolution with their hosts, they both satisfy their own survival requirements and enhance host adaptability to the external environment, creating a mutually beneficial relationship (Rodriguez & Redman, 2008; Laurent et al., 2013; Mendes et al., 2013). This co-evolution has shaped endophytes' unique genetic characteristics and metabolic products, enabling them to directly or indirectly promote plant growth through hormone and secondary metabolite secretion (Ahemad & Kibret, 2014), and assist in coping with biotic stress caused by pathogens and pests through production of antibiotics, hydrolytic enzymes, and alkaloids (Waller et al., 2005; Hayat et al., 2010; Rho et al., 2018; Carrión et al., 2019). Thus, endophytes play crucial roles in plant growth, development, and resistance to adverse conditions.

In recent years, plant diseases caused by pathogens have become increasingly severe, urgently requiring new anti-stress agents and microbial fertilizers to address these biological problems. Most such agents have been discovered through studies of microbial interactions. Previous literature has reported on endophyte characteristics, natural products, and plant interactions (Porras-Alfaro & Bayman, 2011; Wani et al., 2015; Jia et al., 2016). This review comprehensively summarizes the origins, diversity, and biotic stress resistance of plant endophytes, and provides prospects for their development and utilization, aiming to offer references for endophyte product development and crop stress resistance improvement.

1. Sources of Plant Endophytes

Most endophytes are transmitted horizontally, with beneficial host-associated microorganisms colonizing plants from the environment. Soil microorganisms can enter plant roots and establish colonization, while airborne microbes can penetrate through plant surfaces to infect plants (Saikkonen et al., 1998; Compant et al., 2005; Baldotto et al., 2011). When applied to maize and wheat through foliar inoculation, researchers believe that *Azospirillum brasilense* enters plants through stomata and can colonize internal leaf and stem tissues (Fukami et al., 2016). Once endophytes colonize plants and form symbiotic relationships, vertical transmission may evolve to ensure beneficial symbionts are passed to subsequent generations (Herre et al., 1999). Vertical transmission occurs within seeds or pollen infected by endophytes, with germinated seedlings carrying the same endophyte species. For example, *Bacillus* in *Oxalis corniculata* is transmitted through seeds (Jooste et al., 2019). In vertically transmitted symbionts, the symbiont is obligate and spends its entire life cycle within the host, unable to survive in the environment (Bright & Bulghresi, 2010). However, obligate relationships between plants and endophytes appear rare, and not all symbionts undergo vertical transmission—some employ horizontal transmission (Foster & Wenseieers, 2006). Moreover, some bacterial endophytes can use both transmission modes, representing a mixed transmission strategy.

2.1 Distribution Diversity of Endophytes in Plants

Endophytes are ubiquitous across various plants, exhibiting broad distribution and community diversity. To date, numerous endophytes have been discovered and isolated from studied plants, colonizing cells or intercellular spaces in various tissues and organs. This specific distribution may relate to their ability to utilize different substrates (Rodrigues et al., 1994; Huang et al., 2017). The seed-transmitted endophytic fungus *Neotyphodium lolii* shows irregular distribution in plant tissues, colonizing only mature embryos but not during differentiation (Majewska-sawka & Nakashima, 2004). Some species exhibit specific distribution patterns within plant organs. For instance, *Burkholderia* appears only in bamboo rhizome samples, *Pseudomonas* is detected in bamboo shoots and stems but not rhizomes, and *Bacillus* is found only in bamboo shoots (Liu et al., 2017). Additionally, endophytic fungal communities show strong seasonal variation in plant tissues. In January, endophytic fungi content is high in sorrel (*Rumex acetosa*) roots (98.3%) but low in leaves (only 4.4%), while in June, the opposite pattern occurs with leaf content increasing to 90% (Wearn et al., 2012). The temporal and spatial distribution diversity of endophytes reflects both plant-endophyte interactions and the adaptation of the symbiont to the environment.

2.2.1 Endophytic Fungi

Endophytic fungi have been isolated from various plants, including crops, woody plants, and particularly medicinal plants, mosses, ferns, and lichens. Colonization rates are typically higher in stems than leaves, and higher in leaves than roots (Tao et al., 2008). Identified endophytic fungi mainly belong to Ascomycota (89%), Basidiomycota (9%), and Mucoromycota (2%), distributed across genera such as *Fusarium*, *Aspergillus*, *Colletotrichum*, *Penicillium*, and *Gibberella*, demonstrating rich biodiversity (Larran et al., 2007; Wang et al., 2016; Renuka & Ramanujam, 2016; Xing et al., 2018).

2.2.2 Endophytic Bacteria

Research indicates that plant endophytic bacteria predominantly exist in roots and seeds, with relatively fewer in stems and leaves (Afzal et al., 2019). Proteobacteria is the most frequently isolated phylum, including α-, β-, and γ-Proteobacteria, with γ-Proteobacteria being the most diverse and dominant (Miliute et al., 2015; Santoyo et al., 2016). Actinobacteria, Bacteroidetes, and Firmicutes are the most common endophytic bacterial phyla (Reinhold-hurek & Hurek, 1998; Santoyo et al., 2016), with their dominance varying according to host plant species (Bodenhausen et al., 2013; Ding & Melcher, 2016). The most frequently isolated endophytic bacterial genera include *Bacillus*, *Burkholderia*, *Microbacterium*, *Micrococcus*, *Pantoea*, *Pseudomonas*, and *Stenotrophomonas* (Chaturvedi et al., 2016).

2.2.3 Endophytic Actinomycetes

Actinomycetes can produce various antibiotic substances, with the highest isolation rates from roots, followed by stems, and lowest from leaves (Gangwar et al., 2014). Endophytic actinomycetes are distributed across families including Streptosporangiaceae (40%), Streptomycetaceae (27%), Thermomonosporaceae (16%), Micromonosporaceae (8%), Pseudonocardiaceae (8%), and Actinosynnemataceae (2%) (Janso et al., 2010). Currently, most isolated endophytic actinomycetes belong to the genus *Streptomyces*, with additional genera including *Micromonospora*, *Actinopolyspora*, *Saccharopolyspora*, *Nocardia*, *Oerskovia*, *Microhispora*, *Streptosporangium*, *Promicromonospora*, and *Rhodococcus* (Verma et al., 2009; Akshatha et al., 2014).

3. Plant Endophyte Resistance to Biotic Stress

3.1 Resistance to Pathogenic Diseases

Many endophytes can inhibit plant diseases caused by pathogens. For example, Saikia et al. (2021) found that endophytic *Pseudomonas* combined with rhizosphere *Streptomyces fimicarius* and *S. laurentii* significantly reduced rice bacterial blight while producing indole acetic acid, hydrogen cyanide, and siderophores that notably promoted plant growth. Two *Alcaligenes faecalis* and *Bacillus cereus* strains isolated from tobacco, and *Stenotrophomonas maltophilia*, *Bacillus*, *Azotobacter chroococcum*, and *Serratia marcescens* from nightshade plants can all inhibit Fusarium wilt while promoting tomato growth (Aydi-ben-abdallah et al., 2020; Abdallah et al., 2016). Research shows endophytes resist pathogen-induced diseases through multiple pathways: inducing host resistance, competing for niche and nutrient space with pathogens, producing secondary metabolites such as antibiotics, hydrolytic enzymes, and alkaloids, and interfering with pathogen signaling.

3.1.1 Inhibiting Pathogen Growth Through Induced Resistance Van Loon & Bakker (2003) and Van Wees et al. (2008) confirmed that beneficial rhizosphere bacteria can induce plant resistance against pathogen infection, reducing disease severity. This plant response is termed induced systemic resistance (ISR), which confers broad-spectrum resistance and substantially enhances plant defense against pathogens, decreasing disease incidence (Li et al., 2021). In most plants, ISR is regulated by jasmonic acid (JA) and ethylene. For instance, *Bacillus cereus* (EPL1.1.3) and *Serratia nematodiphila* TLE1.1 induce systemic resistance in tomato against *Ralstonia syzigiisub* sp. infection through JA production (Yanti et al., 2019). Saffron endophyte *Burkholderia gladioli* E39CS3 induces resistance against *Fusarium oxysporum* infection by increasing endogenous JA levels, suppressing saffron corm rot (Ahmad et al., 2021). *Bacillus subtilis* DZSY21 isolated from *Eucommia ulmoides* leaves suppresses southern corn leaf blight (*Bipolaris maydis*) by activating SA- and JA-dependent signaling pathways to trigger ISR (Ding et al., 2017).

3.1.2 Inhibiting Pathogen Growth Through Niche and Nutrient Competition Some endophytes share the same ecological niche as pathogens and can reduce pathogen colonization by competing for living space. Tan et al. (2016) found that *Bacillus amyloliquefaciens* T-5 can serve as a biocontrol agent for tomato seedlings. When tomato seedlings were pre-inoculated with T-5GFP, colonization by *Ralstonia solanacearum* QL-Rs was inhibited, alleviating bacterial wilt. The authors attributed this to space-mediated interactions, as T-5 could colonize roots more effectively.

Endophytes also protect host plants by competing for nutrients (e.g., carbohydrates, nitrogen, and oxygen). They can rapidly colonize hosts, deplete available substrates, and cause pathogens to die from nutrient deficiency (Pal & Kgardener, 2006). The yeast *Pichia guilliermondii*, as a unicellular organism, can rapidly proliferate under nutrient-rich conditions in fruit wounds, consuming various carbohydrates (disaccharides and monosaccharides) and nitrogen sources, thereby inhibiting *Penicillium digitatum*, *Botrytis cinerea*, and *Colletotrichum* spp. (Spadaro & Droby, 2016). *Chryseobacterium* sp. WR21 can compete with *Ralstonia solanacearum* for root exudates, inhibiting bacterial wilt pathogen growth and preventing disease (Huang et al., 2017).

Iron is also an essential micronutrient for plant growth, participating in transpiration and enzymatic reactions. The low solubility of Fe^{3+} limits iron availability, potentially restricting microbial growth. Many microorganisms produce low-molecular-weight siderophores with high Fe^{3+} affinity (Van, 2000). Rice blast, caused by *Magnaporthe oryzae*, is strongly inhibited by endophytic *Streptomyces sporocinereus* OsiSh-2, with antagonism related to iron competition. OsiSh-2 contains more siderophore biosynthesis gene clusters, demonstrating superior iron utilization capacity. Under iron-deficient conditions, it can acquire more iron, thereby inhibiting *M. oryzae* growth (Zeng et al., 2021).

3.1.3 Inhibiting Pathogen Growth Through Secondary Metabolite Production Numerous studies have identified endophytic bacterial species that produce secondary metabolites reducing pathogen growth and activity. For example, 43 endophytic bacteria isolated from *Dendrobium* included *Bacillus megaterium* with strong antimicrobial activity (Wang et al., 2019). Peanut endophyte *B. velezensis* LDO2 demonstrates robust capacity to synthesize various antimicrobial metabolites, exhibiting strong antagonistic activity against peanut pathogenic fungi and bacteria, particularly inhibiting *Aspergillus flavus* mycelial growth and causing hyphal malformation, while possessing multiple plant growth-promoting traits (Chen et al., 2019). Endophytes isolated from soybean root nodules, including *Enterobacter*, *Acinetobacter*, *Pseudomonas*, *Ochrobactrum*, and *Bacillus*, showed antimicrobial activity against *Phytophthora sojae* 01, with *Acinetobacter calcoaceticus* DD161 showing the strongest inhibition (71.14%), causing fungal hyphal breakage, lysis, protoplast ball formation at hyphal tips, and fragmentation (Zhao et al., 2018).

Endophytes also exhibit antimicrobial activity against five major foodborne pathogens. Endophytic *Bacillus subtilis* GBF-96 isolated from ginkgo shows antimicrobial activity against *Escherichia coli*, *Salmonella typhimurium*, *B. cereus*, *Listeria monocytogenes*, and *Staphylococcus aureus*. The ethyl acetate extract of GBF-96 metabolites also shows antimicrobial activity, causing pathogen surface rupture, cell shrinkage, and lysis, with the proposed mechanism being cell membrane penetration and induced cell lysis (Islam et al., 2019). Similar effects were observed with *Paenibacillus kribbensis* from yew (Islam et al., 2018). Endophytic *Bacillus* sp. cryopeg and *Paenibacillus* sp. Rif 200865 from the fern *Dryopteris uniformis* also show antimicrobial activity against five foodborne pathogens, with butanol solvent extracts of their metabolites causing irregular cell shapes or rupture (Das et al., 2017).

Plant endophytes can secrete antibiotic substances to inhibit and kill pathogens. Endophytic fungus *Phomopsis heveicola* from tropical medicinal plant *Piper longum* possesses antibacterial, antifungal, and antioxidant potential. Under catalysis by the epigenetic modifier valproic acid, it produces antibiotics that inhibit human pathogens (*Pseudomonas aeruginosa*, *Shigella sonnei*, *Streptococcus pyogenes*, *Salmonella typhi*) and plant pathogens (*Puccinia recondita*, *Rhizoctonia solani*, *Phytophthora infestans*, *Botrytis cinerea*), while enhancing DPPH scavenging activity (Ameen et al., 2021). Rice endophytes *Streptomyces* *fimicarius* and *S. laurentii* produce antibiotics such as pyrimidicin B, kanamycin C, and neomycin A, inhibiting *Xanthomonas oryzae* pv. *oryzae* growth (Saikia & Bora, 2021).

Endophytes also inhibit pathogens by secreting hydrolytic enzymes. Lastochkina et al. (2020) combined *Bacillus subtilis* (0-4, 26D) with salicylic acid as an inoculant, increasing amylase inhibitor activity in *Fusarium oxysporum*-infected tubers while reducing fusarium-induced protease activity, thereby decreasing dry rot incidence. Endophytic *Burkholderia gladioli* E39CS3 from saffron can produce chitinase or β-1,3-glucanase, participating in *F. oxysporum* cell wall degradation and effectively inducing hyphal cell death (Ahman et al., 2021). Tomato endophytes *Stenotrophomonas maltophilia* (S23, S24, S28), *Azotobacter chroococcum* (S11), and *Serratia marcescens* (S14) can produce chitinase and protease to inhibit *F. oxysporum* growth (Aydi-ben-abdallah et al., 2020). *Bacillus cereus* isolated from rice roots produces volatile antibiotics and chitinase, inhibiting mycelial growth of five major rice pathogens: *Fusarium verticillioides*, *F. fujikuroi*, *F. proliferum*, *Magnaporthe oryzae*, and *Magnaporthe salvinii* (Etesami et al., 2019). *Pseudomonas aeruginosa* (H40), *Stenotrophomonas maltophilia* (H8), and *Bacillus subtilis* (H18) isolated from pea, cabbage, and pepper produce compounds including 2,5-dihydroxybenzoic acid, 4-(1-methylethyl)benzaldehyde, geldanamycin, phthalic acid, 2-ethylhexyl ester, 3,4-dimethoxycinnamic acid, 1,3-diazole, and 2-(4-tert-butyl-2,6-dimethyl-3-hydroxybenzyl)-2-imidazoline, which exhibit antifungal and antioxidant activity against rice sheath blight (*Rhizoctonia solani*) (Selim et al., 2017).

Endophyte-produced alkaloids inhibit pathogen growth and metabolic activity. Endophytes in *Catharanthus roseus* can increase alkaloid content (ajmalicine and serpentine) in roots by regulating expression of structural and regulatory genes in the terpenoid indole alkaloid (TIA) biosynthesis pathway, thereby resisting pathogen infection (Singh et al., 2020; Hewitt et al., 2020). Qi et al. (2019) isolated endophytic *Penicillium* sp. CPCC 400817 from mangrove plants that produces a new alkaloid (GKK1032C) with strong antibacterial activity against methicillin-resistant *S. aureus*. Endophytic *Penicillium citrinum*-314 from *Halocnemum strobilaceum* produces a new aminomethylphenolic alkaloid (halociline) that inhibits *B. subtilis*, *S. aureus*, *E. coli*, and *P. aeruginosa* (Abdel et al., 2020).

3.1.4 Inhibiting Pathogen Growth Through Signal Interference Endophytes inhibit pathogen growth by degrading N-acyl-L-homoserine lactone (AHL) signals, blocking quorum sensing. Endophytes with AHL-degrading activity isolated from potato tubers can prevent soft rot caused by *Pectobacterium carotovorum* by degrading pathogen AHL signals and interfering with quorum sensing. These endophytes were identified as *Bacillus* sp., *Variovorax* sp., *Variovorax paradoxus*, and *Agrobacterium tumefaciens* (Ha et al., 2018). Anandan et al. (2019) also found that *Bacillus thuringiensis* KMCL07 produces lactonase, reducing *P. aeruginosa* (PAO1) virulence and inhibiting biofilm formation by disrupting AHL-mediated quorum sensing without any growth inhibition. Kiarood et al. (2020) identified the same mechanism in *B. cereus* and *Pseudomonas azotoformans*, which reduced citrus diseases caused by *Pseudomonas syringae* pv.

3.2 Resistance to Insect Pests

Siddiqui and Shaukat (2003) noted that endophytic bacterial colonization reduces initial root damage and affects host responses to pathogen attack, accelerating plant development and producing abundant root exudates that enhance soil microbial growth and provide substantial opportunities for biological management of plant-damaging nematodes. Endophytes inhibit nematode growth by producing active substances such as hydrolytic enzymes. Liu et al. (2020) demonstrated in greenhouse experiments that *Bacillus halotolerans*, *B. kochii*, *B. oceanisediminis*, *B. pumilus*, *B. toyonensis*, *B. cereus*, *P. aeruginosa*, and *B. pseudomycoides* can effectively suppress root-knot nematodes in soil. Mardhiana et al. (2017) isolated eight endophytes from *Cyperus rotundus* roots that produce protease, chitinase, and HCN, exhibit urease activity, and solubilize phosphates. All endophytic bacteria effectively promoted tomato growth and reduced infection severity by the southern root-knot nematode (*Meloidogyne incognita*) (Mardhiana et al., 2017). Wiratno et al. (2019) also found endophytes isolated from black pepper roots can produce chitinase or protease, exhibiting lethality against *M. incognita*. Rhizosphere endophytes *Paenibacillus* sp. and *Bacillus* produce secondary metabolites that reduce total nematode egg counts in tomato and carrot (Viljoen et al., 2019). *Chaetomium globosum* YSC5 produces metabolites including chaetoglobosin A, chaetoglobosin B, flavipin, 3-methoxyepicoccone, and 4,5,6-trihydroxy-7-methylphthalide, significantly reducing nematode reproduction (Khan et al., 2019). Asyiah et al. (2021) formulated a bacterial consortium combining *Pseudomonas dimunita* with three *Bacillus* strains, adding organic matter and vitamins to create a bionematicide that reduced total root-knot nematode J2 populations in soil and roots by 60.74% and 66.24%, respectively.

4. Conclusions and Prospects

Currently, pesticide application remains the primary method for controlling pathogenic diseases. However, chemical pesticide use causes severe environmental pollution and threatens human health, necessitating more sustainable strategies that are environmentally friendly and safe for human health. Plant endophytes can inhibit pathogen infection through niche and nutrient competition, induce resistance, and synthesize secondary metabolites such as antibiotics, alkaloids, and chitin-like compounds to suppress pathogen and nematode growth, thereby controlling diseases and pests. Consequently, researchers consider endophyte-based biocontrol an environmentally friendly strategy for managing plant pathogens with potential to replace or reduce chemical pesticide use

(Yang & Cao, 2016; Latha et al., 2019).

Future directions include: (1) Plant endophytes are preferred biocontrol strains that originate from and act on plants without harming the environment or human health, though challenges remain regarding their long-term survival in plants or the environment. (2) Endophytes produce various secondary metabolites that antagonize pathogens in vitro, offering opportunities to culture these metabolites or use them as precursor structures for developing new green pesticides. (3) With deepening research on plant microbiomes, combining beneficial endophytes into microbial consortia will greatly enhance biocontrol efficiency, maintain plants free from pathogen infection, and improve plant resistance.

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