BIODIVERSITAS
Volume 25, Number 3, March 2024
Pages: 1143-1150

ISSN: 1412-033X
E-ISSN: 2085-4722
DOI: 10.13057/biodiv/d250329

The suppression of *Ganoderma boninense* on oil palm under mixed planting with taro plants

SUWANDI SUWANDI♥, MONICA ALESIA, RUDI PUTRA MUNANDAR, RAHMAD FADLI, SUPARMAN SUPARMAN, CHANDRA IRSAN, A. MUSLIM
Department of Plant Protection, Faculty of Agriculture, Universitas Sriwijaya. Jl. Raya Palembang-Prabumulih Km 32, Indralaya, Ogan Ilir 30662, South Sumatra, Indonesia. Tel.: +62-711-580059, Fax.: +62-711-580276, ♥email:suwandi@fp.unsri.ac.id

Manuscript received: 18 September 2023. Revision accepted: 24 March 2024.

Abstract. *Suwandi S, Alesia M, Munandar RP, Fadli R, Suparman S, Irsan C, Muslim A. 2024. The suppression of Ganoderma boninense on oil palm under mixed planting with taro plants. Biodiversitas 25: 1143-1150.* Basal stem rot, caused by *Ganoderma boninense*, is highly destructive in monoculture oil palm plantations. This study evaluated *Ganoderma boninense* infections and oil palm growth in mixed plantings of oil palm seedlings and taro plants (Japanese, Bogor, and Indralaya taro). *Ganoderma*, colonizing rubber wood blocks, was inoculated into mixed plants, and the infection was compared to single-inoculated oil palm and taro plants. The interference of mixed planting with taro plants on the growth of oil palm seedlings was compared between inoculated and noninoculated mixed and single planting. *Ganoderma* inoculation caused simultaneous disease (dual-host infection) in mixed oil palm and taro plants. *Ganoderma* infection was less severe in taro plants compared to oil palm, whether in single or mixed planting. Over six months, oil palm root necrosis and disease index were reduced by 82% to 96% and 65% to 71%, respectively, while no significant effect was observed at nine months. The decay of *Ganoderma*-colonized wood improved by 44.1% to 84.0% in mixed planting, with no significant impact on mycelium viability. Taro plants did not inhibit oil palm growth, including plant height, leaf area, and relative growth rate of primary root length, in both the presence and the absence of *Ganoderma* infection. This study highlights the potential of mixed planting with taro to reduce *Ganoderma* disease in oil palm.

Keywords: Dual-host infection, *Ganoderma*, intercrop, oil palm, taro plant

INTRODUCTION

Basal stem rot (BSR), caused by polypore fungi *Ganoderma boninense* Pat. and other *Ganoderma* spp., is the most significant disease affecting oil palm plantations in Southeast Asia (Pilotti 2005; Midot et al. 2019; Paterson 2023). The fungi infect and cause the decay of roots, bole, and trunk tissue, preventing water and nutrient translocation toward the upper portion of oil palm trees. Diseased palm shows the external symptoms of spear leaves not opening, frond yellowing and wilting, and eventually collapse (Khoo and Chong 2023). BSR infections can lead to mass palm mortality and reduced oil palm yields by up to 68% production in severely affected plantations (Ibrahim et al. 2020; Kamu et al. 2021). In certain inland plantations of North Sumatra, BSR killed up to 67% of oil palm trees within 25 planting years (Riyanto et al. 2020). Meanwhile, in a peatland oil palm plantation in Sumatra, *Ganoderma* disease killed 30% to 54% of the palm stand. It resulted in an estimated yield reduction of 0.5 to 0.7 t/ha/yr over 14 planting years (Pujianto et al. 2016). Recent extensive disease surveillance of 37,359.81 ha of smallholder plantations in Malaysia reported that BSR disease had impacted 6.08% to 27.7% of oil palm in different soil types, including inland, coastal, peat, and lateritic areas (Ibrahim et al. 2020).

Controlling BSR is technically challenging due to the fungal pathogen's survival strategy. *Ganoderma boninense* forms melanized compact mycelia on infected roots or inside the basal stem, protecting against chemical and biological degradation and enabling the fungus to survive for extended periods (Rees et al. 2009). The propagules of the BSR pathogen colonize the diseased oil palm roots and survive up to four years (Eris et al. 2020). Infested plantations may harbor a multitude of infected roots in the soil, with even the tiniest infected root piece serving as an infective inoculum (Rees et al. 2007). Root contact with infected debris buried in the soil during replanting is recognized as the primary spreading source of infection (Naidu et al. 2017). The abundance of inoculum sources in recent plantings has contributed to increased disease across plant generations (Priwiratama et al. 2020).

Oil palm, a perennial tree, creates a complex habitat with abundant understory vegetation, even in standard monoculture cropping practices of large-scale plantations; herbaceous weeds dominate the understory vegetation of oil palm (Luke et al. 2019). Although considered unintended vegetation, the understory herbaceous plants in oil palm plantations can benefit both belowground and aboveground biodiversity, including improving soil biodiversity (Ashton-Butt et al. 2018) and supporting aboveground invertebrate communities (Ashraf et al. 2018; Spear et al. 2018). Smallholders often practice mixed planting by intercropping oil palm with annual food and cash crops, such as rice, maize, soybean, and cassava, or with perennial herbaceous crops like pineapple, banana, yam, and taro, especially during the first five years before the harvest period (Teuscher et al. 2016). Intercropping oil palm with food and cash crops such as taro brings mutual economic and environmental benefits (Khasanah et al. 2020).

Moreover, intercropping practices can decrease weed, insect, and disease pressure (Huss et al. 2022). Boudreau (2013) showed that intercropping reduced rot and wilt diseases by 86% in 14 studies comparing monocrops and intercrops. Stomph et al. (2020) reported a similar estimate of 78.6% crop protection benefits from intercropping in 196 cases compared to monocropping. The disease control benefits of intercropping oil palm with taro plants regarding their impact on BSR and the causal pathogen's survival are unknown. Taro plants have a perennial lifecycle, produce corms, and are well-suited for understory intercropping with oil palm. Their extensive root system may potentially influence the survival and growth of soil pathogens. Previous studies have demonstrated the suppression effects of taro plants against the polypore fungal pathogen *Rigidoporus microporus*, which causes white root rot in rubber trees. The viability and growth of rhizomorph-colonized rubber wood blocks (RWB) were suppressed after the RWB blocks were buried for 90 days in soil containing taro plants (Yulianti et al. 2017). Therefore, this research aimed to evaluate *Ganoderma boninense* infections and oil palm growth in a mixed planting of oil palm seedlings and taro plants of Japanese, Bogor, and Indralaya taro species.

MATERIALS AND METHODS

Plant materials and planting system

Germinating oil palm seeds (D×P cross from the Indonesian Oil Palm Research Institute) were pre-grown in trays containing sand media for three months until they had three leaves before being subjected to the mixed cropping treatment. Three cultivars of taro plants (*Colocasia esculenta* (L.) Schott) were tested, namely Japanese taro (previously called *Colocasia esculenta* var. *antiquorum* (Schott) F.T.Hubb. & Rehder), Bogor and Indralaya taro (previously called *Colocasia esculenta* var. *esculenta* (L.) Schott). The plants were generated from corms collected from Bogor, West Java, and Indralaya, South Sumatra local markets. The sprouting corms were pre-grown in a sand medium for three months to obtain homogeneous plants.

Ganoderma inoculation was examined in three planting systems: (i) mixed planting between oil palm seedlings with one of three taro plants, (ii) single planting of oil palm seedlings, and (iii) single planting of taro plants. Two additional planting systems, identical to (i) and (ii) but without pathogen inoculation, were implemented to evaluate the impact of inoculation and mixed planting on oil palm growth. In total, 15 planting systems were implemented, each consisting of 15 plants as replication; the experiment was replicated once. The plants were grown in a 1:1 mixture of field soil and sand, with a total volume of five liters, in a black polyethylene bag (polybag). For mixed planting, the plants were spaced for 10 cm. The polybags were arranged at 90 cm spacing under a 25% paranet, and the plants received monthly fertilization with 0.5% NPK 16-16-16 fertilizer.

Plant inoculation and disease evaluation

The study used a highly aggressive isolate of *G. boninense* (isolate GbA from BSR oil palm in West Sumatra) as the inoculum, prepared as two-month-old mycelium colonizing a 12×5×5-cm RWB (Suwandi et al. 2023). Plants were inoculated by binding a wounded primary root (10 cm long) with a single RWB using parafilm, following Rees et al. (2007). A single RWB was inoculated onto two mixed plants (dual-host inoculation) for mixed planting. Both RWB and inoculated roots were buried five cm below the soil surface. Plants were uprooted at three, six-, and nine-months post-inoculation (MPI) to evaluate root necrosis and disease severity. Root necrosis, indicated by discolored and rotted main roots, was measured to evaluate the extent of root infection. Root infection was confirmed by directly plating necrotic roots on a *Ganoderma*-selective medium (GSM) (Ariffin and Idris 1992). Each plant replication was assessed for *Ganoderma* colonization by examining five replicate roots. Disease index was recorded based on Breton et al.'s (2006) rating, with an additional root rot rating: (0) healthy, (1) rotting on main roots, (2) up to 20% rotting of bole tissues, (3) from 20% to 50% internal rotting, (4) over 50% internal rotting, and (5) total rotting of bole tissues along with total desiccation of the plant.

Inoculum potential and survival

The decay of *Ganoderma*-colonized RWB and mycelial viability were measured to assess the inoculum potential and pathogen survival in response to mixed planting. RWB decay was calculated as the percentage of dry weight loss after nine months of inoculation treatment. *Ganoderma* mycelia viability on RWB was assessed as the percentage of colonized wood fragments from which the mycelia emerged on GSM, with 20 randomly cut wood fragments examined for each RWB.

Growth of oil palm

Plant height, leaf area, and length of main roots were recorded to assess the growth interference of mixed planting with taro plants on oil palm seedlings. Leaf area was measured monthly and predicted using the formula 0.55 × length × width of the leaf blade (Gromikora et al. 2014). Plants were uprooted every three months, and the total length of the main roots was measured using a measuring tape. The relative growth rate of the main roots was calculated at six and nine MPI using the mean natural logarithm-transformed root length (Hoffmann and Poorter 2002).

Data analyses

Data analysis was conducted using R version 4.2.2 (The R Foundation for Statistical Computing). The normal distribution of the data was tested with the Shapiro-Wilk test, and variance homogeneity was checked with Levene's test. Logarithmic transformation was applied to homogenize the variance for the length of root necrosis, which was then subjected to one-way analyses of variance. Mean root necrosis length and disease index were compared using Tukey's honest significance test (HSD test). The mean RWB dry weight loss and percentage of mycelium survival were compared to the control treatment of single oil palm inoculation using the Dunnett test.

RESULTS AND DISCUSSION

Effects on Plant Disease

Root infection of *G. boninense* was determined and confirmed on all inoculated plant species, whether under single or mixed planting, at one MPI. Infected roots exhibited darkening and soft rot. The infection initiated from the inoculation site of roots and extended towards the basal stem for oil palm and the corm for taro plants. In single oil palm planting, *Ganoderma* infection led to complete BSR and plant death at six MPI, with basidiocarp formation on the dead plant. On taro plants, the infection expanded from the roots towards the corm, resulting in corm soft rot or dry rot (Figure 1). Root and corm infections were confirmed by the growth of *G. boninense* mycelium out of diseased plant tissues on GSM (Figure 1). Infection on Indralaya taro caused complete corm rotting and plant mortality under mixed planting with oil palm nine months after inoculation.

Under mixed planting, *Ganoderma* inoculation resulted in simultaneous disease in both oil palm and taro plants, known as dual-host infection. At three MPI, there was no significant difference ($P>0.05$) between oil palm and taro plants in the root length necrosis and disease severity, whether in single or mixed planting. However, by six MPI, the planting system significantly affected oil palm's root necrosis and disease severity. In mixed planting with Japanese taro, Bogor taro, and Indralaya taro, root necrosis of oil palm was reduced by 96%, 91%, and 82%, respectively, compared to single planting. This lower root infection in mixed planting also led to a lower disease index. Mixed planting with Japanese taro, Bogor taro, and Indralaya taro resulted in a disease index of 71%, 71%, and 65% lower than in single planting. In contrast, mixed planting did not influence the disease severity of taro plants, as the length of root necrosis and disease severity did not significantly differ between single and mixed planting. By six MPI, *Ganoderma* inoculations caused less root necrosis and disease severity in taro plants than in oil palm.

Figure 1. Tuber rots of taros (indicated by arrows) six months after *Ganoderma boninense* inoculation in mixed planting of oil palm and taros plants (middle row) compared to healthy, uninfected tubers (top row): A. Japanese taro, B. Bogor taro, C. Indralaya taro, and mycelium of *G. boninense* growing out of rotted tissues of taros root and tuber on GSM (bottom row A, B and C)

However, by nine MPI, the root necrosis and disease severity of oil palm under mixed planting markedly increased and became non-significantly different from disease under single planting. There was no reduction in oil palm root necrosis and disease severity due to taro plants at nine MPI. Similarly, disease development in taro plants under mixed planting was prominent at nine MPI, with the most severe impact observed in Indralaya taro (Figure 2).

Effects on pathogen inoculum potential and survival

The inoculum potential of *G. boninense* was assessed at nine MPI by measuring the dry weight reduction of RWB due to the fungus's decaying activity. *Ganoderma*-colonized RWB exhibited a dry weight loss of 68% (an increase of 56% relative to single planting) and 65% (an increase of 47% relative to single planting) in mixed planting with Bogor and Indralaya taro, respectively. A single inoculation of Japanese or Indralaya taro also resulted in RWB decay of 64% (an increase of 44% relative to single planting) and 81% (an increase of 84% relative to single planting), respectively (Figure 3). In contrast to the higher RWB decay, dual-host inoculation on oil palm and taro plants had a lesser effect on the survival of *G. boninense* mycelia colonizing RWB (Figure 3). The RWB colonized by *Ganoderm*a mycelia, which was used to inoculate the tested plants, remained over 81% viable after being buried for nine months.

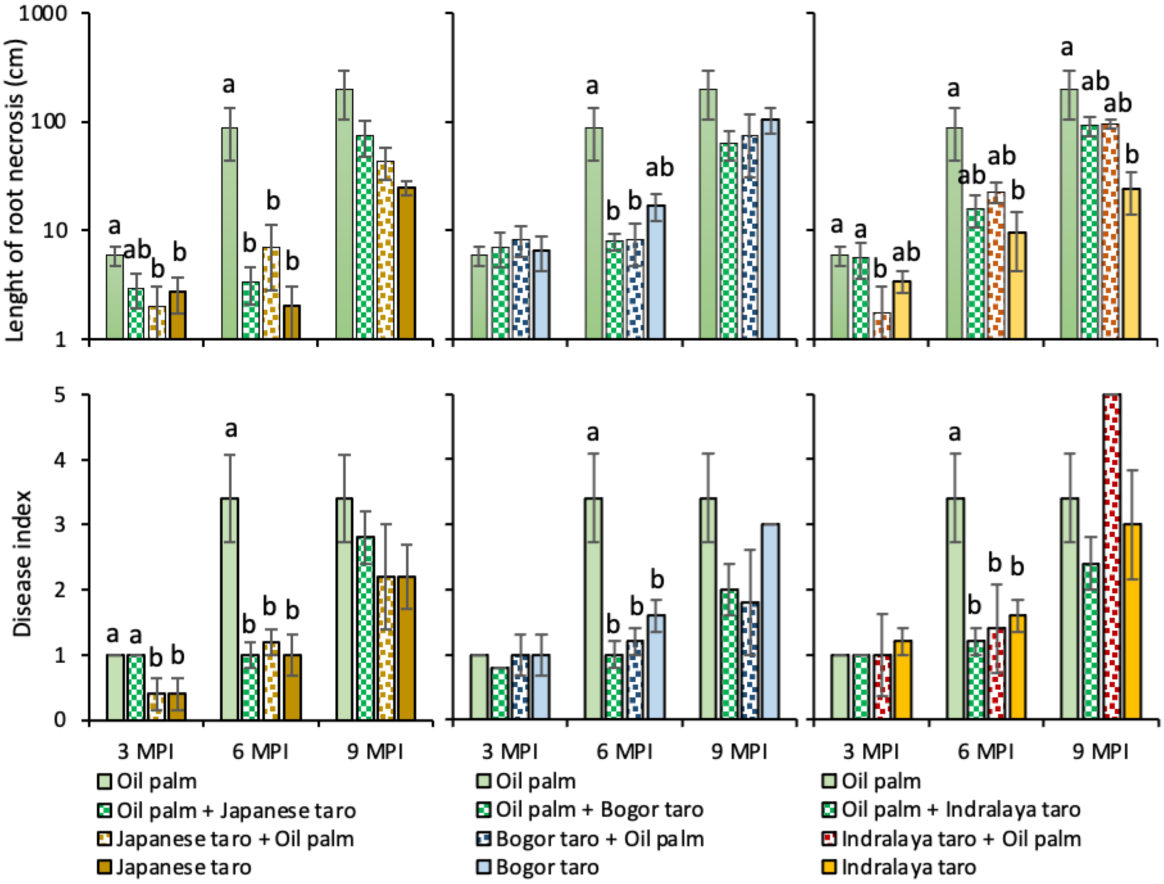

Figure 2. Effects of single or mixed planting of oil palm with taro plants (Japanese taro, Bogor taro, or Indralaya Taro) on *Ganoderma boninense* infection at three, six, and nine MPI (month post-inoculation) on single-host or dual-host plants. Graphic bars with a pattern fill are for plants with mixed planting, and the graphic bar describes the mean for the first mentioned plant. Error bars denote standard error of means (SEM). For each plant species and month, values followed by different letters are significantly different (HSD test)

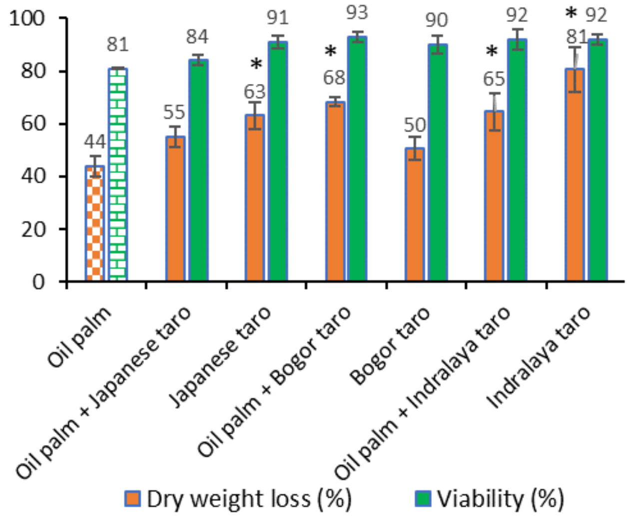

Figure 3. Effects of single or mixed planting of oil palm with taro plants (Japanese taro, Bogor taro, or Indralaya Taro) on the decay of *Ganoderma boninense*-colonized rubber wood block and pathogen viability after burial for nine months. An asterisk (*) denotes a significant difference (Dunnett test) from the respective mean values of oil palm single planting for each dry weight loss and viability.

Effects on oil palm growth

Mixed planting of oil palm seedlings with Japanese or Indralaya taro for ten months (nine MPI) in a small volume of soil (five liters) did not affect oil palm growth, as indicated by plant height (Figure 4A) and leaf area (Figure 4B). Taro plants did not interfere with oil palm growth, whether inoculated with *G. boninense* (+Gb) or not inoculated (-Gb). For mixed planting with Bogor taro, a notable inhibition of plant height and leaf area in the inoculated oil palm was observed at eight and nine MPI. Oil palm and taro plants showed rapid primary root growth, with a significantly higher relative growth rate (RGR) of primary root length from three to six MPI compared to six to nine MPI. Oil palm primary root growth was unaffected by mixed planting for nine MPI, with no significant difference in RGR values between mixed and single planting. However, taro plants exhibited different patterns of primary root growth. Mixed planting did not impact taro primary root growth during the first six MPIs; a variation in primary root growth was observed. From six to nine MPI, Japanese taro displayed a higher RGR of primary root length in mixed planting, while Indralaya taro showed marked inhibition of root growth in mixed planting compared to single planting (Figure 5).

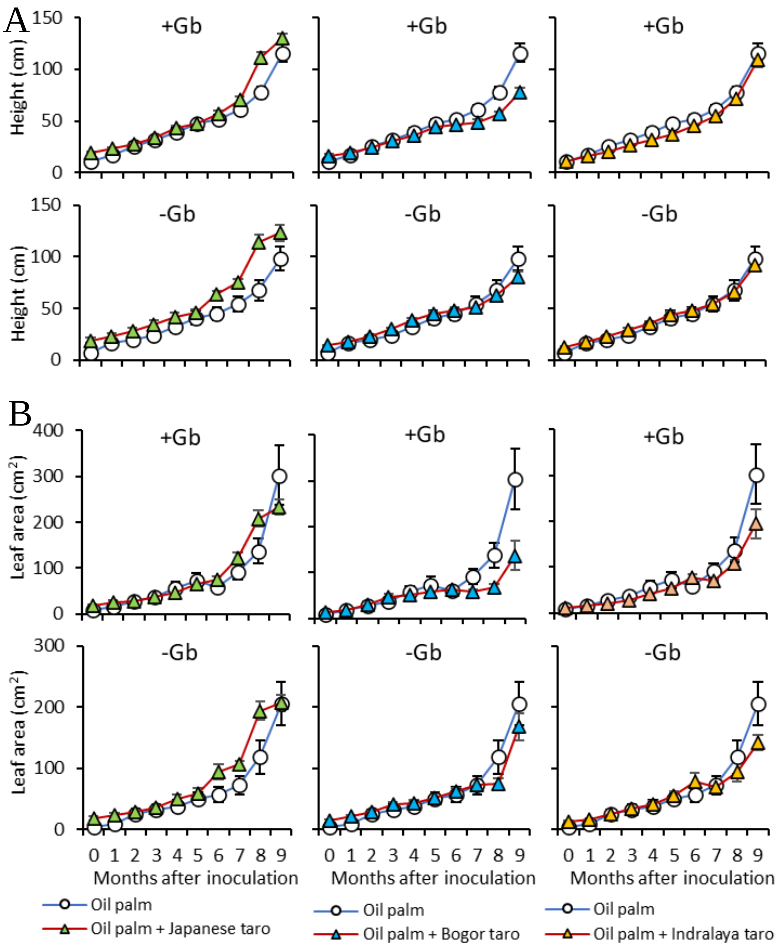

Figure 4. Effects of single or mixed planting with taro plants (Japanese taro, Bogor taro, or Indralaya Taro) on plant height (A) and leaf area (B) of *Ganoderma boninense*-inoculated oil palm (+ Gb) and noninoculated oil palm (- Gb)

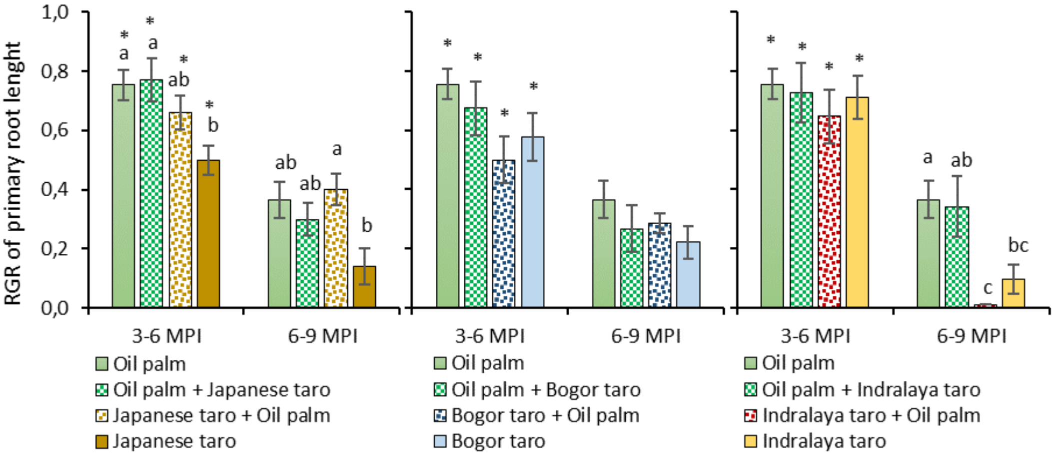

Figure 5. The relative growth rate (RGR) of the primary root length of oil palm and taro plants (Japanese taro, Bogor taro, or Indralaya Taro) under single or mixed planting and inoculated with *Ganoderma boninense*. Graphic bars with a pattern fill represent plants in mixed planting, with the graphic bar indicating the mean for the first mentioned plant. Error bars indicate the standard error of means (SEM). For each plant species and month, values followed by different letters are significantly different (HSD test). An asterisk (*) denotes a significant difference between the values at three to six MPI and the respective bar at six to nine MPI (months post-inoculation), according to the Welch t-test

Discussion

Ganoderma boninense was artificially inoculated onto various taro plants, including Japanese, Bogor, and Indralaya taro, resulting in infection and rot in their roots and tubers. The presence of *G. boninense* mycelium was consistently reisolated from the diseased root and tuber tissue, confirming its pathogenicity to taro plants. This finding aligns with the knowledge that *Ganoderma* spp. has a wide range of host plants, all woody plants (Loyd et al. 2018). Previous studies also demonstrated that *G. boninense* could cause infection in non-woody plants such as ginger, galangal, Java turmeric (Suwandi et al. 2023), and water yam (Fadli et al. 2023). The taro plant infection confirms the pathogen's cosmopolitan nature in using diverse lignin sources, from herbaceous to woody plants. Among the taro varieties tested, Japanese and Bogor taro showed greater resistance to pathogen infection, with root and tuber rot developing more slowly and not leading to plant mortality. Conversely, Indralaya taro proved to be more susceptible to *Ganoderma* infection, with extensive tuber rot development affecting all tubers, although the plant survived.

Inoculation of a single inoculum of *G. boninense* with two different plant species (dual-host inoculation) in a mixed planting of oil palm and taro plants generated multiple host infections on all mixed plants. All taro plants resisted *G. boninense* infection during rapid root growth between three and six MPI. However, pathogen infection increased from six to nine MPI in the post-corm maturity stages with reduced root growth rates. Indralaya taro showed greater vulnerability in mixed planting, showing the highest disease index and total tuber decay. Indralaya taro matured more quickly than the other two taro varieties, as evidenced by a decline in root growth after six MPI. Taro plants are suggested to be susceptible to *Ganoderma* infection during declining root growth. Oil palm responded to different severities under single inoculation than dual inoculation, particularly at six MPI. A marked reduction in disease in oil palm was noticed when mixed planted with an active growing taro plant, whereas the disease was less affected when the taro reached the susceptible stage (post-corm maturity). During extensive root growth, taro plants may secrete allelochemicals that directly influence the growth of *Ganoderma* mycelium. The root exudate from a ten-day-old axenic culture of *Xanthosoma sagittifolium* taro displayed an antifungal effect on *G. boninense* mycelium (Suwandi et al. 2022). Taro plants secrete root exudates rich in organic acids, including oxalic acid, lactic acid, benzoic acid, m-hydroxybenzoic acid, p-hydroxybenzoic acid, vanillic acid, succinic acid, and adipic acid (Ma and Miyasaka 1998; Asao et al. 2003). Some of these acids, like benzoic acid, have demonstrated antifungal properties against *G. boninense* in vitro. The application of benzoic acid reduced pathogen colonization in infected oil palms (Chong et al. 2019). The secretion of an antifungal allelochemical by taro likely contributes to the resistance response in mixed planted oil palm and taro against *Ganoderma* at six MPI. This secretion may decrease as taro plants reach post-corm maturity, but the taro corms remain susceptible to *Ganoderma*. The present study acknowledges certain limitations that should be considered in interpreting the results. Firstly, the relatively short duration of the experiment, spanning nine months, provides insights into the early impact of mixed planting but may not capture the long-term dynamics of *G. boninense* infections in oil palm-taro intercropping systems. Additionally, using artificial inoculation with a highly aggressive isolate of *G. boninense*, while necessary for controlled experimentation, may not fully replicate the complex natural conditions of disease spread in the field. Despite these limitations, our research provides valuable insights into the early stages of disease suppression through mixed planting, and future studies with extended durations and more nuanced inoculation methods can contribute to a greater understanding of these dynamics.

Mixed cropping can increase host diversity, reducing disease pressure through the inoculum dilution mechanism (Zhu and Morel 2019; Villegas-Fernández et al. 2023). However, this mechanism had a minor effect on *Ganoderma* disease reduction, as the disease increased in susceptible mixed planting interactions. Disease reduction in *Ganoderma*-inoculated oil palm was most noticeable during the resistant response of taro plants, as observed in a mixed planting with rhizomatous species like Java curcumin and ginger. Disease suppression was not observed in mixed planting with the susceptible galangal (Suwandi et al. 2023). This highlights the importance of partner plant resistance responses in *Ganoderma* disease suppression in mixed planting.

Reports on the impact of intercropping with taro on the disease of the main crops have been limited, with some concerns that it might increase disease severity. A six-month on-farm trial intercropping black pepper with *Colocasia* taro suggested reduced *Phytophthora* foot rot disease (Silbanus and Raynor 1993). In another study, intercropping with taro (*Colocasia esculenta*) was linked to disease reduction in *Falcataria moluccana*, leading to higher forest tree survival rates (Nandini et al. 2023). Additionally, an artificial inoculation pot trial found that mixed planting with *Xanthosoma* taro suppressed mycelial growth of *Rigidoporus microporus* and reduced rubber seedling taproot disease (Yulianti et al. 2017).

The burial of *Ganoderma*-colonized RWB, whether in single taro plants or mixed taro and oil palm plantings, significantly impacted RWB decay. After 90 days of planting with taro, *Ganoderma*-colonized wood decayed by 64% to 81%, in contrast to the 44% decay observed in single oil palm planting. This increased wood decay surpassed the 58%-to-79% decay induced by 120 days of inoculation with white-rot hymenomycetes reported by Naidu et al. (2017). The highest RWB decay occurred in the inoculated susceptible Indralaya taro. Increased RWB decay was also observed in mixed oil palm plantings with other susceptible hosts, such as galangal (Suwandi et al. 2023) and water yam (*Dioscorea alata*) (Fadli et al. 2023). *Ganoderma boninense* degrades RWB, a lignin and cellulose-rich food base crucial for initiating oil palm infection (Rees et al. 2007). The pathogen likely requires increased wood decomposition activity for severe infection initiation in susceptible hosts. The mechanism underlying how taro plants enhance the decomposition of *Ganoderma*-colonized wood requires further study. However, the increased RWB decay did not lead to reduced mycelial viability. Even after being buried under taro plants for nine months, the viability of *Ganoderma* mycelia in RWB remained unaffected. Although they remained viable, the pathogen's inoculum potential might significantly reduce due to wood decay; *Ganoderma* requires at least nine cm³ of wood as a food base to initiate effective infection (Rees et al. 2007). The potential of taro plants in enhancing *Ganoderma*-colonized wood decay suggests its application as a rotation crop for inoculum removal during oil palm replanting.

Taro plants have consistently not shown allelopathic inhibition on oil palm growth. There is no significant difference in leaf area or height between noninoculated oil palm plants in single and mixed planting for eight months after planting. However, growth inhibition was observed after nine months (eight MPI) of planting with Bogor taro and inoculated with *G. boninense*, likely due to space limitations. Our previous study also observed weak competition in oil palm seedlings mixed with *X. sagittifolium* taro and inoculated with *G. boninense* (Rahmadhani et al. 2020). Numerous reports indicate that intercropping with taro plants in an appropriate population does not harm the growth and yield of the main crop (Kazi et al. 2017; Winara et al. 2022; Nandini et al. 2023). The findings from our study emphasize the beneficial use of mixed planting with taro plants in managing *Ganoderma* BSR and support the need for a long-term field study.

ACKNOWLEDGEMENTS

This work was financially supported by a Basic Research Grant (059/E5/PG.02.00.PL/2023 and 0193.05/UN9.3.1/PL/2023) from the Directorate for Research and Community Service, Ministry of Culture, Research and Technology, the Republic of Indonesia.

REFERENCES

Ariffin D, Idris AS. 1991. A selective medium for isolation of *Ganoderma* from diseased tissues. In: Basiron Y, Jalani BS, Chang KW, Cheah SC, Henson IE, Norman K, Paranjothy K, Mohd Tayeb D, Ariffin D (eds). Proceedings of the 1991 International Palm Oil Conference, Progress, Prospects and Challenges Towards the 21st Century (Module I-Agriculture). Palm Oil Research Institute of Malaysia, Bangi.

Asao T, Hasegawa K, Sueda Y, Tomita K, Taniguchi K, Hosoki T, Pramanik MHR, Matsui Y. 2003. Autotoxicity of root exudates from taro. Sci Hortic 97: 389-396.

Ashraf M, Zulkifli R, Sanusi R, Tohiran KA, Terhem R, Moslim R, Norhisham AR, Ashton-Butt A, Azhar B. 2018. Alley-cropping system can boost arthropod biodiversity and ecosystem functions in oil palm plantations. Agric Ecosyst Environ 260: 19-26. DOI: 10.1016/j.agee.2018.03.017.

Ashton-Butt A, Aryawan AAK, Hood ASC, Naim M, Purnomo D, Suhardi, Wahyuningsih R, Willcock S, Poppy GM, Caliman JP, Turner EC, Foster W A, Peh KSH, Snaddon JL. 2018. Understory vegetation in oil palm plantations benefits soil biodiversity and decomposition rates. Front For Glob Change 1: 10. DOI: 10.3389/ffgc.2018.00010.

Boudreau MA. 2013. Diseases in intercropping systems. Ann Rev Phytopathol 51: 499-519. DOI: 10.1146/annurev-phyto-082712-102246.

Breton F, Hasan Y, Hariadi, Lubis Z, Franqueville HD. 2006. Characterization of parameters for the development of an early screening test for basal stem rot tolerance in oil palm progenies. J Oil Palm Res Special Issue 2006: 24-36.

Chong KP, Lo RKS, Ang ABPS, Ho ST, Ho ESM, Wong LK, Chin PCF, Syahriel A, Alexander A, Cheong SY. 2019. Evaluation on the effectiveness of organic acids combination against *Ganoderma boninense*, the causal pathogen of basal stem rot in oil palm. The Planter 95: 841-856. DOI: 10.56333/tp.2019.011.

Eris DD, Widiastuti H, Taniwiryono D. 2020. Soil biology characteristics of oil palm land endemic to *Ganoderma* after four years conversion to sugarcane. IOP Conf Ser: Earth Environ Sci 482: 012032. DOI: 10.1088/1755-1315/482/1/012032.

Fadli R, Suwandi S, Nurhayati N, Muslim A, Irsan C. 2023. Effect of mixed cropping of water yam (*Dioscorea alata*) on *Ganoderma* disease of oil palm. J Phytol 15: 7-11. DOI: 10.25081/jp.2023.v15.7641.

Gromikora N, Yahya S, Suwarto S. 2014. Growth and production modelling of oil palm at different levels of frond pruning. J Agron Indonesia 42: 228-235.

Hoffmann WA, Poorter H. 2002. Avoiding bias in calculations of relative growth rate. Ann Bot 90: 37-42. DOI: 10.1093/aob/mcf140.

Huss CP, Holmes KD, Blubaugh CK. 2022. Benefits and risks of intercropping for crop resilience and pest management. J Econ Entomol 115: 1350-1362. DOI: 10.1093/jee/toac045.

Ibrahim MS, Seman IA, Rusli M H, Izzuddin MA, Kamarudin N, Hasyim K and Manaf ZA. 2020. Surveillance of *Ganoderma* disease in oil palm planted by participants of the smallholders replanting incentive scheme in Malaysia. J Oil Palm Res 32: 237-244. DOI: 10.21894/jopr.2020.0024.

Kamu A, Phin CK, Seman IA, Gabda D, Mun HC. 2021. Estimating the yield loss of oil palm due to *Ganoderma* basal stem rot disease by using Bayesian model averaging. J Oil Palm Res 33: 46-55. DOI: 10.21894/jopr.2020.0061.

Kazi AA, Tandel MB, Pathak JG, Prajapat DH. 2017. Potentiality of *Colocasia* intercrop under naturally occurring palmyra palm (*Borassus flabellifer* L.). J Tree Sci 36: 58-61. DOI: 10.5958/2455-7129.2017.00008.5.

Khasanah N, van Noordwijk M, Slingerland M, Sofiyudin M, Stomph D, Migeon AF, Hairiah K. 2020. Oil palm agroforestry can achieve economic and environmental gains as indicated by multifunctional land equivalent ratios. Front Sustain Food Syst 3: 122. DOI: 10.3389/fsufs.2019.00122.

Khoo YW, Chong KP. 2023. *Ganoderma boninense*: general characteristics of pathogenicity and methods of control. Front Plant Sci 14: 1156869. DOI: 10.3389/fpls.2023.1156869.

Loyd AL, Linder ER, Anger NA, Richter BS, Blanchette RA and Smith JA. 2018. Pathogenicity of *Ganoderma* species on landscape trees in the Southeastern United States. Plant Dis 102: 1944-1949. DOI: 10.1094/PDIS-02-18-0338-RE.

Luke SH, Purnomo D, Advento AD, Aryawan AAK, Naim M, Pikstein RN, Ps S, Rambe TDS, Soeprapto, Caliman JP, Snaddon JL, Foster WA, Turner, EC. 2019. Effects of understory vegetation management on plant communities in oil palm plantations in Sumatra, Indonesia. Front For Glob Change 2: 33. DOI: 10.3389/ffgc.2019.00033.

Ma Z, Miyasaka SC. 1998. Oxalate exudation by taro in response to Al. Plant Physiol 118: 861-8655. DOI: 10.1104/pp.118.3.861.

Maizatul SM, Idris AS. 2012. Reduction of *Ganoderma* inoculum in infected-oil palm stumps by fumigant dazomet. Proceedings of the 4th IOPRI-MPOB International Seminar: Existing and Emerging Pest and Diseases of Oil Palm: Advances in Research and Management, Bandung, 13-14 December 2012.

Midot F, Lau S, Wong WC, Tung HJ, Yap ML, Lo ML, Jee MS, Dom SP, Melling L. 2019. Genetic diversity and demographic history of *Ganoderma boninense* in oil palm plantations of Sarawak, Malaysia inferred from ITS regions. Microorganisms 7: 464. DOI: 10.3390/microorganisms7100464.

Naidu Y, Siddiqui Y, Rafii MY, Saud HM, Idris AS. 2017. Investigating the effect of white-rot hymenomycetes biodegradation on basal stem rot infected oil palm wood blocks: Biochemical and anatomical characterization. Ind Crops Prod 108: 872-882. DOI: 10.1016/j.indcrop.2017.08.064.

Nandini R, Agustarini R, Susila IWW, Samawandana G. 2023. Evaluating agroforestry patterns to increase land productivity of *Falcataria moluccana* private forests in Central Lombok Regency, West Nusa Tenggara. Forest and Society 7: 247-262. DOI: 10.24259/fs.v7i2.25752.

Paterson RRM. 2023. Future climate effects on basal stem rot of conventional and modified oil palm in Indonesia and Thailand. Forests 14: 1347. DOI: 10.3390/f14071347.

Pilotti CA. 2005. Stem rots of oil palm caused by *Ganoderma boninense*: Pathogen biology and epidemiology. Mycopathologia 159: 29-137. DOI: 10.1007/s11046-004-4435-3.

Priwiratama H, Prasetyo AE, Susanto A. 2020. Incidence of basal stem rot disease of oil palm in converted planting areas and control treatments. IOP Conf Ser: Earth Environ Sci 468: 012036. DOI: 10.1088/1755-1315/468/1/012036.

Rahmadhani TP, Suwandi S, Suparman S. 2020. Growth responses of oil palm seedling inoculated with *Ganoderma boninense* under competition with edible herbaceous plants. J Sci Agric 4: 45-49. DOI: 10.25081/jsa.2020.v4.6231.

Rees RW, Flood J, Hasan Y, Cooper RM. 2007. Effects of inoculum potential, shading and soil temperature on root infection of oil palm seedlings by the basal stem rot pathogen *Ganoderma boninense*. Plant Pathol 56: 862-870. DOI: 10.1111/j.1365-3059.2007.01621.x.

Rees RW, Flood J, Hasan Y, Potter U, Cooper RM. 2009. Basal stem rot of oil palm (*Elaeis guineensis*); mode of root infection and lower stem invasion by *Ganoderma boninense*. Plant Pathol 58: 982-989. DOI: 10.1111/j.1365-3059.2009.02100.x.

Silbanus S, Raynor B. 1993. Intercropping *Colocasia* taro with black pepper (*Piper nigrum*) on Pohnpei. College of Tropical Agriculture and Human Resources University of Hawaii. Res Ext Ser 140: 13.

Spear DM, Foster WA, Advento AD, Naim M, Caliman JP, Luke SH, Snaddon JL, Ps S, Turner EC. 2018. Simplifying understory complexity in oil palm plantations is associated with a reduction in the density of a cleptoparasitic spider, *Argyrodes miniaceus* (Araneae: Theridiidae), in host (Araneae: Nephilinae) webs. Ecol Evol 8: 1595-1603. DOI: 10.1002/ece3.3772.

Stomph T, Dordas C, Baranger A, de Rijk J, Dong B, Evers J, Gu C, Li L, Simon J, Jensen ES, Wang Q, Wang Y, Wang Z, Xu H, Zhang C, Zhang L, Zhang WP, Bedoussac L, van der Werf W. 2020. Designing intercrops for high yield, yield stability and efficient use of resources: are there principles?. Advances in Agronomy 160: 1-50.

Suwandi S, Munandar RP, Suparman S, Irsan C, Muslim A. 2023. Mixed planting with rhizomatous plants interferes with *Ganoderma* disease in oil palm. J Oil Palm Res 35: 354-364. DOI: 10.21894/jopr.2022.0043.

Suwandi S, Rahmadhani TP, Suparman S, Irsan C, Muslim A. 2022. Allelopathic potential of root exudates from perennial herbaceous plants against *Ganoderma boninense.* IOP Conf Ser: Earth Environ Sci 976: 012053 DOI: 10.1088/1755-1315/976/1/012053.

Teuscher M, Gérard A, Brose U, Buchori D, Clough Y, Ehbrecht M, Hölscher D, Irawan B, Sundawati L, Wollni M, Kreft H. 2016. Experimental biodiversity enrichment in oil-palm-dominated landscapes in Indonesia. Front Plant Sci 7: 1538. DOI: 10.3389/fpls.2016.01538.

Villegas-Fernández ÁM, Amarna AA, Moral J, Rubiales D. 2023. Crop diversification to control rust in faba bean caused by *Uromyces viciae-fabae*. J Fungi (Basel) 9: 344. DOI: 10.3390/jof9030344.

Winara A, Fauziyah E, Suhartono, Widiyanto A, Sanudin, Sudomo A, Siarudin M, Hani A, Indrajaya Y, Achmad B, et al. 2022. Assessing the productivity and socioeconomic feasibility of cocoyam and teak agroforestry for food security. Sustainability 14: 11981. DOI: 10.3390/su141911981.

Yulianti S, Suwandi S, Nurhayati N. 2017. Suppression ability of herbaceous plants on inoculum potential of *Rigidoporus microporus*. Jurnal Fitopatologi Indonesia 13: 81-88. DOI: 10.14692/jfi.13.3.81.

Zhu S, Morel JB. 2019. Molecular mechanisms underlying microbial disease control in intercropping. Mol Plant Microbe Interact 32: 20-24. DOI: 10.1094/MPMI-03-18-0058-CR.