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Biosecurity versus Biocontrol: The Impact of *Uromycladium falcatarium* on Pacific Mimosaceae

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ABSTRACT

Uromycladium falcatarium is a gall-forming rust fungus that causes highly damaging disease on *Falcataria moluccana* in commercial plantations in Indonesia, Malaysia, and the Philippines. *Falcataria moluccana* is also an invasive weed that threatens infrastructure and native ecosystems in many Pacific Islands, including Hawaii, and is currently a target for biological control using host-specific natural enemies. Some *Uromycladium* species have been successfully used as biological controls for certain *Acacia* weeds. We conducted artificial inoculations to determine the ability of *U. falcatarium* from Indonesia to control *F. moluccana* in Hawaii, and to assess its impact on non-target Mimosaceae. Inoculations were applied in the laboratory and under net house conditions to three-month-old seedlings of *F. moluccana*, *Acacia koaia*, *Acacia confusa*, *Albizia chinensis*, *Albizia lebbeck*, and *Leucaena leucocephala* from Hawaii, and *F. moluccana* from Moluccas, Indonesia, as a control. Inoculations in the laboratory, monitored by freehand sections at 1, 24, and 48 hours, showed that all species except *A. confusa* supported the early stages of infection by *U. falcatarium*. In the net house, 4 randomized complete blocks with 5 seedlings per unit sample for each species were monitored for 5 months after treatment with sprayed inoculum, as well as continuous exposure to mature teliospore-producing galls placed overhead on shade cloth. All species showed early symptoms of infection after the first month, but only *F. mollucana*, from both Hawaii and the Moluccas, supported full disease development and gall formation over 5 months, ultimately leading to seedling death. The results suggest that *U. falcatarium* may be a suitable candidate for biological control of invasive *F. moluccana*. However, since several non-target species from Hawaii have shown susceptibility to the early stages of infection by the rust fungus, biosecurity precautions should be taken to prevent its introduction until further tests demonstrate safety.

1. Introduction

In 2015, *Uromycladium falcatarium*, a rust gall fungus, was described from *Falcataria moluccana* (a tree species in the Mimosaceae family) and reported to occur only on *F. moluccana* (Doungsa-ard et al. 2015). This extremely damaging disease has been a significant economic issue in plantations outside the tree's native range since 1988. The fungus has spread across commercial *Falcataria* plantations from the Philippines to Malaysia in 1992 and finally entered Indonesia, severely impacting timber production (Palma et al. 2020). The disease has been breaking out from 2004 to 2017 in the Indonesian archipelago, particularly on Java Island. The disease affects both seedlings in the nursery and mature trees in the field. In mature trees, the fungus infects and causes the development of chocolate-brown, cauliflower-like, or whip-like galls on the stem, branches, petioles, shoots, and pods (Rahayu et al. 2010). Trees infected by gall rust become almost leafless, as the galls on the branches absorb all sap nutrients and block the movement of sap beyond the galls, and have sparse crowns and produce fewer flowers and pods (Ambrose et al. 2022). On seedlings, the galls are commonly found near the base of stems, leaf stalks, or shoots (Rahayu et al. 2010). Infected seedlings usually lose their leaves and become stunted, eventually dying, and disease incidence of 90–100% has been reported in nurseries. Twenty days of gall rust fungus infection on the stem, shoot, and leaf stalk separately caused 82%, 70%, and 73% mortality of two-month-old seedlings, respectively (Ambrose et al. 2022). Generally, rust fungus infects young tissue, such as seedling cells, more than mature or old cells of *F. moluccana* trees. The infected seedlings may survive in the nursery; however, they will pass the rust inoculum in the field and develop the symptoms quickly.

Introduced to Hawaii in 1917 as a fast-growing tree with potential for forestry use, *F. moluccana* has become extremely invasive. The trees grow up to 150 feet tall, growing up to 15 feet per year, quickly dominating and replacing Hawaiian forests. They also dramatically increase soil nitrogen levels, altering native ecosystems and creating conditions that benefit other invasive species over native flora (Hughes et al. 2024). While *F. moluccana* grows quickly, its wood is weak and prone to breaking, with limbs and/or entire trees falling. Trees pose a serious hazard to all human structures, including homes, power lines, and highways (Hughes et al. 2024). Conventional management is extremely costly, as removing hazardous trees can cost thousands of dollars per tree. Herbicidal control is highly effective but challenging to sustain across large areas (Hughes et al. 2024). Biological control could offer a valuable additional tool for management, especially by suppressing the natural regeneration of *F. moluccana* seedlings. Impacts of the gall rust fungus *U. falcatarium* suggest that it could be an effective biological control agent of *F. moluccana* in Hawaii.

Relatives of *U. falcatarium* have been successfully deployed in South Africa for biological control of invasive Australian Mimosaceae, which are closely related to *F. moluccana* (Wood and Breeÿen 2021). Although several pathogens are commonly found on acacias in Australia, their use in the biological control program in South Africa has been limited, mainly due to concerns about their impact on vegetative growth and, consequently, on the valuable attributes of this group of plants (Impson et al. 2021). The implementation of classical biological control for invasive species remains a subject for debate. Biological control can be seen as an efficient, low-risk tool for controlling invasions (Day and Riding 2019) or as an intervention with high-risk environmental impact and unpredictable consequences (Day and Bule 2016). Therefore, this study aimed to determine the ability of *U. falcatarium* from Indonesia to control *F. moluccana* in Hawaii, and to assess its impact on non-target Mimosaceae species in Hawaii, through experimental inoculations.

2. Materials and Methods

2.1. Laboratory Experiment

2.1.1. Preparation of inoculum

Rust fungus galls producing fresh spores were collected from *F. moluccana* trees in the infested areas around Merapi Volcano and brought to the Laboratory of Forest Health and Protection, Faculty of Forestry, Universitas Gadjah Mada, Yogyakarta, Indonesia. Spores were propagated from a single pustule isolate using the modified protocol described by Fraser et al. (2019). To establish a single pustule isolate of *U. falcatarium*, teliospores were scraped from a single telium of fresh galls from the field, and suspended in 1–5 ml of distilled water with 0.05% Tween 20 (DWT). This suspension was applied to the young tissue of healthy *F. moluccana* seedlings using a sterile paintbrush. Following a 48-hour incubation at 20°C and 90% relative humidity in the growth chamber, the seedlings were transferred to a greenhouse. Once telia developed (approximately two to three weeks post-inoculation), the spores were harvested and re-applied to new seedlings to bulk up the inoculum. The mass teliospores were then used for either laboratory or net-house artificial inoculation.

2.1.2. Artificial inoculation in the laboratory

Artificial inoculation was performed on Hawaiian *F. moluccana* seedlings in the Laboratory to test their susceptibility to *U. falcatarium* sourced from Java, Indonesia. Since several other Mimosaceae species, both exotic and native, are present in Hawaii, we also tested *Acacia koaia*, *Acacia confusa*, *Albizia chinensis*, *Albizia lebbeck*, and *Leucaena leucocephala*. After we produced mass teliospores, the three-month-old seedlings were sprayed with distilled water, and the spores were applied to the tips and upper leaves of healthy young seedlings using paintbrushes, with 10 replications per species. Freehand sections were made from seedling shoots at 1, 24, and 48 hours after inoculation, with 30 sections per seedling. The number of spores germinated, penetrating basidiospores, and infected tissues were recorded at each time step to calculate their percentages. The observations were documented using a light microscope, Olympus Trinoculars Type CX33.

2.2. Net House Experiment

The experiment used three-month-old seedlings of six species tested: *F. moluccana*, *A. koaia*, *A. confusa*, *A. chinensis*, *A. lebbeck*, *L. leucocephala* (from Hawaii), and *F. moluccana* (from Moluccas, Indonesia). Since there was a gradient in light intensity due to varying shading trees around the net house, we used a randomized complete block design. We established four blocks, with each block comprising six species. Five seedlings were used to represent each species within a block, serving as experimental units (**Fig. 1**).

Every month, seedlings were inspected, and a disease rating from 0 to 5 was assigned. Based on a preliminary study, artificial inoculation with teliospore suspension was applied at a spore density of 5×10^{11}/ml and sprayed onto each seedling at a volume of 2 ml. This volume is sufficient to thoroughly coat the shoot, tip, and leaf area of a seedling without causing excessive runoff.

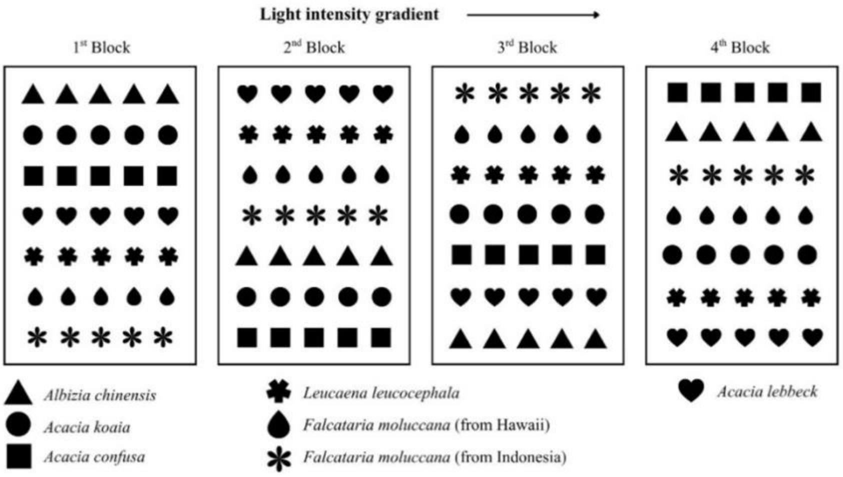

Fig. 1. Randomized complete block design (RCBD) layout for the artificial inoculation of six three-month-old Mimosaceae species with *Uromycladium falcatarium* in a net house experiment.

To allow continuous natural inoculation, fresh rust fungus galls with reddish teliospore color, produced from three to four weeks after artificial inoculation during the preparation of mass inoculum, were placed on shade cloth above the test plants, and spores were allowed to fall naturally. Plants were inspected monthly for 5 months using a magnifying glass until more than 50% of *F. moluccana* seedlings, the target species, died due to the rust fungus. The disease's index score for seedling symptoms was calculated using the modified method from Rahayu et al. (2011), as presented in **Table 1**.

Table 1. Index score for the presence of symptoms and gall-rust in the greenhouse

Index score	Gall on tip/branches	Symptoms on leaves
0	No gall	No symptom
1	No gall	Curly leaf but no gall presence
2	Twisted tip and or branches	Curly leaf with no gall presence
3	Gall forming	Curly leaf with gall presence
4	Gall formation and sporulation	Curly leaf with gall presence and sporulation
5	Gall formation and sporulation Causing the death of the seedling	Dried leaf, seedling death

Based on the index score for gall rust symptoms, gall rust disease severity (DS) was calculated using Equation 1 (Chester 1959) as follows.

$$Disease\ Severity\ (DS) = \frac{(n0\ \times\ z0)\ +\ (n1\ \times\ z1) + \ldots + (n5\ \times\ z5)}{(N\ \times\ Z)} \times 100\% \qquad (1)$$

where *DS* is the disease severity; *n0, n1, n2, n3, n4, n5* is the number of trees with index score 0, 1, 2, 3, 4, 5; *z0, z1, z2, z3, z4, z5* is the index score 0, 1, 2, 3, 4, 5, *N* is the total number of trees in one plot (5), and *Z* is the highest score (5).

2.3. Data Analysis

Qualitative data were analyzed using descriptive methods, while quantitative data were subjected to a one-way analysis of variance (ANOVA). Post-hoc comparisons were performed using Duncan's multiple range test (DMRT) at a 1% significance level ($p \leq 0.01$). All statistical analyses were conducted using R version 4.5.1.

3. Results and Discussion

3.1. Laboratory Inoculation

Falcataria moluccana from both Moluccas and Hawaii was quickly infected by the *U. falcatarium* fungus. The fungal spores germinated, and basidiospores penetrated the tips and began infecting the tissue within 1 to 48 h after artificial inoculation with the teliospore. *U. falcatarium* teliospores germinated on the tip and leaf surface, and the fungi penetrated all the test plant species under laboratory conditions within the first 24 hours, except on *A. confusa*, as presented in **Fig. 2–8**. Only the phyllodes tip of *A. confusa* was entirely uninfected by the fungus. The spores were attached only to the tissue surface and did not germinate into basidiospores (**Fig. 3**).

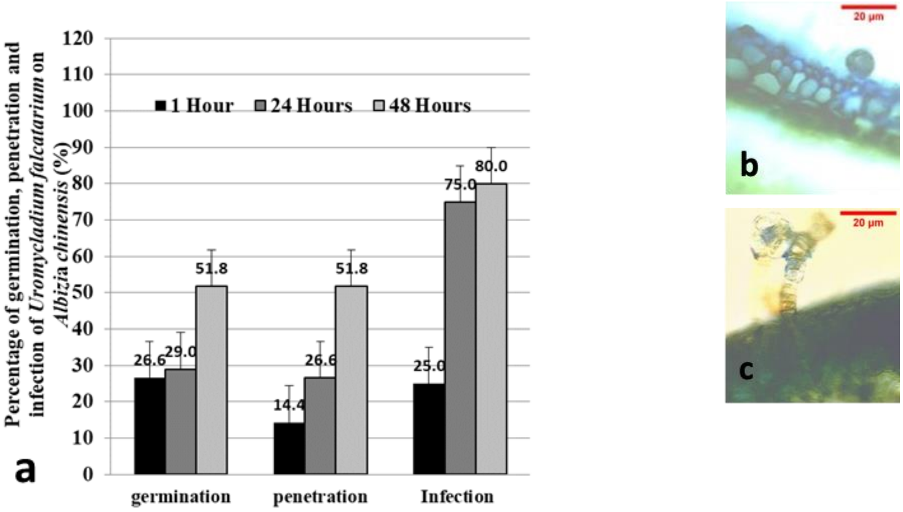

Fig. 2. (a) Percentage of germination, penetration, and infection of *Uromycladium falcatarium* on *Albizia chinensis* from Hawaii, (b) germination and infection, and (c) penetration of basidiospore and infection.

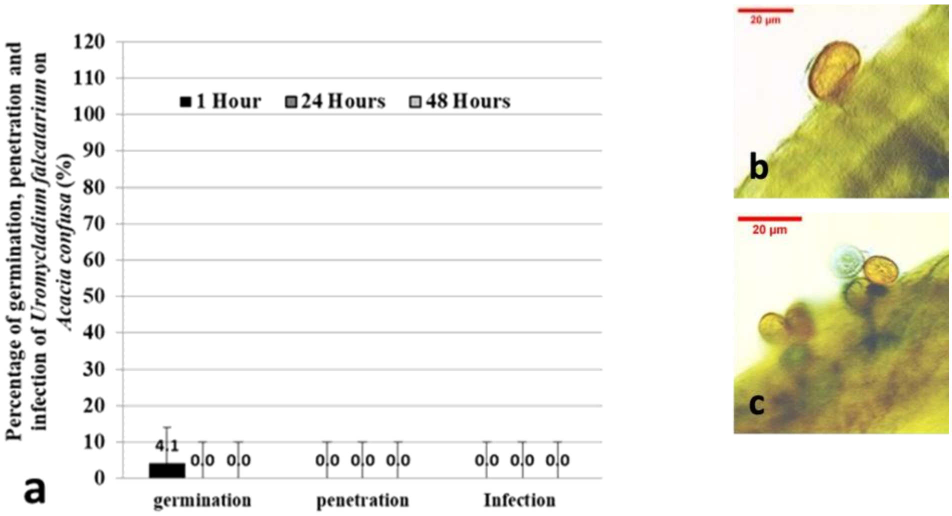

Fig. 3. (a) Percentage of germination, penetration, and infection of *Uromycladium falcatarium* on *Acacia confusa* from Hawaii, (b) landing teliospore, and (c) non-teleomorph teliospore germinates to be a basidiospore.

Young tip material of *A. koaia*, the native species of Hawaii, was infected with this *U. falcatarium* isolate in laboratory tests (**Fig. 4**).

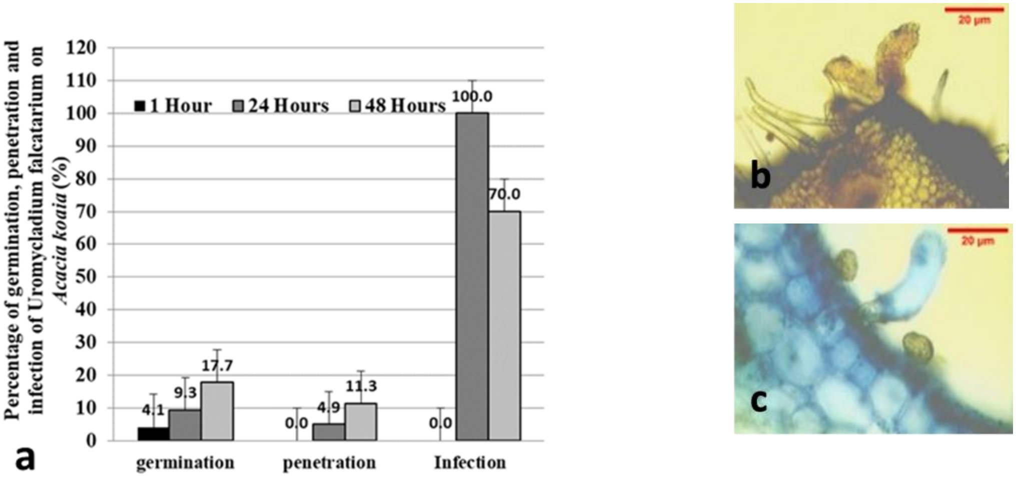

Fig. 4. (a) Percentage of germination, penetration, and infection of *Uromycladium falcatarium* on *Acacia koaia* from Hawaii, (b) penetration of basidiospore, and (c) penetration and infection.

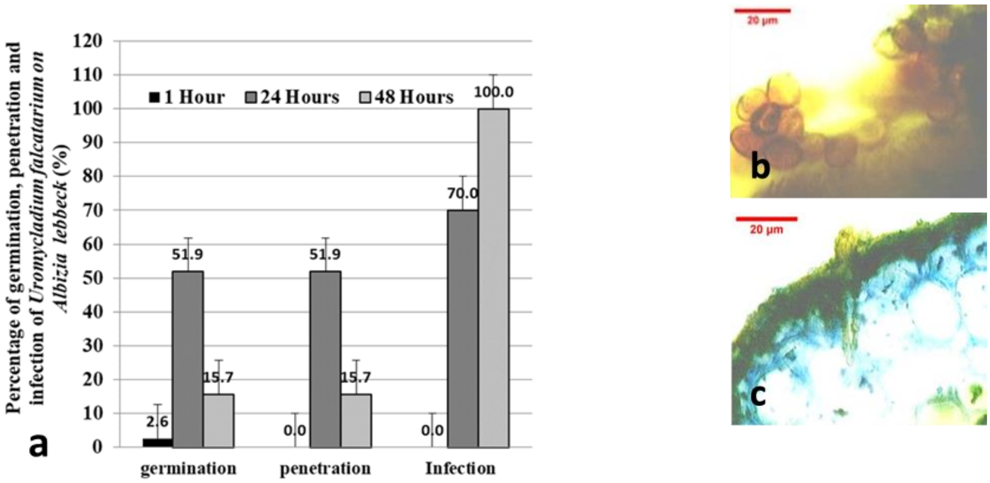

Fig. 5. (a) Percentage of germination, penetration, and infection of *Uromycladium falcatarium* on *Albizia lebbeck* from Hawaii, (b) landing teliospore, and (c) penetration and infection.

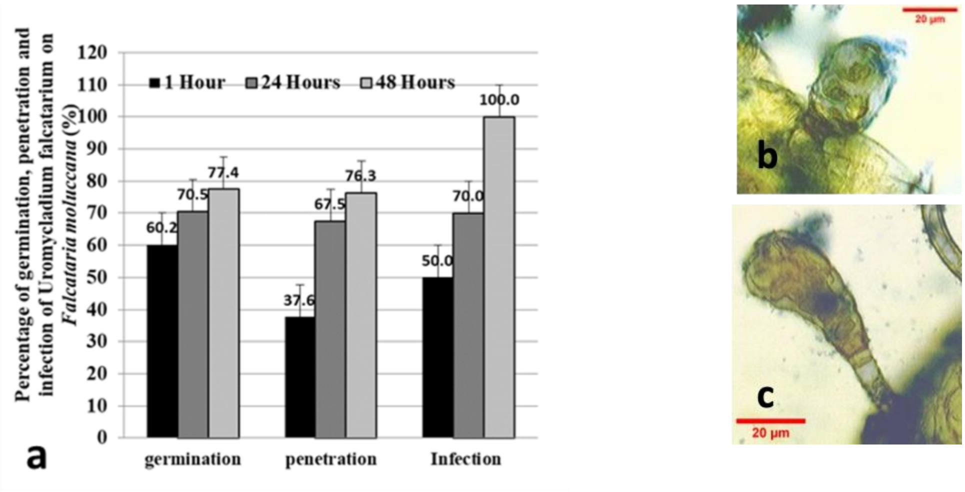

Fig. 6. (a) Percentage of germination, penetration, and infection of *Uromycladium falcatarium* on *Falcataria moluccana* from Hawaii, (b) penetration of basidiospore, and (c) penetration and infection.

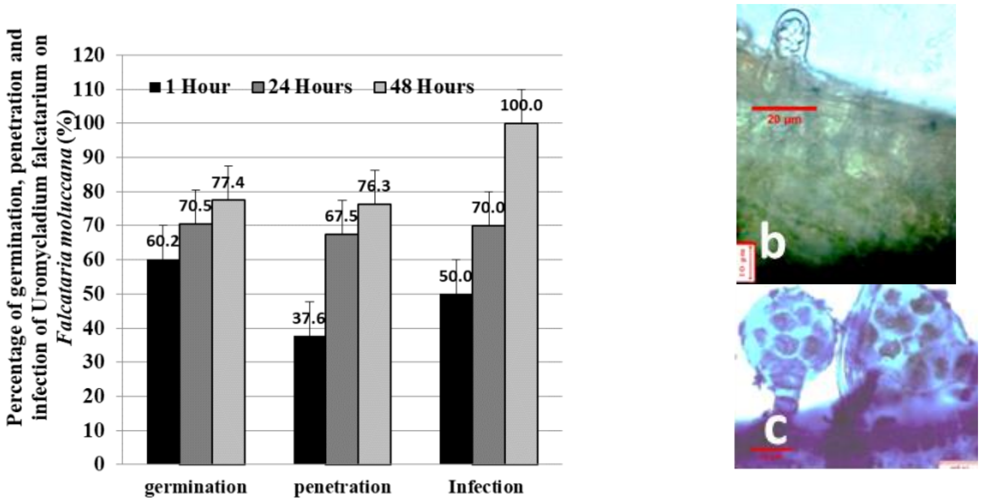

Fig. 7. (a) Percentage of germination, penetration, and infection of *Uromycladium falcatarium* on *Falcataria moluccana* from Moluccas, Indonesia, (b) germination of teliospore to be basidiospore, and (c) penetration and infection.

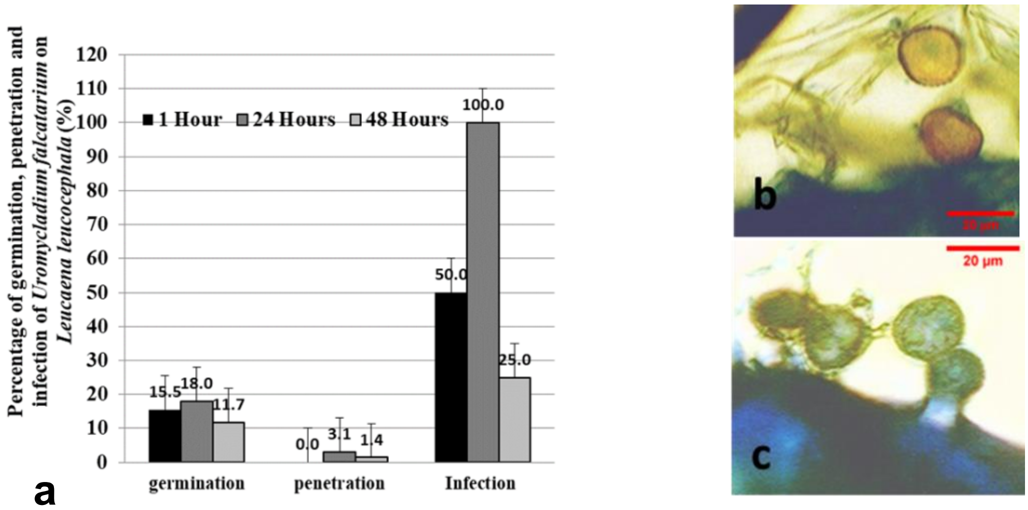

Fig. 8. (a) Percentage of germination, penetration, and infection of *Uromycladium falcatarium* on *Leucaena leucocephala* from Hawaii, (b) landing teliospore, and (c) penetration and infection.

The teliospores are crucial for the overwintering of most rust fungi, and they are primarily responsible for the formation of new physiological races (Omara et al. 2021). The pre-entry or pre-penetration phase of infection by fungi usually commences with the germination of a spore and includes the growth of the resulting germ tube on the surface of the plant. Some pathogens form specialized infection structures (e.g., appressoria and infection cushions), while others enter by direct hyphal growth through wounds or natural openings. The *U. falcatarium* can enter host cells through direct penetration and natural openings (Rahayu et al. 2010). According to the laboratory results, the teliospores of the rust fungus *U. falcatarium* appear to germinate on all species tested, including the target plant *F. moluccana* and non-target species. Environmental conditions, especially relative humidity, strongly influence teliospore germination. The rust fungus *U. falcatarium* requires at least 85% relative humidity for germination (Rahayu et al. 2018; Tering et al. 2025), and this experiment maintained the microenvironment around the seedlings at an optimal 90% relative humidity.

Once a pathogen reaches a suitable infection site at the plant surface, it must breach a series of barriers to gain entry into its host before establishing a parasitic relationship. Pathogens exploit every possible route of entry into plants, but individual pathogens usually follow preferred routes. The *U. falcatarium* enters through natural openings and directly penetrates the plant surface, requiring more sophisticated mechanisms involving adhesion, the formation of appressoria or other infection structures, and infection pegs (Rahayu et al. 2010). Direct penetration of the plant surface is possibly the most common mode of entry for biotrophic fungal pathogens, such as rust fungi. Plant surfaces are complex, robust and resistant to penetration by the vast majority of micro-organisms. During penetration, pathogen genes are expressed in a coordinated sequence, resulting in adhesion, followed by physical pressure on the plant surface and enzymatic degradation of the cuticle and various cell wall layers. Physical and chemical signals precisely switch pathogen genes on and off, so that cutinase, followed by cellulase, then pectinase, and finally protease, digest the host cuticle, cell wall, and middle lamella in the order they are encountered (Lorrain et al. 2019). Among the species tested in this experiment, only *A. confusa* was not penetrated by *U. falcatarium* within 48 hours of inoculation, indicating that it is incompatible with the rust fungus or that the fungus may require more time to infect the host. According to Lin et al. (2018), *A. confusa* exhibited potent antioxidant activity due to its high flavanol content. Thus, this species may be more resistant to many pathogens, including the rust fungus *U. falcatarium*.

3.2. Greenhouse Experiment

Disease severity varied widely among plants inoculated with *U. falcatarium*, ranging from 7% to 96% (**Fig. 9**), and there were significant differences among species from one to five months after inoculation (**Table 2**). Beginning 2 months after inoculation, *F. moluccana* from Hawaii and Indonesia showed significantly higher disease damage from *U. falcatarium* than other species.

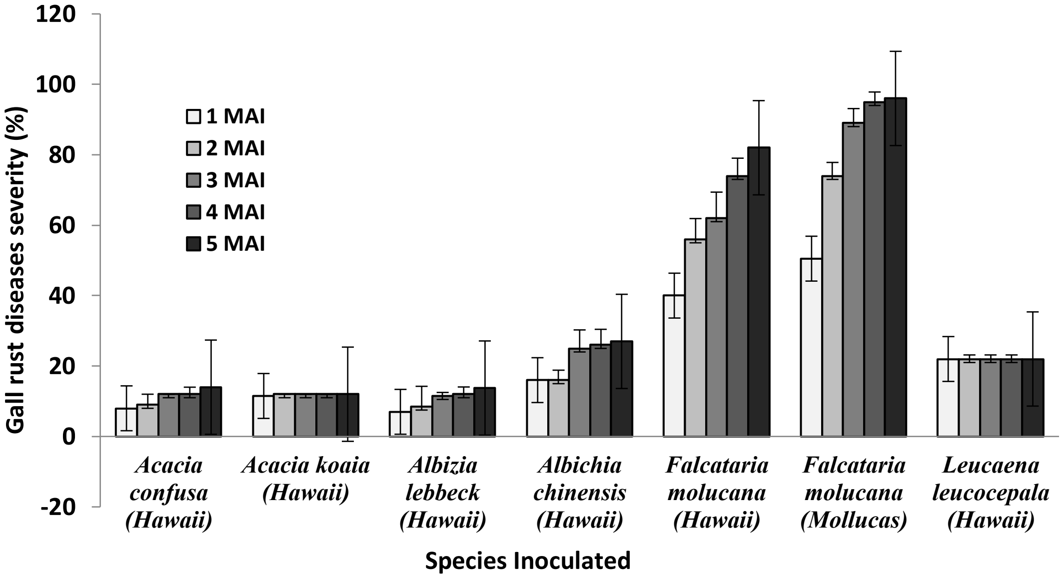

Fig. 9. Gall rust disease severity on 8-month-old seedlings of six species of trees from the Mimosaceae family after 5 months of artificial inoculation (MAI) with *Uromycladium falcatarium* teliospores from *Falcataria moluccana* trees infected with gall rust on Java Island, Indonesia. Significant differences among treatments are based on Duncan's multiple-range test (DMRT) at $p \leq 0.05$.

Table 2. ANOVA results for gall rust disease severity in Mimosaceae species 5 months post inoculation with *Uromycladium falcatarium* under net house experiment

Source of Variation	DF	Sum of square	Mean square	F value	Pr (>F)
One month after inoculation					
Block	3	65.71	21.90	0.43	ns
Species	6	6971.43	1161.90	22.90	***
Error	18	914.28	50.79		
Total	27	7951.43	294.49		
Two months after inoculation					
Block	3	129.71	43.24	0.90	ns
Species	6	15837.71	2639.62	54.85	***
Error	18	866.28	48.13		
Total	27	16833.71	623.47		
Three months after inoculation					
Block	3	288	96	1.78	ns
Species	6	21605.71	3600.95	66.96	***
Error	18	968	53.78		
Total	27	22861.71	846.73		
Four months after inoculation					
Block	3	276	92	1.68	ns
Species	6	27422.86	4570.48	83.61	***
Error	18	984	54.67		
Total	27	28682.86	1062.33		
Five months after inoculation					
Block	3	193.71	64.57	2.10	ns
Species	6	29301.71	4883.62	158.59	***
Error	18	554.28	30.79		
Total	27	30049.71	1112.95		

Gall formation in *F. moluccana* progressed rapidly, resulting in high mortality within 5 months after inoculation, killing most seedlings from Hawaii and Indonesia. However, a small number of *F. moluccana* from Hawaii were impacted less, forming fewer, smaller galls.

All inoculated species, including target and non-target, exhibited some level of disease symptoms. In the first month after inoculation, the disease severity of 5 non-target species remained below 25%, whereas in *F. moluccana* it increased to at least 40%. *A. koaia* showed slight stem enlargement associated with early rust gall formation, although it did not develop into a true gall. Other non-target plants showed slight discoloration or leaflet curling but no signs of disease progression. Only *F. moluccana* from Indonesia and Hawaii appear susceptible to the *U. falcatarium* rust fungus isolate from Merapi Mountain, Yogyakarta. Infections progressed to gall formation and sporulation consistently within 5 months in *F. moluccana* from Indonesia and Hawaii, but never in the non-target species (**Fig. 10**). This result suggests that the fungus could not develop further within the plant tissue of non-target species. This limitation may be due to several factors, including host-pathogen incompatibility, insufficient time for successful gall induction (Harris and Pitzschke 2020), the presence of inhibitory chemical contents within host cells that suppress the development of rust mycelia (Mapuranga et al. 2024), and other currently unidentified causes.

Although symptoms did not progress to gall formation and sporulation in the native Hawaiian species *A. koaia*, early signs of infection raised concern that this species could be negatively affected by *U. falcatarium*. In addition, reports indicate that other *Acacia* species are susceptible to attack by this variety of *U. falcatarium* (Ambrose et al. 2022; Doungsa-ard et al. 2015). We do not know whether the disease progresses to spore formation in these non-target trees, but the pronounced growth of gall tissue warrants caution. Our finding that *U. falcatarium* from Java Island can initiate infection in a variety of non-target Mimosaceae from Hawaii provides support for biosecurity precautions recommended by DeNitto et al. (2015) to protect Hawaii's native forests from risks of *Uromycladium* taxa.

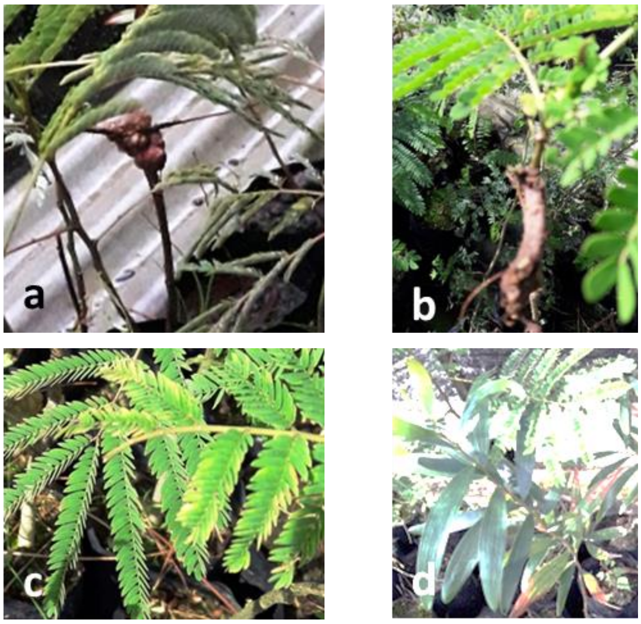

Fig. 10. (a) Gall forming on a *Falcataria moluccana* seedling originated from Indonesia, (b) *Falcataria moluccana* seedling originated from Hawaii, (c) no gall formation on *Albizia cinensis*, and (d) *Acacia koaia*.

The safe application of biological control depends on accurate characterization of the host specificity of a prospective agent. Rust fungi, including *Uromycladium* species, have a reputation for narrow host ranges and successful use in biological control (Morin 2020). In South Africa, *Uromycladium morrisii* has proven highly host-specific and effective for biological control of invasive *Acacia saligna* since 1987 (Doungsa-ard et al. 2018). More recently, *Uromycladium woodii* was released in South Africa for biological control of *Paraserianthes lophantha* after extensive testing demonstrated its specificity (Wood and Breeÿen 2021). These species, along with *U. falcatarium*, were formerly included in a large species complex designated as *Uromycladium tepperianum*, which is now being resolved using molecular methods (Doungsa-ard et al. 2018). Within the former *U. tepperianum sensu lato*, the relationships among species and their host plants suggest patterns of coevolutionary speciation between certain *Acacia* species and their associated *Uromycladium* species. In contrast, Doungsa-ard et al. (2015) hypothesized that host jumping from *Acacia*, rather than coevolution, is a likely explanation for speciation of *U. falcatarium*, given the genetic distance between the host plant taxa: tribe *Acacieae* versus tribe *Ingeae* for *Falcataria*.

Evidence for large host jumps and host-shift speciation may have implications for the use of *Uromycladium* as a biological control agent. A concern for biological control is that the agent might jump or switch from the target species to a non-target plant species. One way to quantify the risk of promiscuity of a potential biological control agent is to analyze the genetic structure of the species in question and its close relatives within its native geographic range (McTaggart et al. 2015). In addition to the evolutionary tendency of *Uromycladium* species toward narrow host specificity, another piece of evidence for the specificity of *U. falcatarium* is its apparent genetic distance from its nearest relatives (Doungsa-ard et al. 2018), suggesting a relatively long period since speciation.

4. Conclusions

Uromycladium falcatarium from Java Island has good potential as a biological control agent for *F. moluccana* in Hawaii. While this rust fungus produced early signs of infection in the laboratory on seedlings of several species from Hawaii (*Acacia koaia, Acacia chinensis, Acacia lebbeck*, and *Leucaena leucocephala*), and all non-target species exhibited mild symptoms over five months following inoculations in a net house, high levels of infection and gall formation occurred only on targeted *F. moluccana* plants from Hawaii and from the Moluccas, Indonesia. Impacts on *F. moluccana* from both sources were substantial, resulting in severe galling and the death of most seedlings after 5 months. Since the native non-target species *Acacia koaia* showed mild symptoms of infection by *U. falcatarium* from Java, the ecological risks and potential impacts on Hawaiian ecosystems require further evaluation before this rust fungus is considered for introduction as a biological control.

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Author Contributions

S.R.: Conceptualization, Methodology, Software, Validation, Formal Analysis, Investigation, Resources, Data Curation, Writing – Original Draft Preparation, Writing – Review and Editing; M.T.J.: Funding Acquisition, Conceptualization, Writing – Review and Editing.

Conflict of Interest

The authors declare no conflict of interest.

Declaration of Generative AI And AI-Assisted Technologies in the Manuscript Preparation

Not applicable.

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