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MIXED PLANTING WITH RHIZOMATOUS PLANTS INTERFERES WITH *Ganoderma* DISEASE IN OIL PALM

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ABSTRACT

Basal stem rot (BSR) caused by Ganoderma boninense *remains the most destructive disease in oil palm monoculture plantations. This study investigates the nature of* Ganoderma *infection and survival under mixed planting with rhizomatous plants and its impact on the growth of oil palm. Two mixed plants (oil palm seedling and Java turmeric, galangal, or ginger) and single planting of those plants were inoculated with* Ganoderma boninense*-colonised rubber wood block (RWB). The results showed that* Ganoderma *inoculation in mixed planting caused an infection on both host species (dual-host infection). Under mixed planting for 9 months with Java turmeric and ginger, the disease index of oil palm was reduced by 47%-59% compared to the single planting. Planting oil palm with rhizomatous plants showed a minor effect on the decay of RWB and fungal survival but planting with ginger induced basidiocarp formation. The rhizomatous plants habitually did not exhibit allelopathic inhibition of oil palm growth. Growth of* Ganoderma*-infected seedlings was recovered under mixed planting. This study highlights a novel insight that mixed planting with rhizomatous plants can interfere with and reduce* Ganoderma *disease in oil palm.*

Keywords: *Ganoderma*, intercrop, infection interference, oil palm, rhizomatous plant.

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INTRODUCTION

Ganoderma spp. are polypore fungi that mainly live saprophytically but can also be pathogenic to most woody plants (Zhou *et al*., 2015). In Southeast Asia, *Ganoderma* spp. play an important role as pathogens of woody plantation plants such as coconut (Kandan *et al*., 2010; Vinjusha and Kumar, 2022), acacia (Glen *et al*., 2009; Page *et al*., 2020) and oil palm (Ariffin *et al.,* 2000; Siddiqui *et al.,* 2021). *Ganoderma boninense* has been identified as the main pathogen of oil palm that causes basal stem rot (BSR) (Midot *et al.,* 2019; Pilotti, 2005; Purba *et al.,* 2020). BSR disease has become a serious problem in all soil types and oil palm planted areas in Indonesia and Malaysia. In some inland plantations of North Sumatra, BSR killed 31%-67% of oil palm trees during its 25 years of planting (Riyanto *et al*., 2020). In a peatland oil palm plantation in Sumatra, *Ganoderma* infection was reported to cause 30%-54% plant mortality and was estimated to reduce 0.5-0.7 t ha^{-1} yr^{-1} yield in its 14 years of planting (Pujianto *et al*., 2016). Recent disease surveillance of 37 359.81 ha of smallholder's plantations in Malaysia reported that BSR disease had affected 8.72%, 14.00%, 6.08% and 27.70% of oil palm in inland, coastal, peat and lateritic area, respectively (Ibrahim *et al*., 2020). BSR disease can reduce oil palm yields in some severely affected plantings by 68% (Kamu *et al.,* 2021). Inocula of *G. boninense* survive for a long time in infested plant debris left in the soil and therefore infect the next generation of plantings. Infested planting may harbour many infested roots, while a small infected root piece could be an infective inoculum (Rees *et al.,* 2007). The abundance of inoculum sources in a recent planting was considered responsible for the disease increase over several plant generations (Priwiratama *et al.,* 2020). Several control measures, including cultural practices, mechanical, chemical and microbial treatments, were applied to control BSR; however, none has been really able to reduce the spread of the disease (Siddiqui *et al*., 2021).

Oil palm plantations in Indonesia generally apply a standard monoculture cropping procedure with 25-30 years of commercial lifespan. This

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perennial tree planting forms a complex habitat of abundant understorey vegetation. This vegetation is dominated by herbaceous weeds (Ashton-Butt *et al.*, 2018; Luke *et al.*, 2019; Rembold *et al.*, 2017). Understorey vegetation in oil palm plantations could benefit both under- and above-ground biodiversity, including improving avian biodiversity (Nájera and Simonetti, 2010; Tohiran *et al.*, 2017), helping above-ground invertebrate communities (Ashraf *et al.*, 2018; Chung *et al.*, 2000; Spear *et al.*, 2018) and improving soil biodiversity and decomposition rates (Ashton-Butt *et al.*, 2018). In contrast to a large-scale plantation, some smallholders intercrop young oil palm with non-permanent food and cash crops, such as rice, maize, soybean, pineapple, cassava, banana, yam and cocoyam, particularly during the preharvest period until five years (Teuscher *et al.*, 2016). Intercropping oil palm with food and cash crops could provide both economic and environmental gains (Khasanah *et al.*, 2020). Boudreau (2013) demonstrated that intercropping practices had reduced rot/wilt diseases in 86% of 14 studies comparing diseases in monocrops and intercrops. The increase in host diversity through mixed cropping can lead either to a decrease in disease pressure (inoculum dilution mechanism) or to induce resistance in neighbouring plants (molecular mechanism) (Zhu and Morel, 2019). Rhizomatous plants from the Zingiberaceae family are among the cash crops adaptable to understorey intercropping with young oil palm or even mature palm (Yusron and Januwati, 2003). In rubber planting, mixed planting with perennial herbaceous plants, including rhizomatous plants, could reduce white root rot disease caused by *Rigidoporus microporous* and improve the decomposition of the infested stump (Silva *et al.*, 2014, Situmorang *et al.*, 2007).

However, it is not known how mixed planting as understorey intercropping with rhizomatous perennial plants influences the infection and survival of *G. boninense* and the growth of oil palm. The present study aimed to determine the effects of mixed planting with rhizomatous plants on the infection, development and survival of *G. boninense* and the growth of oil palm. This study hypothesised that *Ganoderma* infection, survival and development would be negatively interfered by mixed planting. Our findings will have important implications for a new approach to BSR management.

MATERIALS AND METHODS

Plant and Planting System

The rhizomatous plants tested were Java turmeric (*Curcuma xanthorrhiza* D. Dietr.), galangal (*Alpinia galanga* (L.) Willd.), and ginger (*Zingiber officinale* Roscoe). Rhizomes as planting materials were collected from local markets in South Sumatra and allowed to sprout for one month in sand medium to obtain plants of homogenous size. Oil palm material was obtained as germinated *dura* x *pisifera* (D×P) seeds from the Indonesian Oil Palm Research Institute. Seedlings were pregrown in a sand culture for two months until they had two leaves.

Three planting systems with *Ganoderma* inoculation were evaluated in this study: (i) mixed planting between oil palm seedlings and one of three rhizomatous plants, (ii) single planting of oil palm seedlings, and (iii) single planting of rhizomatous plants. Two additional planting systems equal to (i) and (ii) but without pathogen inoculation were also implemented to determine the effect of inoculation and mixed planting on the growth of oil palm. Each planting system comprised 15 plants. The experiment was replicated once. A mixture of field soil and sand (1:1) with a total volume of 5 L was filled within a black polyethylene bag (polybag) and used to grow plants in all planting systems. For mixed planting, plants were spaced 10 cm apart. Polybags were arranged at 90 cm spacing under a 25% paranet. Plants were fertilised every month with 0.5% NPK 16-16-16. Plant inoculation was performed one month after mixed planting (at the three-leaf stage for oil palm).

Inoculum and Inoculation of *G. boninense*

G. boninense isolate GbA from diseased oil palm identified based on morphology and the ITS sequences showed high aggressiveness (Rahmadhani *et al*., 2020) was used throughout the study. Pathogen inoculum was prepared as a two-month-old mycelium colonising a 12×5×5 cm rubber wood block (RWB). Inoculation was performed following Rees *et al.* (2007) by binding a wounded primary root (10 cm in length) with a single RWB using a parafilm. For mixed planting, a single RWB was inoculated onto two mixed plants (dual-host inoculation). Inoculated roots and RWB were buried at a 10 cm depth.

Disease Evaluation

Inoculated plants were uprooted every three, six and nine months post-inoculation (mpi) to examine root necrosis and disease severity. The length of root necrosis, as shown by discoloured and rotted primary roots, was recorded to measure the degree of root infection. Root infection was confirmed by direct plating of rotted roots on the *Ganoderma*-selective medium (GSM) (Ariffin and Seman, 1991). Five roots were examined for the presence or absence of *Ganoderma* infection. Disease severity was recorded following the rating of Breton *et al.* (2006) with an additional root rot rating: (0) healthy,

(1) rotting on primary 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.

Pathogen Development and Survival

Basidiocarp formation either on RWB as a source of inoculum or diseased plants was recorded as a variable for fungal development. The number of basidiocarps was counted, and the fresh weight was measured after detaching from its substrates. The decay of RWB and mycelial viability were recorded to measure pathogen survival within RWB in response to the planting system. RWB decay was calculated as the percentage of dry weight loss (Fernanda *et al*., 2021) after inoculation treatment for nine months. The viability of *Ganoderma* mycelia colonising RWB was assessed as the percentage of colonised wood fragments from which the *Ganoderma* mycelia emerged on GSM, out of 20 randomly cut wood fragments for each RWB (Chang, 2003).

Growth of Oil Palm

The leaf area and plant height of oil palm were recorded monthly to assess the growing interference of rhizomatous plants against oil palm seedlings. Leaf area was predicted by 0.55 × length × width of each of the whole plant leaves (Gromikora *et al.*, 2014).

Data Analyses

Data were analysed using R studio Version 1.4.1106 (RStudio PBC, Boston, MA, USA). The data were tested for normal distribution using the Shapiro-Wilk test and for variance homogeneity by Levene's test. Logarithmic transformation was performed to homogenous variance for the length of root necrosis before being subjected to one-way analyses of variance. The mean root necrosis length and disease index were compared using Tukey's honestly significant test (HSD). The mean RWB dry weight loss, percentage of mycelium survival, and fresh weight of basidiocarp were compared to the control treatment of single oil palm inoculation using the Dunnett test. The palm leaf area and height of single planting were compared to those of mixed planting by Student's t-test for equal variance and Welch t-test for unequal variance.

RESULTS AND DISCUSSION

Effects of Mixed Planting on Plant Disease

Ganoderma boninense infection occurred in all plants either under inoculation in a single or mixed planting. Root infection was observed on all inoculated plant species at one month post-inoculation (mpi). Infected roots were rotted and slightly darkened in colour. Oil palm infection (inoculation on a single oil palm) started to cause complete basal stem rot and plant death (mortality 80%) with basidiocarp formation on the dead plant at 6 mpi (*Figure 1*). On rhizomatous plants, root infection was extended towards the rhizome, causing rhizome root rot/rhizome rot (*Figures 2b*, *3b* and *4b*). Root and rhizome infections were confirmed by the recovery of *Ganoderma* mycelium on GSM (*Figures 2d*, *3d* and *4d*). Root and rhizome rot caused by *G. boninense* infection was more severe in galangal with a disease index of 1.8-3.4 at 6 mpi than in Java turmeric and ginger with a disease index of 0.6-0.8 and 1.0-1.4, respectively (*Figure 5*). *Ganoderma* infection caused galangal mortality (20%-60%) with basidiocarp formation (*Figure 2c*) under either single or mixed planting after 6 months of inoculation. In contrast to infection on galangal, root and rhizome rot of infected Java turmeric and ginger did not cause plant mortality even though the basidiocarp was also formed on the infected ginger rhizome at 9 mpi.

Artificial inoculation of *G. boninense* on rhizomatous plants, *viz.* Java turmeric, galangal, and ginger caused infection and rotting in the root and rhizome. Mycelium of *G. boninense* was consistently reisolated from the diseased root and rhizome tissue. This is the first study reporting that *G. boninense* is also pathogenic to rhizomatous plants. It is reported that *Ganoderma* spp. have a wide range of host plants, and all of them are woody plants (Loyd *et al.*, 2018b). Galangal was susceptible to *G. boninense* infection because fungal inoculation resulted in severe disease, plant death, and the formation of basidiocarps on diseased plants. Java turmeric and ginger were more resistant to pathogen infection, as root and rhizome rot developed slowly and did not cause plant mortality. *Ganoderma* spp. are known

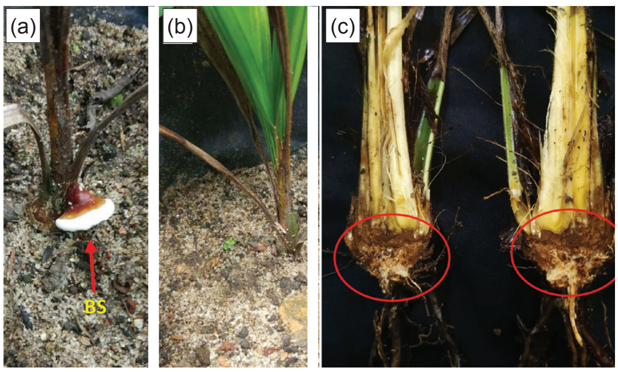

Figure 1. Symptoms of basal stem rot on inoculated oil palm seedlings under single planting at 6 months post-inoculation with Ganoderma boninense-*colonised rubber wood block showing dead palm with the formation of basidiocarp (BS) of* G. boninense *(a) drying of lower leaves without formation of basidiocarp (b) and complete basal stem (bole) and root rotting (red circle) (c).*

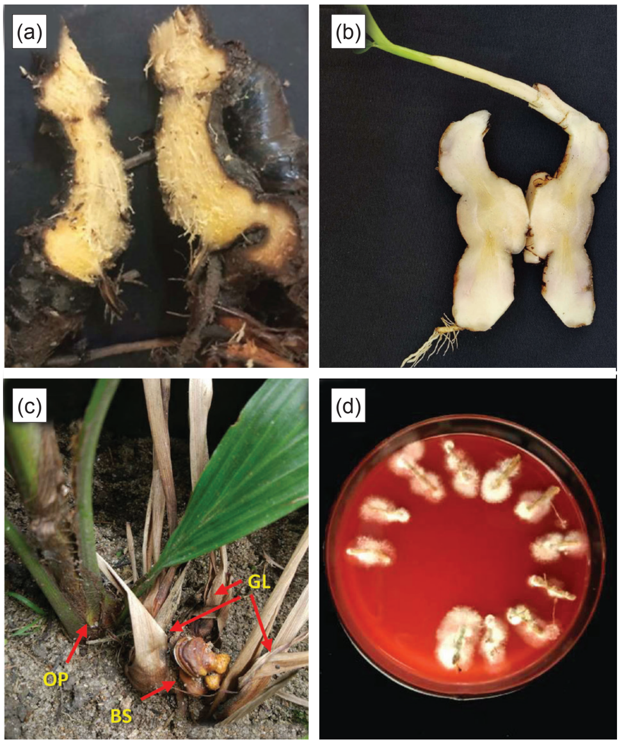

Figure 2. Symptoms of Ganoderma boninense *inoculation on mixed planting of oil palm and galangal at six months post-inoculation (mpi). (a) Complete rotting of infected roots and rhizomes relative to (b) the healthy uninoculated galangal plant. (c) Basidiocarp (BS) emerging from dead, diseased galangal plants (GL) with adjacent root-infected oil palm (OP) (the palm showed leaf symptoms at 9 mpi) and (d) mycelium of* G. boninense *growing out of infected tissues of galangal root and rhizome on GSM.*

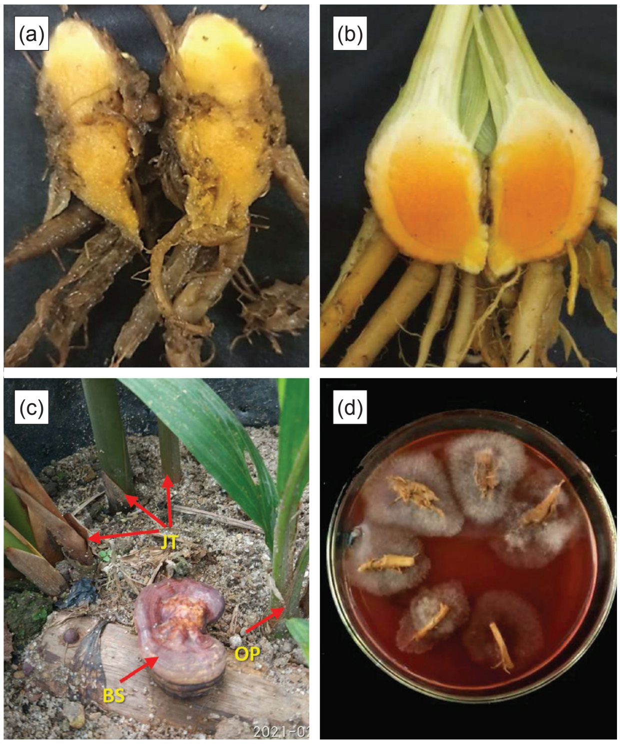

Figure 3. Symptoms of Ganoderma boninense *inoculation on mixed planting of oil palm and Java turmeric at six months post-inoculation (mpi). (a) Complete rotting of infected root dan rhizome relative to (b) the healthy uninoculated turmeric plant. (c) Basidiocarp (BS) emerging from rubber wood block as a source of inoculum with adjacent root infected oil palm (OP) and Java turmeric (JT) and (d) mycelium of* G. boninense *growing out infected tissues of Java turmeric root and rhizome on GSM.*

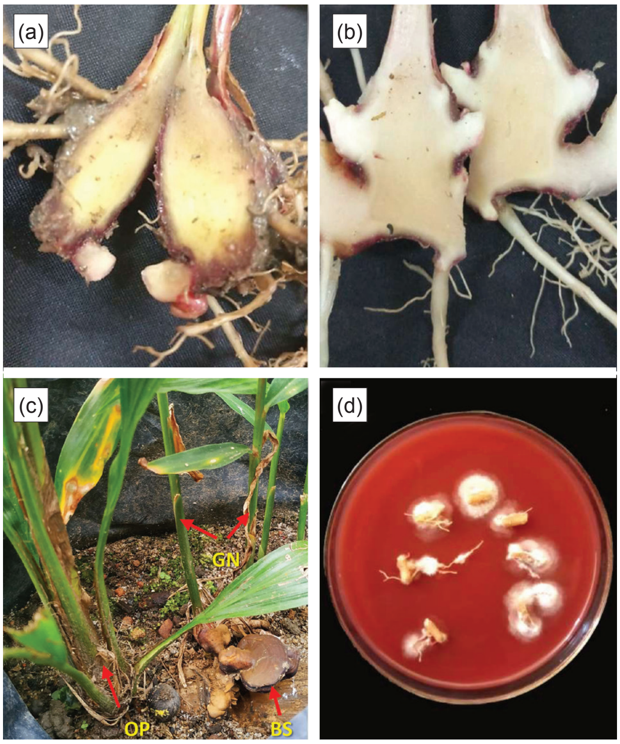

Figure 4. Symptoms of Ganoderma boninense *inoculation on mixed planting of oil palm and ginger at six months post-inoculation (mpi). (a) Partial rotting of infected root dan rhizome relative to (b) the healthy uninoculated ginger plant. (c) Basidiocarp (BS) emerging from rubber wood block as a source of inoculum with adjacent root infected oil palm (OP) and ginger (GN) and (d) mycelium of* G. boninense *growing out of infected tissues of ginger root and rhizome on GSM.*

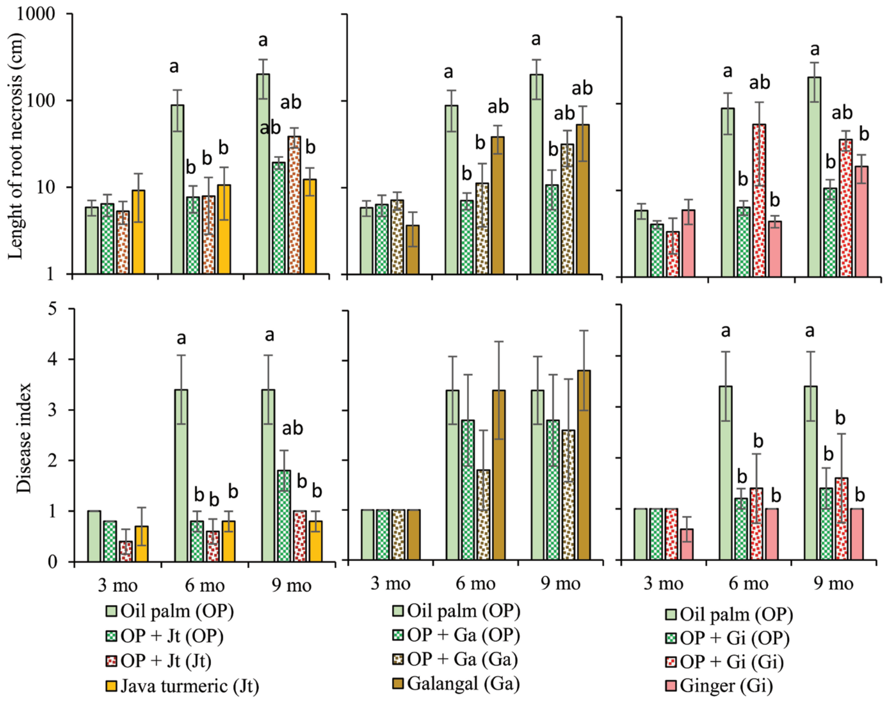

Figure 5. Effects of single or mixed planting of oil palm with rhizomatous plants (Java turmeric, galangal, and ginger) on Ganoderma boninense *infection on single host or dual host plants. Graphic bars with a pattern fill are for plants with mixed planting, and the graphic bar describes the mean for the plant name within the bracket. Error bars denote standard error of means (SEM). For each plant species and month, values followed by different letters are significantly different (HSD test).*

to secrete cell wall-degrading enzymes, which are considered the main infection mode used by wood decay fungi to infect a wide variety of woody plants (Dhillon *et al.*, 2021; Ramzi *et al.*, 2019; Rees *et al.*, 2009). Infection of rhizomatous plants, as described in this study, confirmed the cosmopolitan nature of the pathogen, which can utilise a wide variety of lignins from herbaceous to woody plants.

Dual host plant inoculation by a single mycelium inoculum under mixed planting caused *G. boninense* infection at 1 mpi on all mixed plants. The disease developed in a similar manner until 3 mpi in all planting systems. There was no significant ($p \geq 0.05$) effect of single versus mixed planting on root necrosis or the disease index on either mixed plants at the initial infection stage at 3 mpi. Dual host inoculation started to significantly ($p<0.05$) affect root necrosis at 6 mpi and continued similarly at 9 mpi. Root necrosis of oil palm in dual host inoculation was significantly ($p<0.05$) lower, ranging from 6.4-19.3 cm in length compared to that of single inoculation (88.1-200.8 cm). In contrast to oil palm infection, there was no difference ($p \geq 0.05$) in the length of root necrosis between single and dual inoculation of rhizomatous plants. A reduction of oil palm infection for dual inoculation treatment was significantly ($p<0.05$) described for disease index for mixed planting with Java turmeric and ginger but did not occur ($p \geq 0.05$) for galangal. Under mixed planting for nine months with Java turmeric and ginger, the disease index of oil palm was reduced by 47%-59% compared to the single planting. Infection suppression through mixed planting with Java turmeric and ginger constantly occurred at 6 and 9 mpi (*Figure 5*).

Inoculating a single inoculum of *G. boninense* with two different plant species (dual host inoculation) in mixed planting of oil palm and rhizomatous plants resulted in multiple host infections on all mixed plants. The present study described the evidence of dual or multiple host species infections by a single individual fungal mycelium network under artificial inoculation. Since understorey growth by herbaceous vegetation is common in oil palm fields, multiple host infections by *G. boninense* can also occur in nature. Multiple host species infections have been reported in *Rigidoporus microporus*, in which a single individual mycelium, as revealed by somatic compatibility, infected four woody and two herbaceous plant species, galangal and banana (Suwandi, 2007). In this study, the responses of rhizomatous plants were parallel in severity either in dual hosts (under mixed planting) or in single hosts (under single planting). Galangal was susceptible, whereas Java turmeric and ginger were resistant in both inoculation methods. Conversely, oil palm responded to different severities under single inoculation compared to dual inoculation. A marked reduction in disease index was noticed when mixed planting with a resistant host, whereas the disease was less affected when inoculated with mixed planting with a susceptible host. However, host resistance was unlikely to be the only contributing factor to the reduced disease of oil palm under mixed planting. In our other experiment, there was no disease suppression of *Ganoderma*-inoculated oil palm in a mixed planting with a resistant rhizomatous plant, arrowroot (*Maranta arundinacea*) (Rahmadhani *et al.,* 2020).

The disease was significantly reduced on oil palm as the primary host, suggesting infection interference by Java turmeric and ginger against *Ganoderma* in a mixed planting. Suppression of fungal growth and disease under mixed planting with rhizomatous plants has been reported against *R. microporus*, a white root rot pathogen of rubber trees, but with different magnitudes of activity. In the present study, planting with ginger resulted in disease suppression on oil palm, whereas ginger did not show a suppressive effect against white root rot caused by *R. microporus* on rubber trees (Silva *et al.,* 2014, Situmorang *et al.,* 2007). In this study, Galangal was susceptible and could not protect oil palm from *Ganoderma* infection. Still, the plant had potent allelopathic inhibition of *R. microporus* either *in vitro* or in soil and even markedly suppressed white root rot in field trials (Silva *et al.,* 2014, Situmorang *et al.,* 2007). In contrast, Java turmeric established a similar suppression activity against either *G. boninense* or *R. microporus.* Planting with Java turmeric decreased white root rot and rubber tree death by 38% and 44%, respectively (Situmorang *et al.*, 2007), and reduced fungal rhizomorph growth by 56% (Yulianti *et al.*, 2017). Rhizomatous plants likely have different magnitude activity in infection interference against root rot pathogens, *Ganoderma* and *Rigidoporus.* Under mixed planting, Java turmeric could interfere with infection of both *Ganoderma* and *Rigidoporus*, whereas ginger showed a more specific interference infection of *Ganoderma* on oil palm as the main host. Galangal did not interfere with *Ganoderma* infection but showed an interference against infection of *Rigidoporus*. Further field studies are needed to assess the host specificity/preference of the rhizomatous plants.

Effect on Pathogen Development and Survival

The development of *G. boninense,* as manifested by basidiocarp formation, was favoured following attachment and burial in the root zone of rhizomatous plants (*Figures 2c*, *3c* and *4c*). Basidiocarp started to produce on RWB after 3 mpi in a single inoculation of rhizomatous plants compared to that produced after 6 mpi of oil palm inoculation. Basidiocarps were more produced on RWB in all planting types (3-9 basidiocarps on RWBs relative to 0-1 basidiocarps on host plants), except for single oil palm planting (4 basidiocarps on RWBs close to 3 basidiocarps on host plant) (*Table 1*). The average fresh weight of basidiocarps developed on all substrates or hosts was much higher (p<0.05) on Java turmeric single planting and mixed planting of oil palm and ginger plants (oil palm + ginger) than on those inoculated on single oil palm planting (*Table 1*).

The colonisation of *G. boninense* mycelia on RWB used to artificially inoculate tested plants resulted in dry weight loss at 9 mpi. The present observation confirmed the typical characteristics of *Ganoderma* fungus as a decaying fungus. Single inoculation did not affect RWB decay, as there was no difference (p≥0.05) in the RWB dry weight losses between single plantings of different plants. A reduction in RWB decay was observed when RWB was dual inoculated on oil palm and Java turmeric with 55.7% RWB weight loss. In contrast, dual inoculation on oil palm and galangal significantly (p<0.05) increased RWB decay to be 82.4% compared to single inoculation on the palm with 71.8% RWB decay (*Figure 6*).

Mycelia of *G. boninense* colonising the most fragments (>82%) of RWB remained viable after being buried for nine months. Dual host inoculation on oil palm and rhizomatous plants had less effect on the survival of *G. boninense* mycelia colonising RWB. A slightly reduced (p<0.05) viability by 14.6% was only observed with dual inoculation of oil palm and ginger (*Figure 6*).

Mixed planting for nine months of oil palm and rhizomatous plants had less effect on the decaying of RWB colonised with *Ganoderma* after nine months. A slight increase in RWB decay was observed in the interaction of two susceptible hosts, galangal and oil palm. Wood decaying fungi will utilise any wood's lignin and polysaccharide components (Loyd *et al.*, 2018a; Naidu *et al.*, 2017; Zabel and Morrell, 2020) in the present case, RWB as nutrient sources. Once the RWB is completely decayed, the fungi will obtain nutrients from the host oil palm/ rhizomatous plant as the nutrient-depleted from the RWB. Therefore, infection will occur as a result of the decaying process as manifested by the bole infection and foliar symptoms (Naidu *et al.*, 2017; Rees *et al.*, 2009). The severe infection occurred due to inoculum intensity or other environmental factors conducive to the fungi development (Breton *et al.*, 2006; Rees *et al.*, 2007). A similar higher RWB decay was also noted on other mixed plantings of oil palm with susceptible hosts, taro plants (Alesia *et al.*, 2021) and winged yam (*Dioscorea alata*) (unpublished result). However, planting rhizomatous plants for a longer period (two years) increased the decay of *Rigidoporus*-colonised rubber stumps by 46%-85% (Situmorang *et al.,* 2007).

A minor effect of mixed planting was also shown on the survival of *Ganoderma* mycelia colonising RWB in the 9-mpi study. A slight reduction in mycelial viability was noticed on mixed plantings of oil palm and ginger. Reduced *Ganoderma*

TABLE 1. FORMATION OF *G. boninense* BASIDIOCARPS AFTER INOCULATION ON SINGLE OR TWO MIXED PLANTS FOR NINE MONTHS

Planting type (n=10)	Fresh weight (g) and number (value within brackets) of basidiocarp emerging from			
	Rubber wood block	Oil palm	Rhizomatous plants	All substrates
Oil palm	6.62 (4)	3.63 (3)	NA	5.34 (7)
Oil palm + Java turmeric	7.08 (3)	0.30 (1)	0	5.39 (4)
Java turmeric	19.01 (9)*	NA	0	19.01 (9)*
Oil palm + Galangal	5.51 (5)	0	2.51 (1)	5.01 (6)
Galangal	5.14 (7)	NA	0	5.14 (7)
Oil palm + Ginger	11.40 (9)	0	34.50 (1)	13.71 (10)*
Ginger	8.33 (9)	NA	4.71 (1)	7.97 (10)

Note: NA - not available, * - denotes a significant difference (Dunnett test) from the respective mean values of oil palm single planting (oil palm).

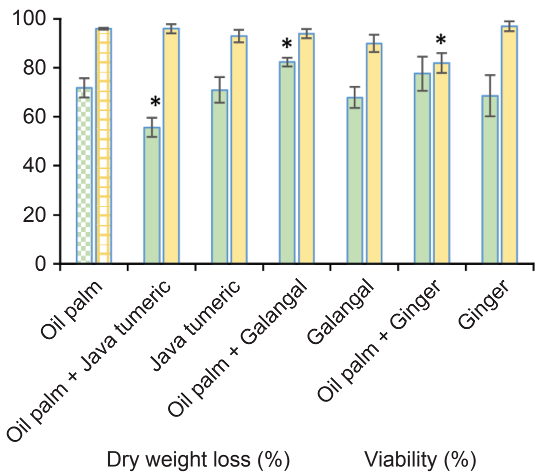

Figure 6. Effects of single or mixed oil palm planting with rhizomatous plants (Java turmeric, galangal, and ginger) on the decay of G. boninense*-colonised rubber wood block and pathogen viability after burial for nine months. For each dry weight loss and viability, * denotes a significant difference (Dunnett test) from the respective mean values of oil palm single planting.*

survival and disease severity under mixed cropping with ginger were possibly associated with allelochemical substances secreted in the rhizome. Ginger has been widely reported to have anti-fungal allelochemicals against numerous fungi. For example, ginger essential oil and gingerol showed anti-fungal activity against *Pestalotiopsis microspora* and suppressed fruit rot caused by the fungus on Chinese olive via a membrane-targeted mechanism with alteration of membrane permeability (Chen *et al.*, 2018). The anti-fungal activity also occurred on Java turmeric essential oil, xanthorrhizol (Akter *et al.*, 2018; Rukayadi *et al.*, 2006). Further study is needed to elaborate on the role of the anti-fungal allelochemical on disease suppression in a mixed planting with these plants. Although both ginger and Java turmeric potentially have allopathic activity against *G. boninense*, both essential oil-producing plants could trigger the basidiocarp formation of *G. boninense.* The induction of basidiocarp formation by the rhizomatous plant can be used further as an indicator plant for monitoring the colonisation of *G. boninense* on wood or palm debris in the field.

Effects on Oil Palm Growth

Mixed planting in a small volume of soil (5 L) between oil palm seedlings and rhizomatous plants for eight months (7 mpi) had less effect on the growth of oil palm as measured by leaf area and plant height. On non-inoculated control plants (-Gb, roots were tied with RWB without *G. boninense*) up to 7 mpi, there were no significant differences recorded in leaf area (*Figure 7a*) or plant height (*Figure 7b*) of oil palm between single and mixed planting. Significant growth inhibition on oil palm in leaf area and plant height was observed at 8 and 9 mpi under mixed planting with Java turmeric and galangal. Among the three rhizomatous plants, ginger showed less negative interference in the growth of oil palm seedlings. Differences between the growth of oil palm under mixed planting with ginger compared with single planting were observed only in the leaf area at 9 mpi. There were no significant differences between the leaf area and plant height of inoculated oil palm under single and mixed planting. The growth of inoculated single planting oil palm was suppressed, whereas oil-palm growth under inoculated mixed planting was less affected (*Figure 7*).

Rhizomatous plants habitually have not exhibited allelopathic inhibition on oil palm growth, as there was no significant difference between leaf area and height for eight months of planting of non-inoculated oil palm between single and mixed planting. Growth inhibition was observed after nine months of planting (8 mpi), which was likely due to limitations of growing space. It has been widely reported that intercropping with rhizomatous plants in an appropriate population is harmless to the growth and yield of the main crop (Chapagain *et al.*, 2018; Kathwal *et al.*, 2019).

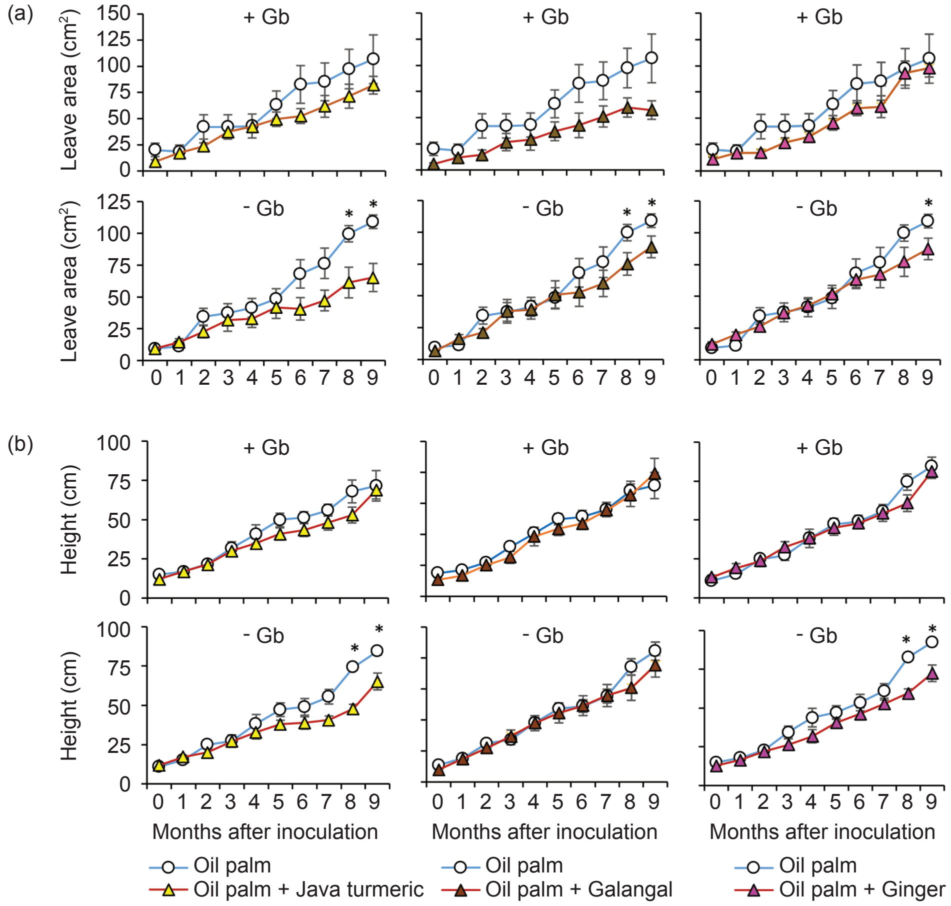

Figure 7. Effects of single or mixed planting with rhizomatous plants (Java turmeric, galangal, and ginger) on (a) leaf area and (b) plant height of Ganoderma boninense*-inoculated oil palm (+ Gb) and non-inoculated oil palm (- Gb). For each plant species and month, * denotes a significant difference (t-test) between the mean values of oil palm in single planting compared to mixed planting.*

The growth of inoculated single planting oil palm was suppressed eight months after inoculation. This growth retardation was not observed in mixed planting, suggesting the growth recovery of infected seedlings. Reduction in disease severity under mixed planting contributed to the growth recovery of infected seedlings. The indirect mechanism through beneficial soil microbial community can also enhance growth under mixed planting and needs further exploration. In the pathosystem of apple replant disease caused by numerous soil-borne fungi such as *Cylindrocarpon*, *Rhizoctonia*, *Phytophthora*, and *Pythium*, enhanced growth of apple seedlings under mixed cropping with *Allium fistulosum*, or *Brassica juncea* had been mediated through modifying the resident fungal community (Zhao *et al*., 2022). Zeng *et al.* (2020) demonstrated that intercropping turmeric and ginger with patchouli could improve the contents of the active ingredient in the main crop (patchouli) by enhancing the beneficial soil microbial community and modifying soil enzyme activity, soil pH, and soil exchangeable Ca. The results from our study highlight the beneficial use of rhizomatous plants in the management of *Ganoderma* basal stem rot. The rhizomatous plant is potentially applied as an understorey intercrop for young replanted plantations or planted locally in the area of the excavated or chipped diseased palms, and further field study is needed to assess the long-term control efficacy.

CONCLUSION

Ganoderma inoculation on mixed planting of oil palm seedling with rhizomatous plants, *i.e.*, Java turmeric (*C. xanthorrhiza*), galangal (*A. galanga*), or ginger (*Z. officinale*) caused an infection on both host species (dual-host infection). The disease was significantly reduced on oil palm as the main host, suggesting infection interference by Java turmeric and ginger in a mixed planting. The rhizomatous plants habitually did not exhibit allelopathic inhibition of oil palm growth. Growth of *Ganoderma*-infected seedlings was recovered under mixed planting. This study highlights a novel insight that dual-host species infection in a mixed planting with rhizomatous plants can interfere with and reduce *Ganoderma* disease on oil palm as the main host.

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