Journal of Oil Palm Research
DOI: https://doi.org/10.21894/jopr.2025.0020

PARADIGMS AND KNOWLEDGE GAPS IN OIL PALM STEM ROTS CAUSED BY *Ganoderma*

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ABSTRACT

Stem rots of oil palms caused by Ganoderma boninense *(basal stem rot and upper stem rot) were first reported in Southeast Asia some 90 years ago. Despite considerable observation and research since that date and the construction of various paradigms, they remain the biggest threat to sustainable oil palm production in SE Asia and Oceania. In this article, we discuss some of the paradigms developed in* Ganoderma *research over many decades and identify some "knowledge gaps" that may be significant for developing improved disease control. Fourteen, specific recommendations on several different aspects of the disease, its control, and palm husbandry are provided and we believe, these should be considered by researchers who continue to study these economically important diseases.*

Keywords: *Ganoderma boninense* research, knowledge gaps, oil palm, recommendations.

Received: 28 March 2024**; Accepted:** 19 December 2024**; Published online:** 28 March 2025.

INTRODUCTION

Stem rots caused by *Ganoderma boninense* remain the greatest challenge to sustainable oil palm production in Southeast Asia and the Pacific (Flood *et al.*, 2022). In Malaysia, fresh fruit bunches (FFB) yield reduction at the rate of 0.04 t to 4.34 t/ha at 10 to 22 years of planting respectively was reported by Roslan and Idris (2012) with economic losses reported of up to USD500 million (Bharudin *et al.*, 2022; Zakaria, 2023). In North Sumatra, by the time of replanting (25 years), 40%-50% of palms in some fields were lost with the majority of those remaining showing disease symptoms (Rees *et al*., 2007). The level of basal stem rot (BSR) in Papua New Guinea (PNG) is not as high as in Southeast (SE) Asia although 50% has been recorded (Pilotti *et al.*, 2018).

In recent years, there have been numerous reviews about *Ganoderma*-induced stem rots in oil palm (*e.g.*, Bharudin *et al*., 2022; Chong *et al*., 2017a; 2017b; Mercière *et al*., 2017; Siddiqui *et al*., 2021; Supramani *et al*., 2022; Zakaria, 2023). Although these publications have, to varying degrees, considered both historical perspectives and new research, several basic questions remain to be answered before much of the existing research can be fully utilised for possible control strategies. Siddiqui *et al*. (2021) and Flood *et al*. (2022) both published updated reviews of the current knowledge on BSR of oil palm and also briefly highlighted some of the key challenges that remain for researchers and the oil palm industry in general. This approach was expanded by Pilotti and Bridge (2023) who reviewed *Ganoderma* diseases of several tropical crops and also identified several fundamental issues and areas where further research and interpretation are required.

In this article, we have attempted to discuss the paradigms that have impacted *Ganoderma* research over many decades and have identified the "knowledge gaps" that we believe may be significant for the development of robust monitoring and husbandry required to improve disease control. We have considered the historical and current information in two sections that are essentially "What do we know?" (Current Knowledge) and "What are we unsure of?" (Uncertainties). We have then attempted to identify what activities may be required to clarify the uncertainties that remain in *Ganoderma* research that require further investigation. These are provided as several specific recommendations in different aspects of

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Ganoderma research that we believe should be considered by researchers who continue to study this economically important disease.

CURRENT KNOWLEDGE

The Fungus

Historically, various species of *Ganoderma* were suggested as responsible for BSR in oil palms. In 1985, Ho and Nawawi determined that all occurrences of BSR in Malaysia were due to the single species *G. boninense* (Ho & Nawawi, 1985). Subsequently, all instances of BSR on oil palm in Southeast Asia and Oceania have been identified as *G. boninense*. Although the names *G. miniatocinctum* and *G. zonatum* have been used for some collections in Malaysia, molecular and mating studies have repeatedly confirmed that these isolates have been misidentified and that they are examples of *G. boninense* (Flood *et al*., 2022; Fryssouli *et al*., 2020; Midot *et al*., 2019; Pilotti & Bridge, 2023). *Ganoderma boninense* was first described in 1888 and has been recorded from a wide range of palm hosts throughout SE Asia and Oceania (Patouillard, 1889; Pilotti & Bridge, 2023; Steyaert, 1975). The species was therefore present in the region and probably widely distributed on native palms before the commercial introduction of oil palm (Mercière *et al*., 2017; Midot *et al*., 2019).

Systematically, *G. boninense* has been placed together with a small number of other species in a distinct clade within the genus (Fryssouli *et al*., 2020). This clade was originally termed the "palm clade" by Moncalvo (2000) and includes *G. zonatum* and *G. ryvardenii* which occur on palms in the Americas and Africa respectively. Modern species within *Ganoderma* are thought to be relatively young in evolutionary terms and probably diverged around 30 million years ago (MYA). This is after the origin of palms (around 100 MYA) and the formation of the modern continents (around 60 MYA (Flood *et al*., 2022). *Ganoderma* species are largely associated with soil and plant debris and recent studies suggest that there may be significant biogeographic distributions within the genus (Fryssouli *et al*., 2020; Moncalvo & Buchanan, 2008). It is therefore likely that the modern palm pathogens have evolved independently on each continent from a common ancestor (Loyd *et al*., 2019; Pilotti & Bridge, 2023).

The fungus is typical of many basidiomycetes in that the fruiting body (bracket) produces monokaryotic spores. These basidiospores germinate to produce monokaryotic mycelium and this then fuses with mycelium from another compatible spore to produce dikaryotic mycelium that ultimately, produces a new fruiting body. *Ganoderma boninense* has a tetrapolar mating system and this favours outbreeding between spores from different fruiting bodies (Pilotti *et al*., 2002). [Bharudin *et al*., (2022) and Pilotti & Bridge, (2023)] described the detailed life cycle of *G. boninense*.

The Disease

Ganoderma diseases are generally confined to woody plants and palms. A small number of species can infect many tropical and sub-tropical crops including rubber, tea, other beverage crops, citrus, and *Acacia* spp. as well as betel, coconut and oil palms (Pilotti & Bridge, 2023). The fungi occur as decomposers of dead wood in natural ecosystems and no doubt have evolved with specific enzyme systems capable of degrading a variety of materials (Papp, 2019; Pilotti & Bridge, 2023). This is evident in the 'palm specific' species that appear to have become specialised and pathogenic on palms *viz*. *G. boninense, G. ryvardenii* and *G. zonatum* (see previous section).

Basal stem rot (BSR). Most instances of *Ganoderma* diseases on palms manifest as a basal rot of the bole tissue which may subsequently move into the roots. Initially, infection in oil palms was thought to begin in root tissue and move into the bole area, but it is believed that the inoculum potential in single palm roots is inadequate to initiate infection in basal tissue and multiple infections would be needed (Rees *et al*., 2009). Anecdotal evidence indicates that the infection may begin in the base of the palm, *via* pruned frond butts, a route first suggested some 90 years ago by Thompson (1931). Panchal and Bridge (2005) detected the pathogen's DNA in the tissue behind pruned frond bases while *G. boninense* has also been detected in inoculated cut fronds (Rees *et al.,* 2009). These findings were from palms before disease symptoms were apparent and so suggest early colonisation in the frond bases might occur. Unlike other palms such as coconut, it is necessary to prune the green fronds of oil palm to allow access to the fruit bunches during harvest. Pruning typically begins two to two and a half years after planting and continues throughout the economic life of the palm. It is possible that mechanical injury at the bole-root interface of palms caused by strong winds could also provide an avenue for the entry of fungal inoculum in the form of basidiospores. Mechanical weeding could also cause wounds to the base of the palms and the root ring providing an avenue of infection.

The decay is typically a tan-coloured dry rot with or without darker 'zone' lines and an advancing yellow margin. The latter area is believed to be composed of extracellular fungal enzymes that begin the decay process, possibly by removing hemicellulases and starting to expose the target constituents of cellulose and lignin (Ariffin *et al*., 2000).

The duration of the disease cycle may depend on the susceptibility of the breeding line and the time of infection. Diseased palms have been known to survive after early symptom expression from as little as six months to as long as two to three years (Ariffin *et al*., 2000; Zakaria, 2023). However, this field-based evidence does not take into account the incubation period which is as yet unknown but appears to be variable, possibly relating to the genetics or nutritional status of the palm. Some evidence from field trials in PNG shows that the application of Muriate of Potash (MoP) may play a role in reducing *Ganoderma* disease incidence (PNG OPRA, 2002). It is generally believed that the disease cycle will be faster and disease incidence will increase with increasing replantings. This is generally true for areas with relatively high initial disease incidence (<10%>) but there may be some exceptions to this general assumption, especially in areas where oil palms have been planted into primary or secondary forested areas. Under this scenario, the build-up of disease inoculum may take longer to manifest since the initial inoculum source is likely to be basidiospores liberated from naturally decaying native palms or distant fields of coconut or oil palm (Sanderson, 2005).

The association of previous plantings of coconut with *Ganoderma* disease of oil palms is well established (Abdullah, 2000; Ariffin, 2000; Sanderson *et al*., 2000) and isolates from both hosts are conspecific (Pilotti *et al.*, 2002). Although the disease incidence in individual plantation blocks is variable, the incidence of basal stem rot is generally higher in plantings after coconut (Ariffin, 2000; Pilotti, 2005; Singh, 1991). Stem rots of coconut have not been of consequence in most countries except India where the disease has a different and as yet unresolved etiology (Pilotti & Bridge, 2023). The fungus does however, grow saprophytically on dead coconut trunks in most countries where oil palm is planted and these are believed to be an initial source of infection for newly planted oil palms, either through basidiospores liberated from basidioma, or mycelium. A similar situation exists for ornamental palms attacked by *G. zonatum* in North America where initial infections are believed to be initiated by basidiospores (Elliot & Broschat, 2000; Loyd *et al*., 2018; Pilotti & Bridge, 2023).

Expression of symptoms is similar among palm species with progressive wilting and yellowing of fronds as the disease advances throughout the basal elements (Pilotti & Bridge, 2023). Usually when symptoms are observed in oil palms, it is not possible to apply remedial treatments and the palm will eventually succumb to the infection. Basidioma of *Ganoderma* will be evident when symptoms (and assumed bole decay) are at an advanced stage in infected palms. It has been observed in PNG and Solomon Islands (SI) that about 10% of palms expressing varying levels of disease symptoms do not produce basidioma on the exterior of the trunk (PNG OPRA, 2007). The reasons for this are unknown but could relate to the state of the fungal mycelium (monokaryotic, see *The Fungus* section) or secondary infections by other fungi or bacteria that may out-compete the initial infection by *G. boninense.*

The spread of *Ganoderma* differs among crops; particularly between palms and hardwood trees. However, molecular evidence suggests that both basidiospores and mycelium play a role in the persistence and spread of stem rots (Flood *et al*., 2022; Pilotti & Bridge, 2023). In a plantation environment such as for oil palm, disease spread will differ for different stages of the planting cycle. For example, in a first-generation planting, basidiospores will largely be responsible for disease initiation, and spread away from initial foci will become evident as palms reach the end of the first planting cycle of normally, 25 years. Under this scenario, disease patterns will generally be random in the first half of the planting cycle and become more aggregated in the latter half due to hypothetical spread between palms, although the overall disease pattern will still be considered random (Pilotti, personal communication, 2023; Pilotti & Bridge, personal communication, 2023). Evidence for this has been obtained from molecular and somatic incompatibility studies between isolates from field palms (Miller *et al*., 2000; Pilotti, 2018; Pilotti *et al*, 2018). As the planting cycles increase, it is considered that the fungal mycelium will feature more prominently in disease spread. This is by way of residual inoculum in the debris remaining in the soil from the previous planting as well as increased spread between palms with readily available routes for mycelium to follow (*e.g.* dead and severed roots) from the previous planting. Such a scenario leads to more aggregated disease patterns but this does not rule out the continuing establishment of new infection foci by basidiospores in secondary infections. Sanderson (2005) estimated that around 2 million spores could be released from a 100 x 50 mm bracket every minute (equating to 2.9 x 10-12 spores per day) and although the great majority of these will fall to the ground, Rees *et al*. (2012) reported 2–11,000 spores/m^{-3} in oil palm plantation air samples.

Upper stem rot (USR). The incidence of USR in oil palms tends to increase towards the end of the planting cycle. Low incidences of USR were observed in the first-generation oil palm plantings (Pilotti, 2005) and may increase in subsequent plantings, although this may be correlated to the expected increase in the incidence of basal stem rot. Current thinking is that USR is initiated from secondary infections by basidiospores liberated from basidioma produced from palms with basal stem rot in the same field or plantation. It is known that basidiospores can travel and survive long distances (Pilotti *et al.*, 2003) and that mating between compatible monokaryons (to form dikaryons) takes place readily in a plantation environment (Pilotti, 2005; Pilotti & Bridge, 2023). Therefore, chance infections in the upper portion of palm trunks are possible and do occur. Data collected on USR incidences in oil palm seed gardens in PNG and Indonesia indicate that higher levels of USR are observed, probably due to mechanical injury to palm trunks with regular climbing of mother palms for hand pollination. Insects and small mammals may also play a role in disseminating basidiospores but obtaining proof of this would require careful observation and study.

Early Detection

One major barrier to the management of BSR is early detection. The earlier the disease is detected, the quicker management options can be considered. Traditionally, this was done using a six-month census of the estates by trained staff based on external symptoms or detection through culturing of the fungus; both are time-consuming and labour-intensive so new technologies have been investigated. These have been reviewed in detail by Flood *et al*. (2022) and Pilotti and Bridge (2023) and only broad details of the main remote detection methods and laboratory methods will be provided here.

Remote detection methods. Geospatial technologies have been increasingly used with varying degrees of success. These include hyperspectral remote sensing, multispectral remote sensing, terrestrial laser scanning tomography, intelligent electronic nose, micro-focus X-ray fluorescence, spatial maps, and the increased use of machine learning methods. These methods are discussed in detail in Flood *et al*. (2022).

Khosrokhani *et al.* (2016) concluded that hyperspectral remote sensing (HRS) was capable of detecting BSR in oil palm estates using either aerial or ground-based sensors and that these technologies could also determine disease severity, but differentiation between healthy and slightly infected palms was more difficult. HRS sensors work well in combination with other data sets and models. Modified red edge simple ratio (MRS) sensors can discriminate between healthy and infected palms but can less differentiate infection severity. The intelligent nose system (Abdullah *et al.*, 2011; 2012a; 2012b) can also distinguish infected and non-infected using artificial neural network algorithms (ANN) and multivariate statistics but more research is needed to determine BSR severity. Electrical capacitance volume tomography is a quick and non-destructive method and sonic tomography combined with expert knowledge can detect BSR and determine severity levels. Micro X-ray fluorescence (uXRF) sensors have some potential but distinguishing BSR severity is difficult. Santoso *et al.* (2011; 2017) used spatial maps to determine BSR distribution and using the Kriging interpolation method, the distribution appeared as random. However, QuickBird imaging-derived maps, showed that disease distribution was sporadic in older palms and dendritic in young palms which may be linked to different methods of disease spread (see *Basal Stem Rot* section). Izzuddin *et al.* (2020) analysed BSR in the field using unmanned aerial vehicles linked to field-based ground truthing. A three-band combination of the multispectral images plus object-based analysis did detect moderately and severely infected palms. However, as with many of these technologies, detection of slightly infected palms from healthy ones was problematic and this distinction is key for early detection.

LiDAR (Light detection and ranging) works well in forestry applications (Lefsky *et al*., 2002) and in oil palm (Shafri *et al*., 2012). LiDAR technologies have shown promise for early detection of BSR. Khairunniza-Bejo and Vong (2014) used a ground-based LiDAR technique, known as Terrestrial Laser Scanning (TLS) and their results indicated correlations between the oil palm trunk's perimeter, Diameter-Based Height (DBH) and canopy area, with BSR disease although *Ganoderma* incidence is known to increase with age. Subsequently, Husin *et al.* (2020) used TLS as a means of early detection of BSR in nine-year-old palms. Palms were categorised into four health levels - T0, T1, T2 and T3, representing healthy, mildly infected, moderately infected and severely infected, respectively. Statistical analysis revealed that frond number was the best single parameter to detect BSR disease as early as T1 (slightly affected). In classification models, although a linear model with a combination of parameters, ABD – A (frond), B (frond angle) and D (S200 - canopy strata at 200 cm from the top) delivered the highest average accuracy (86.7%) for classification of healthy/unhealthy trees.

Much research effort has been undertaken into remote sensing but problems remain including differentiating between slightly infected palms and healthy palms in the field which is vital for early detection.

Laboratory methods. Over the last 50 years, numerous researchers have looked at methods to detect *Ganoderma* in palm tissues and their potential to provide early diagnostic tests. Essentially, the methods can be grouped under the four headings culture, physiology, immunology, and molecular (Pilotti & Bridge, 2023).

Culturing. The ability to isolate and culture a viable fungus from plant material may indicate a disease, but this approach has many complications. Failure to isolate an organism may not indicate its absence as the isolation methods and the culture medium need to be optimal and the location of viable fungal material in the plant sample needs to be considered. Similarly, positive isolation may be due to fungal propagules on the surface of the sample or in soil associated with the sample, so considerable care has to be taken with any isolate and culture method including appropriate and thorough surface sterilisation of the sample. A significant barrier to identifying *Ganoderma* by isolation and culture is that the mycelial form of the fungus has few diagnostic characteristics to differentiate it from many other basidiomycetes. A selective culture medium (GSM) (Ariffin & Idris, 1992) has been developed but this is only semi-selective and it will also support the growth of other genera of wood-rotting fungi (Farid *et al.*, 2018). Unfortunately, some components of GSM are either not widely available or considered environmentally unacceptable and so a replacement medium is needed (Amanda & Prakoso, 2018; Pilotti & Bridge, 2023).

Physiology. Various workers have attempted to detect *Ganoderma* in palm material by identifying or assaying different fungus components or the biochemical activity associated with infection. Probably the earliest of these were the studies of *Ganoderma* in coconut palms which measured some physiological properties and developed colorimetric and spectroscopic assays for some chemical properties (Natarajan *et al*., 1986; Pilotti & Bridge, 2023) and reviewed by Raju *et al*. (2015). In oil palm, several chemical components of either the fungus or of the plant defenses have been considered, and these are detailed in Pilotti and Bridge (2023), but to our knowledge, none of these methods has been widely adopted in practice.

Immunology. The first attempts to obtain specific antibodies to *Ganoderma* and to use them to detect the fungus in palm tissue were with betel nut and coconut palms (Ananthanarayanan & Reddy, 1984; Reddy & Ananthanarayanan, 1984). Subsequently, Indonesian researchers developed both polyclonal and monoclonal antibodies and they were able to detect *Ganoderma* in diverse oil palm tissues (including leaves) at various stages of the disease (Darmono, 2000; Utomo & Niepold, 2000a). These antibodies can be linked to various markers to provide ELISA and dot blot-based diagnostic tests for plant tissue (Darmono, 2000; Rajendran *et al*., 2009). Although some questions have been raised regarding specificity, and these need to be considered alongside what other fungi might be expected in the samples, immunological tests can be easily automated to allow for bulk screening of multiple tissue samples (Hushiarian *et al*., 2013; Pilotti & Bridge, 2023; Utomo & Niepold, 2000b).

Molecular. DNA sequence data is now a fundamental character for classifying and identifying fungi (Borman & Johnson, 2020; May, 2020). Although DNA sequences obtained from numerous genes have been used by various workers for both classification and identification, the internal spacer regions (ITS) of the nuclear ribosomal RNA gene cluster have been adopted as a universal marker for fungi (Schoch *et al*., 2012). ITS sequences have been widely considered in the classification and identification of *Ganoderma* species (*e.g.*, Frysouli *et al*., 2020; Moncalvo, 2000). A benefit of ITS sequences is that they contain various variable regions that can be correlated with species identity and so can be used to develop primers that can then be used to selectively amplify DNA from individual species by the Polymerase Chain Reaction (Atkins & Clarke, 2004). This approach was developed to allow specific detection of *Ganoderma* in oil palm tissues in the late 1990s and several specific primers and associated methodologies have been published (Bridge *et al*., 2000; Pilotti & Bridge, 2023; Utomo & Niepold, 2000a; 2000b). ITS-PCR methodology has been used for palm samples obtained in surveys and has shown the presence of *Ganoderma* in frond bases and root material of young palms that subsequently developed BSR (Panchal & Bridge; 2005; Utomo *et al*., 2005).

More recently ribosomal nucleic acid (RNA) markers that occur during early disease stages have been investigated as potential diagnostic markers (Faizah *et al*., 2020). There are indications that the detection of these markers in palm tissue through reverse transcriptase (RT) PCR could also provide a potential early diagnostic test (*e.g.* Permatasari *et al*., 2023). However, RNA can be somewhat transient in samples.

Management of BSR

Management of BSR is currently based on a combination of cultural, biological, and breeding approaches; chemical control has also been attempted. These aspects have been discussed in depth in Flood *et al.* (2022) and Pilotti and Bridge (2023). What follows are short summaries of various aspects of BSR management in SE Asia and the Pacific.

Cultural control. When BSR emerged as a serious problem of oil palm in SE Asia, cultural control was all that was available. The disease incidence was low and cultural approaches were confined to treating individual palms. Initially, the removal of the decayed part of the bole and trunk sometimes accompanied by the application of chemicals was tried, as was mounding of palms using soil around the palm base and isolation of symptomatic palms, by digging trenches to prevent the possible mycelial spread of the pathogen to neighbouring healthy palms or root contact between diseased and healthy palms; all were generally ineffective. Measures were only applied to visibly diseased palms; untreated symptomless palms remained a potential source of infection. Also, this strategy assumed that infection occurred by mycelial spread or root-to-root between neighbouring palms. As disease incidence increased in first-generation plantings, the recommendation to isolate individual palms was changed to the removal of these palms. However, after 10 years of growth, it is not feasible to continue to resupply and any management is left to replant. Economically, the labour costs needed became prohibitive for many oil palm plantations as well as for smallholders and many infected palms remained *in situ* (Chung, 2011; Flood *et al.*, 2022).

As the industry in SE Asia faced replanting of the first generation of oil palm, it was recommended that preparation of the site at replanting time (clean clearing) offered the best practical opportunity to remove infected material (Ariffin *et al*., 2000; Singh, 1991). Such practices have been subsequently widely adopted throughout the region, to different degrees, dependent on BSR incidence in previous plantings, labour availability, and costs involved. These practices have continued as more generations of oil palm have been planted. Removing stumps and large pieces of debris will reduce viable residual inoculum in the form of mycelium from the field before planting the next crop. Whilst "clean-clearing" practices generally result in lower disease incidence in replanted oil palms (in comparison with other replanting techniques), the incidence of the disease may still be unacceptably high (Pilotti & Bridge, 2023). In cases where debris from the first generation remained buried (or partially buried) and seedlings were planted near this material, disease incidence was observed earlier in the replanted field (e.g., within 2 years of planting) (Flood, personal communication, 2023). Windrowing was practised, where all palm material (trunks, boles and roots) was placed unshredded in rows on the soil surface. Later, shredding of oil palm material was advocated to allow natural microorganisms to colonise the material to out-compete the pathogen, and this method is widely used in Malaysia. In Sumatra, Virdiana *et al.* (2012) reported 13 years of field observation and suggested seedlings be planted at least 2 m away from the edge of windrows to delay infection in the next generation. Fallowing for one year also significantly reduced *Ganoderma* infection in the subsequent planting and shredding reduced infection in the next generation (Virdiana *et al*., 2012).

Fallowing has major economic implications for estates (Virdiana *et al*., 2019) but fallowing can be a useful option for smallholders and is already recommended to them in PNG where half of the block is felled and fallowed with the other half still under production. For replanting in larger plantations, field preparation includes machine-felling, windrowing of trunks and removal of all bole tissue remaining in the planting holes when palms are felled. Holes created by felling are immediately back-filled and the boles of infected palms exposed during felling are chipped with an excavator bucket. Shredding is not practiced due to the high cost of the machinery required and its questionable benefit compared to mechanical chipping. Burial of whole palm trunks is strongly discouraged unless they can be buried at depths >3 m from the surface, a practice that would incur considerable cost.

Monitoring through regular surveys and removal of BSR palms in PNG and SI begins at six years of age and is a continuous annual activity until replanting at 23-25 years. The rationale behind the recommended sanitation program in these countries was based on both field evidence and later, on scientific evidence obtained from studies on the population biology of *G. boninense* (Pilotti *et al*., 2003; Sanderson, 2000; Sanderson & Pilotti, 1997; 1998). Emphasis was placed on the presence of *G. boninense* fruiting bodies and infected boles as potential sources of inoculum with little or no regard for subsurface roots and higher portions of the trunk, unless they were infected with upper stem rots. Palm removal was critical as the recommended procedure also prevented the regrowth of *Ganoderma* brackets, considered a high risk for new infections by basidiospores (Sanderson *et al*., 2000). At low levels of disease (<5%), manual removal of palms identified in biannual disease surveys was manageable and cost-effective (Griffiths *et al*., 2001; Marshall *et al*., 2004).

In addition, it is thought that continuous and regular removal of diseased palms potentially reduces the inoculum levels remaining from the previous crop at replanting. Sanitation practices continue to be implemented in PNG and SI although much of the plantations have undergone replanting in the last 10 years. The true effects of the recommended disease management strategies in PNG and SI should be seen in 10-15 years although recommendations in both PNG and SI, now include early replanting in blocks severely affected by BSR disease (Pilotti, 2019). The uptake of this recommendation remains to be seen.

Management of USR is similar to that of BSR. USR is usually only detected when palms fracture after severe wind events or when heavily laden with fruit bunches (Sanderson, 2000). Diseased palms are removed following the same procedures for palms with BSR where diseased portions are manually chipped with harvesting chisels and scattered on the plantation floor (Pilotti, personal communication, 2023).

Chemical control. Early studies indicated some success with the use of various chemicals and application methods including pressure injection of fungicides (Ariffin *et al*., 2000) but Chung (2011) stated that while chemicals such as hexaconazole had been investigated, the approach was rarely practiced as it did not provide effective control. Additional difficulties include the effective placement of fungicides where they are needed and significantly, food safety problems as concentrations of fungicide residues in palm oil may prevent adoption within the industry.

More recently, novel chemical methodologies have been undertaken. Maluin *et al.* (2020) reported more than 74% disease reduction in seedlings compared to untreated seedlings where hexaconazole and/or dazomet were encapsulated into chitosan nanoparticles for the formulation of chitosan-based agro-nanofungicides. Further work on the effect of surfactants on the fungitoxicity of a dazomet-micelle nano delivery system against *G. boninense* has also been reported (Mustafa *et al*., 2023). Whilst interesting research, field-orientated work is needed to demonstrate the effectiveness of these new methodologies at the field level. Currently, for smallholders and plantations alike, chemical control remains an expensive option and is not recommended at all in PNG/SI due to RSPO guidelines.

Biological control. Biological control refers to the use of one organism to limit the growth and multiplication of another and the degree of disease suppression achieved with biological agents can be comparable to that achieved with chemicals (O'Brien, 2017). Modes of action include antibiosis, hyper-parasitism, induced resistance, competition, and toxin inactivation (Kohl *et al*., 2019). Usually, Biological Control Agents (BCA) are isolated by screening organisms from the rhizosphere or endophyte populations in host plants, and control is based on the inhibition of growth of the target pathogen *in vitro*. The use of BCA to control BSR on oil palm has been extensively studied in both Malaysia and Indonesia (Sariah & Zakaria, 2000; Susanto *et al*., 2005). Various microorganisms are antagonistic to *Ganoderma* including fungi such as *Penicillium, Aspergillus, Hendersonia,* and *Trichoderma* along with various mycorrhizal fungi, and bacteria largely from the genera *Bacillus, Burkholderia* and *Pseudomonas* as well as Actinomycetes. Combinations of various amendments such as calcium nitrate have been recommended (Sariah & Zakaria, 2000) and mixed antagonists have also been studied (Sundram *et al*., 2015). Different application methods such as soil augmentation, in combination with mulches, as seed coatings, and in conjunction with composting have been proposed (Jawak *et al*., 2018).

An alternative biocontrol approach is removing nutrients available to the pathogen through degrading the diseased material. *Ganoderma* is known to be a poor competitor in soil (Rees *et al*., 2007), and increasing the rates of decay of oil palm material in the field would be an attractive solution for estates- reducing both *Ganoderma* inoculum and *Oryctes* spp. nesting sites, reducing nutrient loss and so reducing fertiliser application. Rees (2006) identified several basidiomycetes that successfully degraded oil palm wood blocks *in vitr*o and then trialed candidates in the field in Sumatra but with only limited success. Early unpublished studies in PNG using field-isolated basidiomycetes arrived at the same conclusion as decay was slow in inoculated oil palm trunks. Studies using *Thielaviopsis paradoxa* were promising and rapid degradation of the upper portions of the mostly hemicelluose-containing oil palm trunks was achieved (50% degradation within 3 weeks). However, due to the apparent implication of *T. paradoxa* in other palm diseases, this avenue of control was not pursued (PNG OPRA, 2000). More recently, Naidu *et al*. (2017) reported *in vitro* degradation of oil palm wood blocks but degradation was mainly of wood polysaccharides with only minimal degradation of lignin. Nevertheless, these authors considered the work to be a first step toward developing a solution to degrading palm waste.

Host resistance. Breeding programs for resistant planting material have been set up across SE Asia (Wening *et al*., 2020). Many companies and institutes involved have extensive germplasm collections from diverse origins to allow screening and selection. Sources of resistance within existing *Elaeis guineensis* commercial germplasm include material from the centre of origin of *E. guineensis* (West Africa) and *E. oleifera* (South American oil palm).

Breeding for resistance/tolerance in oil palm is not easy. Durand-Gasselin *et al.* (2005) reported field observations on a series of planting materials of *E. guineensis* and *E. oleifera* of known origins which showed differences in disease susceptibility. *E. guineensis* material was highly variable, and material of Deli origin (used as female parental palms for seed production) was highly susceptible to *Ganoderma* compared to material of African origin. Differences in reactions between parents and between crosses from within a given origin were observed. Durand-Gasselin *et al*. (2005) also reported variable resistance in clones derived from palms of the same origin and concluded that an early selection test in the nursery was needed. Due to space and time constraints, it is essential to screen out very susceptible material and allow only the most promising material to be screened in the field. Screening at the nursery stage with artificial inoculation with rubber wood blocks is a common approach (Breton, *et al.*, 2006). Purba *et al.* (2012) suggested that the inheritance of *Ganoderma* tolerance is generally additive and therefore, the performance of crosses can be predicted if parental genotypes have been tested for susceptibility/ tolerance or the Deli *dura* material is introgressed with *Ganoderma* tolerant material.

Tisné *et al*. (2017) identified four *Ganoderma* resistance loci in oil palm from data obtained from 25 years of field observations. Two loci control the development of the first *Ganoderma* symptoms while the other two are related to the death of the palms. Favourable haplotypes were detected among a major gene pool from the ongoing breeding programs. This provided important information for the selection and improvement of resistant varieties. However, the long-term nature of breeding for resistance to *Ganoderma* is very costly and requires reliable access to the field so, many researchers have started to examine alternative approaches to aid breeding programs.

Daval *et al*. (2021) reported the use of computer modelling using extensive data sets derived from an ongoing breeding program. A pedigree-based Quantitative Trait Loci (QTL) mapping approach was applied to more than 10 years of data collected during pre-nursery tests. The study revealed the quantitative nature of *Ganoderma* resistance and identified underlying loci segregating which were relevant to the breeding program. To assess the reliability of QTL effects between the pre-nursery and the field, data was also collected on the disease status of specific individuals planted in the field and modelled with the pre-nursery-based QTL genotypes. Results indicated that in the field, individuals were less likely to be infected with *Ganoderma* when they carried more favourable alleles at the pre-nursery QTL. Daval *et al*. (2021) suggested that their studies provided proof of concept for an approach that was both efficient and cost-effective and could be applied to other breeding programs.

Another alternative to traditional breeding is mutation breeding (Nur *et al*., 2018) which is faster than traditional approaches but is not a genetic modification (GM) technology. However, for oil palm, the length of time needed to develop mutant varieties as well as the need for field access to allow populations to mature does mean that constraints are similar to those of traditional breeding. New tissue culture approaches may allow more efficient methods for the selection and development of mutant lines. Genomic screening in early generations could provide a means to short-cut generations and accelerate mutation breeding in perennial crops. Haploid production methods have been developed for oil palm (Dunwell *et al*., 2010), and these now offer a new target for mutation induction, as homozygous mutants can be produced instantly by the conversion of haploids to double haploids. This is significant, as the vast majority of induced mutations are recessive, and therefore their phenotype cannot be seen until the mutant alleles are made homozygous. Ithnin and Kushari (2020) provided a comprehensive review of breeding and genetic improvement in oil palm while Martin *et al*. (2022) summarised biotechnological methods that can transform traditional breeding including genomics, marker-assisted breeding, genetic engineering and genome editing techniques; these authors also address the concerns connected to these techniques and their applications in practical breeding.

Breeding for resistance to *Ganoderma* is a major goal in the management of BSR strategy. Such improved material would benefit both the commercial sector and smallholders, and could reduce financial investment in sanitation practices. However, Purba *et al*. (2012) considered it essential that the SE Asian oil palm industry continues to investigate alternative management options as breeding is such a long-term enterprise. An integrated approach to BST management is expected for the foreseeable future.

THE UNCERTAINTIES

Having summarised the current knowledge of *Ganoderma* disease in oil palms, we now examine the uncertainties within the study of this pathogen and its effects. Many of these uncertainties relate to the lack of fundamental research that remains to be done including the gaps in knowledge that exist around the infection process, disease spread, identification of the pathogen, mechanisms of resistance, *etc*. While management practices are being conducted, without greater knowledge of these fundamental gaps, such management practices will continue to fail.

The Fungus

Although *G. boninense* has been studied extensively (see Current Knowledge) there are some areas and aspects where some uncertainties remain.

Systematics. Modern mycological systematics is determined by phylogenetic analyses. The rDNA ITS sequence has been adopted as a universal "barcode" for fungi. Still, there are some limitations in the use of this sequence and so it is desirable also to consider DNA sequences obtained from additional genes (Nilsson *et al*., 2008; Schoch *et al*., 2012; 2014; Simon & Weiss, 2008). Wide-scale taxonomic studies of the genus or specific sections of it, generally use only a few representatives of each species and so although other gene sequences have been used for *G. boninense*, they are available for only a few isolates (Hapuarachchi *et al*., 2015; Tchoumi *et al*., 2019). Another concern with *Ganoderma* species is that reference DNA sequences are frequently not linked to type material. In the case of *G. boninense*, two sequences from later collections from Bonin Island are generally used although the type collection is available in at least two public herbaria (Kew & Paris, see Pilotti & Bridge, 2023).

Many of the molecular studies of *Ganoderma* have included only a small number of ITS sequences from *G. boninense* but Fryssouli *et al*. (2020) included over 80 ITS sequences obtained from different isolates, and Flood *et al*. (2022) considered some 143 sequences. Both of these studies demonstrated around 2% variation within the sequences, and Fryssouli *et al*. (2020) suggested that some of these could be considered as new "cryptic" species. High sequence variability and multiple ITS forms are not uncommon in basidiomycete fungi (Chen *et al*., 2016; Lindner & Banik, 2011; Simon & Weiss, 2008), but have not been widely considered in *G. boninense*.

Wang and Yao (2005) recovered multiple ITS sequences from single strains of four *Ganoderma* species. Most molecular studies with *G. boninense* have used either fruiting bodies or mycelial cultures derived from these. Both types of material are dikaryotic and have resulted from a previous mating between monokaryotic basidiospores. To our knowledge, there have not been any studies that have considered ITS sequence variation or inheritance during this process in *G. boninense.*

Ecology/disease initiation and spread. *Ganoderma* species are prevalent on oil palm throughout Southern Asia and Oceania. They also occur and cause disease on other perennials to varying extents from limited (*e.g., Casuarina* spp.) to extensive (*e.g., Acacia* spp.) (Pilotti & Bridge, 2023). The differences in prevalence may be largely attributed to the level at which different crops are cultivated with more intensively cultivated crops having the highest incidences of stem and butt rots caused by *Ganoderma.* The species identified on oil palm appear to be very closely related and have probably originated from other naturally occurring palms (Mercière *et al*., 2017). Although *G. boninense* has been implicated in Thanjuvar wilt of coconut, this identification has not been confirmed and further investigations on this disease in coconuts are warranted, particularly since this species occurs prolifically as a saprophyte on dead coconut in SE Asia but does not appear to cause disease in living palms outside the Indian subcontinent.

The widespread occurrence of BSR on new oil palm plantings suggests that potential inoculum is relatively common in the surrounding environment. In a "new" planting, the first occurrence of *G. boninense* will probably originate from either debris from previous vegetation, or the surrounding vegetation. There are however relatively few reports of *G. boninense* on native palms and we are not aware of any surveys for the pathogen that have been conducted before planting. This information could be important as planting in an area where the pathogen was already present, would likely lead to earlier and greater infection levels compared to areas where the pathogen was either absent or only present at low levels.

The relatively high level of variability in ITS sequences seen in *G. boninense* is unusual when compared to the other *Ganoderma* palm pathogens. Midot *et al.* (2019) identified eight ITS haplotypes for *G. boninense* from oil palm in Sarawak, Malaysia and Flood *et al.* (2022) found some 59 distinct ITS sequence types among all sequences available from multiple countries and hosts. Fryssouli *et al*. (2020) suggested that the ITS sequences from some oil palm isolates from Indonesia were sufficiently different to possibly constitute a separate "cryptic" species. In contrast, Elliott *et al*. (2018) reported very little ITS sequence variation in *G. zonatum* isolates from multiple palm hosts in the US, and the same is true for the Thanjuvar wilt pathogen of coconut in Southern India, which could be a single homothallic population (Rolph *et al.,* 2000).

It is unclear if the ITS sequence variation seen in *G. boninense* is the result of the huge numbers of individuals present, segregation or crossover from multiple mating events, or if there are multiple species involved. Some recent research has suggested that both non-random mating and bottlenecks occur in *G. boninense* in oil palm plantations (Wong *et al*., 2022). Although there have been some studies linking mating events and some microsatellite markers (Pilotti *et al.,* 2021) it would be useful to ascertain what effect mating has on ITS sequences and if isolates from the different ITS sequence groups are all interfertile.

For disease initiation in the field, it is well established that in the absence of larger mycelium-bearing inoculum sources such as palm trunks or root debris, the fungus primarily establishes in the field as basidiospores (Miller *et al*., 1999; Pilotti *et al*., 2003; 2018). Although a large number of isolates derived from spore inoculum have been observed in seedlings growing near *Ganoderma*-infected oil palms (Pilotti *et al.,* 2018), it is not clear how, when, or if, the disease manifests in young seedlings and the conditions necessary for disease initiation *via* either spores or mycelia in young palms are uncertain. Nursery testing currently requires a large mycelial inoculum source to initiate infections in young seedlings (Flood *et al*., 2022).

The survival of both basidiospores and fungal mycelia under natural conditions has not been investigated fully. It is known that *G. boninense* can survive for several years in oil palm and coconut trunks but the fate of liberated basidiospores and movement and translocation away from infected trunks is still unclear. Unlike fungi such as *Armillaria, Ganoderma* does not form rhizomorphs although it does form mycelial cords in sterilised soil (Rees, 2006). The fungus is considered to be a poor soil competitor (Rees *et al*., 2007) and requires plant material to survive and persist within the soil thus forming inoculum for subsequent planting.

Evidence for both mycelial spread and spore spread between mature oil palms has been obtained from several studies using vegetative compatibility and mating studies on field isolates of *G. boninense.* It is clear that disease is spread between neighbouring mature palms but what is not clear is when and how palms become infected after replanting as well as during the entire planting cycle. In a mature plantation, disease foci do not necessarily expand continuously, and in fields with high disease incidence, 'hotspots' tend to develop in confined areas with continuous initiation of new foci and subsequent expansion of these to varying extents (Pilotti, personal communication, 2023). Both anecdotal and scientific evidence for disease spread between mature oil palms is available but clear spatial and space-time studies of these relationships are rare.

Infection. To date, artificial inoculation has only been achieved using inoculated rubber wood blocks attached to roots or by coating roots in mycelial suspensions. While these are useful tools for inducing infections for detailed laboratory-based studies (resistance mechanisms *etc*.) and for nursery screening in association with breeding trials, they are unlikely to represent the natural infection process in the field. One significant feature of BSR in oil palm is the high level of infection, which is much greater than is seen in other crops such as rubber and tea where infections are usually restricted to local clusters of plants. *Ganoderma* species are widely regarded as "wound pathogens" and cut frond bases could provide a "natural" infection route. However, to date**,** artificial inoculation of stems, peduncles, frond bases, and cut fronds with a range of inocula has failed to initiate infection, although *G. boninense* has been detected at these locations in both symptomatic and asymptomatic palms in the field (Panchal & Bridge, 2005; Pilotti & Bridge, 2002; Rees *et al*., 2007).

Oil palm is largely planted commercially from seeds produced through sexual mating, therefore plantings consist of groups of genetically different individuals. Similarly, *G. boninense* is an outbreeding dikaryotic fungus and so also represents a genetically heterogeneous population. Alleles associated with resistance have been identified in some plants (see earlier) and it is also possible that individual strains of *G. boninense* may show differing levels of vigour or pathogenicity. A molecular survey has shown that not all young palms shown to carry *G. boninense* subsequently went on to develop BSR (Panchal & Bridge, 2005; Pilotti & Bridge, 2002) and this will have implications for both developing pathogenicity tests and early detection methods.

Early Detection

Remote sensing. Despite investment in various forms of remote sensing methods, detection of slightly infected palms (as compared to healthy palms) has remained a challenge and this is crucial for early detection. Terrestrial Laser Scanning (TLS) has shown some promise in the detection of slightly infected palms and may be developed further using a combination of techniques but challenges remain. These technologies are costly in terms of equipment and the technical analysis needed and skilled technical advice would be needed to advise producers. These costs may put these remote sensing technologies beyond the budget of smallholders and even plantations.

Laboratory tests. At present, most laboratory-based detection methods have been developed with artificially inoculated plants or environmental samples from single time points. Costs for simple molecular and immunological tests have decreased in recent years, particularly with the wider adoption of laboratory automation. Although immunological and molecular methods for detecting *G. boninense* have been available for over 20 years, we are only aware of one published study that has used any of these (specific ITS primers) to follow infection in the field as an oil palm block becomes established (Panchal & Bridge, 2005; Pilotti & Bridge, 2002). As a result, it is not possible to compare the comparative predictive performance of these methods. As mentioned above early detection of the pathogen needs to be shown to give rise to subsequent disease.

Management. Many studies of biocontrol of BSR, concentrate on *in vitro* work or nursery trials on seedlings. While these are useful for understanding the host/pathogen interaction and help with the selection of effective candidates, more field studies are needed (Sundram *et al.,* 2015, Virdiana *et al*., 2019). These trials need to include those where BCAs in the oil palm ecosystem are quantified over time so that persistence and activity in the field are more fully understood. Ease of mass production of the putative BCA is needed and *Trichoderma* is easily mass produced on many estates throughout SE Asia and is consequentially routinely used as a soil amendment both at replanting and after diseased palms are removed. Many of the larger estates manufacture their formulations and basic techniques are available for the multiplication and application of *Trichoderma* (Virdiana *et al.*, 2019). Commercial formulations containing a range of microorganisms are also available (Idris *et al*., 2014) for use by both estates and smallholders but independent comparisons of the different commercially available formulations are lacking.

Mature oil palms planted in soil are known to support an extensive mycorrhizal community (Kaonongbua, 2018; Phosri *et al*., 2010). It is generally assumed that this community is acquired naturally from the planting environment, largely after the nursery stage (Phosri *et al*., 2010). The natural acquisition of a mycorrhizal community will depend on the levels of suitable inoculum available in the soil and the species diversity will vary depending on soil type, location, and fertiliser usage (Kaonongbua, 2018; Phosri *et al*., 2010). Early inoculation with various mycorrhizae has been proposed on many occasions to help increase the growth and vigour in young plants on planting out (Galindo-Castañeda & Romero, 2013; Phosri *et al*., 2010; Widiastuti & Tahardi, 1993). There have also been some reports that suggest the presence of mycorrhizae may reduce the incidence of basal stem rot (Rini *et al*., 2022). Commercial formulations such as MycoGold are available but at the current time there is probably insufficient detailed information on natural mycorrhizal species diversity at the various sites (and soils) where oil palm is grown and the full range of interactions that may occur. For example, how do added mycorrhizal products interact with natural indigenous populations?

One of the main uncertainties for the management of BSR is access to the field where cultural approaches, putative BCA, and resistant/tolerant material can be tested (and independently) verified as part of an integrated approach. Many approaches to control are undertaken *in vitro* or in glasshouses as there is little access to the field for students and researchers alike and this inevitably leads to a lack of what is practical to the industry. Whilst the development of resistant/tolerant material would be very beneficial to estates and smallholders alike, the development of such material is long term even with the development of novel approaches such as QTLs, potential use of biomarkers, and mutant breeding. It is essential that the use and efficacy of BCA (whilst interesting in the laboratory or glasshouse as the first steps in a selection process) can be verified in the field. Understanding the ecology of any BCA in different environments and under different management practices is essential. Similarly, the long-term effects of cultural controls such as delayed replanting (fallowing), windrowing, shredding and removal of fruit bodies need to be investigated as does the potential for the use of improving the degradation of palm waste at replanting to deny the pathogen a base for colonisation, survival and subsequent infection of the next generation.

RECOMMENDATIONS

Given the uncertainties listed above, we have listed some specific recommendations but in general, it would be sensible for the public and private funded sectors of the oil palm industry to work more closely together. This could include sites for long-term field access for the testing of new management options but also would allow increased dialogue of the practicalities that producers (estates and small-holders) are facing. This is particularly true of the costs of some high-tech approaches and the need for highly skilled technical support for the producers. In addition, some fundamental questions remain to be answered and some of the paradigms that have been developed over decades need to be challenged and tested further. We have recommended some specific areas for further research and development.

Systematics

Recommendation 1. When compared to many other species of *Ganoderma*, *G. boninense* is relatively well-defined. The ITS sequences that have been proposed as reference sequences are from later collections made from the Type location and are "typical" for the species (Pilotti & Bridge, 2023). Further gene sequences have been obtained from these collections (Zhou *et al*., 2015) and are also considered to be "typical" of the species (Ćilerdžić *et al*., 2018; Nguyen *et al*., 2023). However, the species name is tied to the historic Type collection, and material from this is available in at least two herbaria. It would appear sensible to obtain further reference sequences from the Type material to fully validate the species.

Recommendation 2. The ITS sequence range discussed above is relatively wide for a single species and further investigation with additional gene sequences is required to fully resolve any subgroups or possible cryptic species [*e.g.*, the "d3" group identified by Fryssouli *et al*. (2020)]. In addition, relationships between ITS sequence variation and mating events need to be considered. For example, if monokaryons with different ITS sequences mate, do a single or both ITS sequence types occur in the subsequent dikaryon? This needs to be undertaken in conjunction with the species/cryptic species delineation to determine if any "molecular" species are interfertile or if there is a level of sequence variation above which mating will not occur.

Ecology/ Disease Initiation and Spread

Recommendation 3. There is a need to determine further, where and at what levels, the fungus occurs in the natural environment as done by Pilotti *et al.* (2018). Ideally, this would require surveys of both the planting area and the surrounding environment before planting or replanting. Historically, *Ganoderma* colonisation of debris and nearby non-oil palm plants has often been reported in single studies at a single time point. We need to ensure a timeline can be established to determine the direction of transfer between oil palm and the surrounding environment as well as understand *Ganoderma* colonisation in the previous vegetation before planting *e.g.* in native palms.

Recommendation 4. The origins of fungal inoculum in the field remain an important question to answer. Progress has been made and although it may not be fully resolved, new insights may be gained by understanding the relationships between saprophytic and pathogenic isolates. The collection of *Ganoderma* from natural environments and research into their genetic and host relationships could provide added insight into what is already known (and assumed) regarding the opportunistic nature of *Ganoderma* infections. Such studies, while useful from a taxonomic and evolutionary perspective would also begin to establish the foundation for disease initiation in monoculture crops growing in the vicinity of natural fungal populations.

Recommendation 5. Once established, the spread of BSR requires long-term monitoring through accurate data collection and is one reason why long-term access to the field is required. This is necessary to determine spatial patterns in the spread of BSR and assess the survival and infection potential of infected palms in the field (over several generations). Such studies would allow management decisions to be made on the value of roguing in fields with varying disease incidence levels. Where successive generations of oil palm are planted, and even at first plantings, it may be useful to attempt to quantify the levels of inoculum when fields are being prepared for planting (see Recommendation 3). This would provide some idea of the potential disease incidences that could be expected within a given plantation.

Recommendation 6. Assessing levels of inoculum should include quantifying spore loads in the air as well as inoculum in the soil. The value of such an exercise, on its own, would be questionable without continuous monitoring following planting and other management interventions during the planting cycle. The application of such techniques might be more applicable where fallowing is an option and inoculum levels above a determined threshold at planting could trigger decisions on the need for a fallow period.

Recommendation 7. From experience, the long-term control of *Ganoderma* largely depends on reducing inoculum levels. This can only be achieved by continuous vigilance, monitoring, and application of practices to reduce soil and airborne inocula throughout the growing cycle. Given the large numbers of basidiospores produced into the environment by mature fruiting bodies, it would seem likely that the removal of fruiting bodies from the plantings and windrows will help to reduce the inoculum potential. Aside from the roguing of diseased palms, novel ways that can be applied in the future to reduce inoculum levels could be through the use of tolerant planting material and replanting at an earlier palm age, for example between 16-20 years. The use of more tolerant material may be some years away but early replanting is a good option provided plantations can sustain yields at suitable levels to remain profitable. Other management techniques such as the application of biological control agents, require further investigation into their mechanism and effectiveness in reducing *Ganoderma* inoculum resident in the soil.

Infection

Recommendation 8. Given that the only successful inoculation method involves artificially inoculated blocks, closely attached to roots, a greater understanding of how the fungus becomes established in the oil palm in the field would be useful. This should include inoculation of recently cut fronds and inoculation of the root ring. Thompson (1931) suggested that infection was possible via cut and broken frond bases, which would be in keeping with the view that *Ganoderma* is generally a wound pathogen. Although sealing pruned frond bases to prevent subsequent infection (as is practiced with various other tree crops) has been suggested as a possible control method (Hushiarian *et al*., 2013; Paterson *et al*., 2009; Pilotti & Bridge, 2023) we are not aware of any extended field trials for this. Given that cut and open frond bases are a continuing feature of both new and established plantings, they could provide a route to the bole tissue in young palms and the upper trunk tissue in older palms. We suggest that this is a significant gap in the knowledge for infection control and some initial trials with wound dressings/coverings should be established for both newly planted and established palms to determine their effect on BSR and USR.

Early Detection Methods - Remote Sensing

Recommendation 9. Some methods such as Terrestrial Laser Scanning (TLS) which have shown promise in differentiation of slightly affected palms (Husin *et al.*, 2020) could be developed further. Specifically, about answering practical questions eg early detection to identify individual palms that could receive specific management measures early in the planting cycle or for assessing disease severity to guide the timing of replanting the estate or specific areas of the estate where more intensive management activities could be undertaken.

Early Detection Methods - Laboratory Methods

Recommendation 10. A single study in PNG combined molecular detection of the pathogen in the tissue of young palms with continued monitoring of the palms for disease symptoms over some years (Panchal & Bridge, 2005; Pilotti & Bridge, 2002). We are not aware of any similar long-term published studies linked to either molecular or immunological detection methods. When first developed, the molecular and immunological methods could potentially be expensive and time-consuming but the wider availability of reagents, equipment and increased laboratory automation will have substantially reduced those costs. All such methods are highly dependent on tissue handling and extraction again these have been extensively examined in the subsequent years (Karthikeyan *et al*., 2006; Rajendran *et al*., 2009). The PNG study showed that while early detection could identify the fungus in palms in the field, not all of these palms went on to develop significant BSR. We recommend that there should be a wider assessment of the accuracy and outcomes available from existing methodology before further methods for "early detection" are developed.

Management

Recommendation 11. There are many commercial formulations available that claim efficacy to BSR but they need to be tested and verified independently through field trials. This is also true of many BCA formulations *e.g. Trichoderma*. Do they actually reduce *Ganoderma* infection in the field? This needs to be demonstrated over several years. Linked to this there is a need for an improved understanding of the interactions of the BCA with the host plant and other members of the oil palm microbiome to fully achieve the potential of biocontrol for BSR. Trials with mixtures of organisms, application methods, testing the longevity in different soils and the effect of environmental conditions are also needed. In short, a more ecological approach is needed. In addition, improved molecular approaches could allow the identification of effective BCA based on a genetic profile and could allow a more directed approach (Benítez & McSpadden-Gardener, 2009).

Recommendation 12. The role of mycorrhizae needs to be considered in both the infection and establishment stages of basal stem rot. Current pathogenicity tests with rubber wood blocks and exposed roots will probably not include any naturally occurring mycorrhizae and so we have no information on any competitive effects that may reduce pathogenicity. As with disease progression, mycorrhizal effects are likely to occur over relatively long periods. Phosri *et al.* (2010) suggested that the natural mycorrhizae on newly planted palms become established after around 6 months, and beneficial effects are unlikely to be seen before this. Similarly, any "added" mycorrhiza will need to be able to compete with the natural microbiota and the interactions of these two populations are not understood.

Recommendation 13. Rees (2006) suggested that targeting windrowed material at replanting with fungi that had enhanced degradative abilities (as he had attempted) was unrealistic and an alternative approach was to target individual palms that succumbed to *Ganoderma* in the first year after replanting. To our knowledge, this has not been attempted but could be and linked to the early detection of palms in the early year after replanting. Longer-term field trials targeting the degradation of oil palm material at replanting combined with shredding or other replanting practices are also needed.

Recommendation 14. Breeding for disease resistance will always be an important part of the management of diseases and breeding oil palm for resistance to *Ganoderma* is no exception. Daval *et al*. (2021) combined the use of data sets derived from the breeding programme with QTLs described from pre-nursery tests. More of this approach of combining computing methods with long-term breeding trials would be very beneficial. The uses of biomarkers for evaluating the resistance of oil palm progenies in the field should also be investigated further.

CONCLUSION

Considerable research has been undertaken into *Ganoderma* diseases of oil palm and although this has resulted in many publications and reviews, the disease continues to be a major concern for the industry. It is clear that there are gaps in our knowledge and that some of these relate to fundamental issues. These need to be investigated before we can fully understand and accurately interpret the various processes occurring and treatments suggested.

Some gaps, such as the variability of some DNA sequences and the incorporation of current taxonomic concepts and validated reference materials can be met from existing methodologies and a wider incorporation of existing literature. Many of the others relate to the use and performance of laboratory-derived tests and processes in a field environment. It is perhaps surprising that we have not found any instances of the quantitative measurement of sealing cut fronds, or the effects of biological control agents, in the field over a planting cycle. Similarly, while early detection methodologies such as molecular and immunological tools, and remote sensing methods, can provide an initial insight into disease occurrence, this relates only to the single point in time when the work was undertaken. For the predictive performance of these methods to be demonstrated they need to be considered in the long term. Probably the most basic question for such methods is - do all early detections result in subsequent disease? and do interventions provide a positive benefit over the life of the crop?

There are considerable practical problems with assessing laboratory-derived research in the field. These include costs and logistics in obtaining and transporting samples, the availability of training and instrumentation, and the available personnel. A further complication is that much scientific research is funded through short-term grants with sponsors expecting a "result" within the grant period. There may therefore be a need to consider how a long-term monitoring and survey programme could be established for the industry.

In 1994, the failures of morphological taxonomy for *Ganoderma* were summarised by Ryvarden who proposed that "no new species be described in *Ganoderma* in the decade to 2005 and those authors breaking this law be sentenced to do taxonomic work on at least 10 old names" (Ryvarden, 1995). The application of molecular methods has now provided a lot more clarity in the taxonomy of the genus but this in turn did require considerable re-examination of older names. It may be appropriate to consider a similar moratorium on the introduction of further methods for *Ganoderma* disease detection and control until the existing knowledge has been clarified and tested in context.

ACKNOWLEDGEMENT

JF is a CABI Emeritus Fellow, and acknowledges CABI's ongoing support. CABI as an international, intergovernmental, not-for-profit organisation, gratefully acknowledges the generous support received from our many donors, sponsors and partners. In particular, we thank our Member Countries for their vital financial and strategic contributions**.** CP acknowledges the support of SPC through scientific and technical advice to member countries.

REFERENCES

Abdullah, A. H., Adom, A. H., Md. Shakaff, A. Y., Ahmad, M. N., Saad, M. A., Tan, E. S., Fikri, N. A., Markom, M. A., & Zakaria, A. (2011). Electronic nose system for *Ganoderma* detection. *Sensor Letters*, *9*(3), 353–358. https://doi.org/10.1166/sl.2011.1479

Abdullah, A. H., Adom, A. H., Shakaff, A. Y., Ahmad, M. N., Zakaria, A., Saad, F., & Kamarudin, L. (2012a). Hand-held electronic nose sensor selection system for basal stem rot (BSR) disease detection. In *Proceedings of the Third International Conference on Intelligent Systems Modelling and Simulation* (pp. 737–742). IEEE Computer Society. https://doi.org/10.1109/ISMS.2012.139

Abdullah, A. H., Shakaff, A. M., Adom, A. H., Ahmad, M. N., Zakaria, A., Ghani, S. A., & Seman, I. A. (2012b). Exploring MIP sensor of basal stem rot (BSR) disease in palm oil plantation. In *Proceedings of the 14th International Meeting on Chemical Sensors* (pp. 1348–1351). AMA-Science.

Abdullah, F. (2000). Spatial and sequential mapping of the incidence of basal stem rot of oil palms (*Elaeis guineensis*) on a former coconut (*Cocos nucifera*) plantation. In J. Flood, P. D. Bridge, & M. Holderness (Eds.), Ganoderma *diseases of perennial crops* (pp. 183–194). CABI. https://doi.org/10.1079/9780851993881.0183

Amanda, W. I., & Prakoso, H. T. (2018). Modified *Ganoderma* selective medium to meet Indonesia's government regulation. *IOP Conference Series: Earth and Environmental Science, 183*, 012020. IOP Publishing. https://doi.org/10.1088/1755-1315/183/1/012020

Ananthanarayanan, T. V., & Reddy, M. K. (1984). Serological test for the diagnosis of *Ganoderma lucidum*. *Current Science, 53*(2), 97–98.

Ariffin, D. (2000). Major diseases of oil palm. In Y. Basiron, B. S. Jalani, & K. W. Chan (Eds.), *Advances in Oil Palm Research* (pp. 596–623). MPOB.

Ariffin, D., & Idris, A. S. (1992). The *Ganoderma* selective medium (GSM). *PORIM Information Series No. 8*. Palm Oil Research Institute Malaysia.

Ariffin, D., Idris, A. S., & Singh, G. (2000). Status of *Ganoderma* in oil palm. In J. Flood, P. D. Bridge, & M. Holderness (Eds.), Ganoderma *diseases of perennial crops* (pp. 49–68). CABI. https://doi.org/10.1079/9780851993881.0049

Atkins, S. D., & Clark, I. M. (2004). Fungal molecular diagnostics: A mini review. *Journal of Applied Genetics, 45*(1), 3–15. https://www.ncbi.nlm.nih.gov/pubmed/14960763

Benítez, M. S., & McSpadden Gardener, B. B. (2009). Linking sequence to function in soil bacteria: Sequence-directed isolation of novel bacteria contributing to soilborne plant disease suppression. *Applied and Environmental Microbiology, 75*(3), 915–924. https://doi.org/10.1128/AEM.01296-08

Bharudin, I., Ab Wahab, A. F. F., Abd Samad, M. A., Xin, Y. N., Zairun, M. A., Abu Bakar, F. D., & Abdul Murad, A. M. (2022). Review update on the life cycle, plant-microbe interaction, genomics, detection and control strategies of the oil palm pathogen *Ganoderma boninense*. *Biology, 11*(2), 251. https://doi.org/10.3390/biology11020251

Borman, A. M., & Johnson, E. M. (2020). Sequence-based identification and classification of fungi. In P. D. Bridge, D. Smith, & E. Stackebrandt (Eds.), *Trends in the systematics of bacteria and fungi* (pp. 198–216). CABI. https://doi.org/10.1079/9781789244984.0198

Breton, F., Hasan, Y., Hariadi, S., Lubis, Z., & de Franqueville, H. (2006). Characterization of parameters for the development of an early screening test for basal stem rot tolerance in oil palm progenies. *Journal of Oil Palm Research (Special Issue-April 2006)*, 24–36. http://palmoilis.mpob.gov.my/publications/jopr2006sp-ms24.pdf

Bridge, P. D., O'Grady, E. B., Pilotti, C. A., & Sanderson, F. R. (2000). Development of molecular diagnostics for the detection of *Ganoderma* isolates pathogenic to oil palm. In J. Flood, P. D. Bridge, & M. Holderness (Eds.), Ganoderma *diseases of perennial crops* (pp. 225–234). CABI.

Chen, J., Moinard, M., Xu, J., Wang, S., Foulongne-Oriol, M., Zhao, R., Hyde, K. D., & Callac, P. (2016). Genetic analyses of the internal transcribed spacer sequences suggest introgression and duplication in the medicinal mushroom *Agaricus subrufescens*. *PLoS ONE, 11*(5), e0156250. https://doi.org/10.1371/journal.pone.0156250

Chong, K. P., Dayou, J., & Alexander, A. (2017a). Current detection methods of *G. boninense* infection in oil palm. In K. P. Chong, J. Dayou, & A. Alexander (Eds.), *Detection and control of* Ganoderma boninense *in oil palm crop* (pp. 13–20). Springer. https://doi.org/10.1007/978-3-319-54969-9_3

Chong, K. P., Dayou, J., & Alexander, A. (2017b). Control methods of *G. boninense* in the oil palm industry. In K. P. Chong, J. Dayou, & A. Alexander (Eds.), *Detection and control of* Ganoderma boninense *in oil palm crop* (pp. 21–30). Springer. https://doi.org/10.1007/978-3-319-54969-9_4

Chung, G. F. (2011). Management of *Ganoderma* diseases in oil palm plantations. *The Planter, 87*(1022), 325–339.

Ćilerdžić, J. L., Vukojević, J. B., & Stajić, M. M. (2011). Dynamics of ligninolytic enzyme production in *Ganoderma applanatum* depending on cultivation type. *Proceedings for Natural Sciences, Matica Srpska, Novi Sad, 120*, 323–329. https://doi.org/10.2298/ZMSPN1120327C

Darmono, T. W. (2000). *Ganoderma* in oil palm in Indonesia: Current status and prospective use of antibodies for the detection of infection. In J. Flood, P. D. Bridge, & M. Holderness (Eds.), Ganoderma diseases *of perennial crops* (pp. 249–266). CABI. https://doi.org/10.1079/9780851993881.0249

Daval, A., Pomiès, V., le Squin, S., Denis, M., Riou, V., Breton, F., Nopariansyah, Bink, M., Cochard, B., Jacob, F., Billotte, N., & Tisné, S. (2021). *In silico* QTL mapping in an oil palm breeding program reveals a quantitative and complex genetic resistance to *Ganoderma boninense*. *Molecular Breeding, 41*(53). https://doi.org/10.1007/s11032-021-01246-9

Dunwell, J. M., Wilkinson, M. J., Nelson, S., Wening, S., Sitorus, A. C., Mienanti, D., Alfik, Y., Croxford, A. E., Ford, C. S., Forster, B. P., & Caligari, P. D. S. (2010). Production of haploids and doubled haploids in oil palm. *BMC Plant Biology, 10*, 218. https://doi.org/10.1186/1471-2229-10-218

Durand-Gasselin, T., Asmady, H., Flori, A., Jacquemard, J. C., Hayun, Z., Breton, F., & De Franqueville, H. (2005). Possible sources of genetic resistance in oil palm (*Elaeis guineensis* Jacq.) to basal stem rot caused by *Ganoderma boninense*-Prospects for future breeding. *Mycopathologia, 159*, 93–100. https://doi.org/10.1007/s11046-004-4429-1

Elliott, M. L., & Broschat, T. K. (2000). *Ganoderma butt rot of palms*. University of Florida IFAS Extension Bulletin, 5, Fact Sheet PP54, 7 pp.

Elliott, M. L., Des Jardin, E. A., Ortiz, J. V., & Macias, T. (2018). Genetic variability of *Ganoderma zonatum* infecting palms in Florida. *Mycologia, 110*(2), 339–346. https://doi.org/10.1080/00275514.2018.1442083

Faizah, R., Putranto, R. A., Wening, S., Sukma, D., Raharti, V. R., Budiani, A., & Sudarsono, S. (2020). Differential expression of root specific genes of oil palm seedlings at early stage of *Ganoderma boninense* infection. *Proceedings of the IOP Conference Series: Earth and Environmental Science, 418*(1), 012044. IOP Publishing. https://doi.org/10.1088/1755-1315/418/1/012044

Farid, A. M., Wan Muhd Azrul, W., Syazwan, S. A., Lee, S., & Mohamed, R. (2018). First record of basal stem rot of foxtail palm (*Wodyetia bifurcata*) caused by *Ganoderma boninense* in Malaysia. *Plant Disease, 102*(7), 1461–1461. https://doi.org/10.1094/PDIS-12-17-2027-PDN

Flood, J., Bridge, P. D., & Pilotti, C. (2022). Basal stem rot of oil palm revisited. *Annals of Applied Biology, 181*(2), 160–181. https://doi.org/10.1111/aab.12772

Fryssouli, V., Zervakis, G. I., Polemis, E., & Typas, M. A. (2020). A global meta-analysis of ITS rDNA sequences from material belonging to the genus *Ganoderma* (Basidiomycota, Polyporales) including new data from selected taxa. *MycoKeys, 75*, 71–143. https://doi.org/10.3897/mycokeys.75.59872

Galindo-Castañeda, T., & Romero, M. (2013). Mycorrhization in oil palm (*Elaeis guineensis* and *E. oleifera* x *E. guineensis*) in the pre-nursery stage. *Agronomía Colombiana, 31*(1), 95–102. https://repositorio.unal.edu.co/handle/unal/41452

Griffiths, W., Castle, J., Sanderson, F. R., Pilotti, C. A., & Bridge, P. D. (2001). Control of *Ganoderma* stem rot in the Pacific Rim palm oil plantation limited estates in Papua New Guinea. In *Proceedings of the 2001 International Palm Oil Congress, Agriculture Conference* (AP40). PORIM, Kuala Lumpur, Malaysia.

Hapuarachchi, K. K., Wen, T. C., Deng, C. Y., Kang, J. C., & Hyde, K. D. (2015). Mycosphere essays 1: Taxonomic confusion in the *Ganoderma lucidum* species complex. *Mycosphere, 6*(5), 542–559. https://doi.org/10.5943/mycosphere/6/5/4

Ho, Y. W., & Nawawi, A. (1985). *Ganoderma boninense* Pat. from basal stem rot of oil palm (*Elaeis guineensis*) in Peninsular Malaysia. *Pertanika, 8*, 425–428.

Hushiarian, R., Yusof, N. A., & Dutse, S. W. (2013). Detection and control of *Ganoderma boninense*: Strategies and perspectives. *SpringerPlus, 2*, 555. https://doi.org/10.1186/2193-1801-2-555

Husin, N. A., Khairunniza-Bejo, S., Abdullah, A. F., Kassim, M. S. M., Ahmad, D., & Azmi, A. N. N. (2020). Application of ground-based LiDAR for analysing oil palm canopy properties on the occurrence of basal stem rot (BSR) disease. *Scientific Reports, 10*, 6464. https://doi.org/10.1038/s41598-020-62275-6

Idris, A. S., Mohd Shukri, I., Norman, K., Kushairi, A., Choo, Y. M., Hanafi, M. M., Talib, R., & Sofian, M. Y. (2014). *GanoCare™ – Reducing risk of* Ganoderma *infection in oil palm*. MPOB Information Series No. 545.

Ithnin, M., & Kushairi, A. (Eds.). (2020). *The oil palm genome*. Springer. https://doi.org/10.1007/978-3-030-22549-0

Izzuddin, M. A., Hamzah, A., Nisfarzia, M. N., & Idris, A. S. (2020). Analysis of multispectral images from unmanned aerial vehicles (UAV) using object-based image analysis for detection of *Ganoderma* disease in oil palm. *Journal of Oil Palm Research, 32*(3), 497–508.

Jawak, G., Palupi, E. R., Widajati, E., & Toruan-Mathius, N. (2018). Oil palm seed coating with enriched *Trichoderma asperellum* (T13) to suppress infection of *Ganoderma boninense* Pat. *Jurnal Perbenihan Tanaman Hutan, 6*(2), 121–132. https://doi.org/10.20886/bptpth.2018.6.2.121-132

Kaonongbua, W. (2018). Preliminary study on biodiversity of arbuscular mycorrhizal fungi (AMF) in oil palm (*Elaeis guineensis* Jacq.) plantations in Thailand. In *Proceedings of the IOP Conference Series: Earth and Environmental* (Vol. 144, No. 1, p. 012010). IOP Publishing. https://doi.org/10.1088/1755-1315/144/1/012010

Karthikeyan, M., Radhika, K., Bhaskaran, R., Mathiyazhagan, S., Samiyappan, R., & Velazhahan, R. (2006). Rapid detection of *Ganoderma* disease of coconut and assessment of inhibition effect of various control measures by immunoassay and PCR. *Plant Protection Science, 42*, 49–57. https://doi.org/10.17221/2771-PPS

Khairunniza-Bejo, S., & Vong, C. N. (2014). Detection of basal stem rot (BSR) infected oil palm tree using laser scanning data. In *Proceedings of the 2nd International Conference on Agricultural and Food Engineering; New Trends Forward* (pp. 156–164). Elsevier B.V. https://doi.org/10.1016/j.aaspro.2014.11.023

Khosrokhani, M., Khairunniza-Bejo, S., & Pradhan, B. (2016). Geospatial technologies for detection and monitoring of *Ganoderma* basal stem rot infection in oil palm plantations: A review on sensors and techniques. *Geocarto International, 33*(3), 260–276. https://doi.org/10.1080/10106049.2016.1243410

Kohl, J., Kolnaar, R., & Ravensberg, W. J. (2019). Mode of action of microbial biological control agents against plant diseases: Relevance beyond efficacy. *Frontiers in Plant Science, 10*, 845. https://doi.org/10.3389/fpls.2019.00845

Lefsky, M. A., Cohen, W. B., Parker, G. G., & Harding, D. J. (2002). Lidar remote sensing for ecosystem studies. *Bioscience, 52*, 19–30. https://doi.org/10.1641/0006-3568(2002)052[0019:LRSFES]2.0.CO;2

Lindner, D. L., & Banik, M. T. (2011). Intragenomic variation in the ITS rDNA region obscures phylogenetic relationships and inflates estimates of operational taxonomic units in genus *Laetiporus*. *Mycologia, 103*, 731–740. https://doi.org/10.3852/10-331

Loyd, A. L., Barnes, C. W., Held, B. W., Schink, M. J., Smith, M. E., Smith, J. A., & Blanchette, R. A. (2018). Elucidating "lucidum": Distinguishing the diverse laccate *Ganoderma* species of the United States. *PLoS ONE, 13*(7), e0199738. https://doi.org/10.1371/journal.pone.0199738

Loyd, A. L., Smith, M. E., Blanchette, R. A., & Smith, J. A. (2019). Cultural characterization and chlamydospore function of the *Ganodermataceae* present in the eastern United States. *Mycologia, 111*(1), 1–12. https://doi.org/10.1080/00275514.2018.1543509

Maluin, F. N., Hussein, M. Z., Yusof, N. A., Fakurazi, S., Idris, A. S., Hilmi, N. H. Z., & Daim, L. D. J. (2020). Chitosan-based agronanofungicides as a sustainable alternative in the basal stem rot disease management. *Journal of Agricultural and Food Chemistry, 68*(15), 4305–4314. https://doi.org/10.1038/s41598-020-79335-6

Marshall, R., Hunt, R., & Pilotti, C. A. (2004). Low cost control for basal stem rot. *The Planter, 80*, 173–176.

Martin, J. J., Yarra, R., Wei, L., & Cao, H. (2022). Oil palm breeding in the modern era: Challenges and opportunities. *Plants, 11*(11), 1395. https://doi.org/10.3390/plants11111395

May, T. W. (2020). Identification of fungi: Background, challenges and prospects. In P. Bridge, D. Smith, & E. Stackebrandt (Eds.), *Trends in the Systematics of Bacteria and Fungi* (pp. 21–29). CABI. https://doi.org/10.1079/9781789244984.0021

Mercière, M., Boulord, R., Carasco-Lacombe, C., Klopp, C., Lee, Y.-P., Tan, J.-S., Sharifah, S. R., Alwee, S., Zaremski, A., De Franqueville, H., Breton, F., & Camus-Kulaivelu, L. (2017). About *Ganoderma boninense* in oil palm plantations of Sumatra and Peninsular Malaysia: Ancient population expansion, extensive gene flow, and large-scale dispersion ability. *Fungal Biology, 121*, 529–540. https://doi.org/10.1016/j.funbio.2017.01.001

Midot, F., Lau, S. Y. L., Wong, W. C., Tung, H. J., Yap, M. L., Lo, M. L., Jee, M. S., Dom, S. P., & 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. https://doi.org/10.3390/microorganisms7100464

Miller, R. N. G., Holderness, M., Bridge, P. D., & Chung, G. F. (1999). Genetic diversity of *Ganoderma* in oil palm plantings. *Plant Pathology, 48*, 595–603. https://doi.org/10.1046/j.1365-3059.1999.00390.x

Miller, R. N. G., Holderness, M., & Bridge, P. D. (2000). Molecular and morphological characterization of *Ganoderma* in oil palm plantings. In J. Flood, P. D. Bridge, & M. Holderness (Eds.), Ganoderma *Diseases of Perennial Crops* (pp. 159–182). CABI. https://doi.org/10.1079/9780851993881.0159

Moncalvo, J. (2000). Systematics of *Ganoderma*. In J. Flood, P. D. Bridge, & M. Holderness (Eds.), Ganoderma *Diseases of Perennial Crops* (pp. 23–48). CABI. https://doi.org/10.1079/9780851993881.0023

Moncalvo, J. M., & Buchanan, P. K. (2008). Molecular evidence for long distance dispersal across the southern hemisphere in the *Ganoderma applanatum–australe* species complex (Basidiomycota). *Mycological Research, 112*, 425–436. https://doi.org/10.1016/j.mycres.2007.12.001

Mustafa, I. F., Hussein, M. Z., Idris, A. S., Hailini, N. Z. H., Ramli, N., & Fakurazi, S. (2022). The effect of surfactant type on the physico-chemical properties of hexaconazole/dazomet-micelle nanodelivery system and its biofungicidal activity against *Ganoderma boninense*. *Colloids and Surfaces A: Physicochemical and Engineering Aspects, 640*, 128402. https://doi.org/10.1016/j.colsurfa.2022.128402

Naidu, Y., Siddiqui, Y., Rafii, M. Y., Saud, H. M., & Idris, A. S. (2017). Investigating the effect of white-rot Hymenomycetes biodegradation on basal stem rot infected oil palm wood blocks: Biochemical & anatomical characterization. *Industrial Crops and Products, 108*, 872–882. https://doi.org/10.1016/j.indcrop.2017.08.064

Natarajan, S., Bhaskaran, R., & Shanmugam, N. (1986). Preliminary studies to develop techniques for early detection of Thanjavur wilt in coconut. *Indian Coconut Journal, 17*(3), 3–6.

Nguyen, T. T. T., Nguyen, H. D., Bui, A. T., Pham, K. H. T., Van, K. T. P., Tran, L. T., & Tran, M. H. (2023). Phylogenetic analysis and morphology of *Ganoderma multipileum*, a *Ganoderma* species associated with dieback of the metropolitan woody plant *Delonix regia* (Boj. ex Hook.) Raf. in Vietnam. *Science Progress, 106*(3), 368504231195503. https://doi.org/10.1177/00368504231195503

Nilsson, R. H., Kristiansson, E., Ryberg, M., Hallenberg, N., & Larsson, K. H. (2008). Intraspecific ITS variability in the kingdom fungi as expressed in the international sequence databases and its implications for molecular species identification. *Evolutionary Bioinformatics Online, 4*, 193–201. https://doi.org/10.4137/EBO.S653

Nur, F., Forster, B. P., Osei, S. A., Amiteye, S., Ciomas, J., Hoeman, S., & Jankuloski, L. (2018). Mutation breeding in oil palm: A manual. In *Techniques in Plantation Science*. CABI. https://doi.org/10.1079/9781786396211.0000

O'Brien, P. A. (2017). Biological control of plant diseases. *Australasian Plant Pathology, 46*(4), 293–304. https://doi.org/10.1007/s13313-017-0481-4

Panchal, G., & Bridge, P. D. (2005). Following basal stem rot in young oil palm plantings. *Mycopathologia, 159*, 123–127. https://doi.org/10.1007/s11046-004-4434-4

Papp, V. (2019). Global diversity of the genus *Ganoderma*. In K. R. Sridhar & S. K. Deshmukh (Eds.), *Advances in Macrofungi: Diversity, Ecology and Biotechnology* (pp. 10–33). CRC Press.

Paterson, R. R., Moen, S., & Lima, N. (2009). The feasibility of producing oil palm with altered lignin content to control *Ganoderma* disease. *Journal of Phytopathology, 157*(11–12), 649–656. https://doi.org/10.1111/j.1439-0434.2009.01553.x

Patouillard, N. (1889). Le genre *Ganoderma*. *Bulletin de la Société Mycologique de France, 5*(2,3), 63–80.

Permatasari, G. W., Puspita, M., Kresnawaty, I., Mulyatni, A. S., Eris, D. D., Widiastuti, H., Triyana, K., & Priyono, P. (2023). Validation of early infection markers for *Ganoderma* in oil palm at three endemic *Ganoderma* locations. *Jurnal Penelitian Kelapa Sawit, 31*(1), 1–12. https://doi.org/10.22302/iopri.jur.jpks.v31i1.195

Phosri, C., Rodriguez, A., Sanders, I. R., & Jeffries, P. (2010). The role of mycorrhizas in more sustainable oil palm cultivation. *Agriculture, Ecosystems & Environment, 135*(3), 187–193. https://doi.org/10.1016/j.agee.2009.09.006

Pilotti, C. A. (2005). Stem rots of oil palm caused by *Ganoderma boninense*: Pathogen biology and epidemiology. *Mycopathologia, 159*, 129–137. https://doi.org/10.1007/s11046-004-4435-3

Pilotti, C. A. (2018). Epidemiology of basal stem rot in first and second generation oil palm plantings. *PNG OPRA Project PP07 Interim Report*, PNG OPRA, Kimbe: WNBP, Papua New Guinea.

Pilotti, C. A. (2019). Interim report. *PNG OPRA*, Kimbe: WNBP, Papua New Guinea.

Pilotti, C. A., & Bridge, P. D. (2002). Basal stem rot: Probing the facts. *The Planter, 78*(916), 365–370.

Pilotti, C. A., & Bridge, P. D. (2023). Ganoderma *Diseases of Tropical Crops*. CABI. https://doi.org/10.1079/9781800620780.0000

Pilotti, C. A., Gorea, E. A., & Bonneau, L. (2018). Basidiospores as sources of inoculum in the spread of *Ganoderma boninense* in oil palm plantations. *Plant Pathology, 67*, 1841–1849. https://doi.org/10.1111/ppa.12915

Pilotti, C. A., Killah, G., Rama, D., Gorea, E. A., & Mudge, A. M. (2021). A preliminary study to identify and distinguish southern tropical populations of *Ganoderma boninense* from oil palm via mating assays, sequence data, and microsatellite markers. *Mycologia, 113*(3), 574–585. https://doi.org/10.1080/00275514.2020.1858687

Pilotti, C. A., Sanderson, F. R., & Aitken, E. A. B. (2003). Genetic structure of a population of *Ganoderma boninense* on oil palm. *Plant Pathology, 52*, 455–463. https://doi.org/10.1046/j.1365-3059.2003.00870.x

PNG OPRA. (1997). *Annual Research Report 1997*. West New Britain Province, Papua New Guinea: PNG OPRA Dami Research Station, Papua New Guinea.

PNG OPRA. (1998). *Annual Research Report 1998*. West New Britain Province, Papua New Guinea: PNG OPRA Dami Research Station, Papua New Guinea.

PNG OPRA. (2000). *Annual Research Report 2000*. West New Britain Province, Papua New Guinea: PNG OPRA Dami Research Station, Papua New Guinea.

PNG OPRA. (2002). *Annual Research Report 2002*. PNG Oil Palm Research Association, Dami Research Station, Papua New Guinea.

PNG OPRA. (2007). *Annual Research Report 2007*. PNG Oil Palm Research Association, Dami Research Station, Papua New Guinea.

Purba, A. R., Setiawati, U., Susanto, A., Rahmaningsih, M., Yenni, Y., Tahmadi, H. Y., & Nelson, S. P. (2012). Indonesia's experience of developing *Ganoderma*-tolerant/resistant oil palm planting materials. In *Proceedings of the International Seminar on Breeding for Oil Palm Disease Resistance and Field Visits* (pp. 21–24). Bogota, Colombia: International Society for Oil Palm Breeders, Kuala Lumpur, Malaysia.

Rajendran, L., Kandan, A., Karthikeyan, G., Raguchander, T., & Samiyappan, R. (2009). Early detection of *Ganoderma* causing basal stem rot disease in coconut plantations. *Journal of Oil Palm Research, 21*(1), 627–635.

Raju, J., Naik, S. T., Priti, S., Suryanarayana, V., Benagi, V. I., Nirmalanath, J., & Giri, M. S. (2015). Rapid detection of *Ganoderma* disease of coconut by using ITS-PCR and assessment of inhibition effect of various control measures by fungicides and bioagents. *Journal of Pure and Applied Microbiology, 9*(4), 3325–3331.

Reddy, M., & Ananthanarayanan, T. V. (1984). Detection of *Ganoderma lucidum* in betelnut by the fluorescent antibody technique. *Transactions of the British Mycological Society, 82*(3), 559–561. https://doi.org/10.1016/S0007-1536(84)80026-1

Rees, R. W. (2006). Ganoderma *stem rot of oil palm* (Elaeis guineensis)*: Mode of infection, epidemiology and biological control* (Ph.D. Thesis). Bath University, UK.

Rees, R. W., Flood, J., Hasan, Y., & Cooper, R. M. (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 Pathology, 56*, 862–870. https://doi.org/10.1111/j.1365-3059.2007.01621.x

Rees, R. W., Flood, J., Hasan, Y., & Cooper, R. M. (2009). Basal stem rot infection of oil palm: Mode of root and lower stem invasion by *Ganoderma*. *Plant Pathology, 58*, 982–989. https://doi.org/10.1111/j.1365-3059.2009.02100.x

Rees, R. W., Flood, J., Hasan, Y., Wills, M. A., & Cooper, R. M. (2012). *Ganoderma boninense* basidiospores in oil palm plantations: Evaluation of their possible role in stem rots of *Elaeis guineensis*. *Plant Pathology, 61*, 567–578. https://doi.org/10.1111/j.1365-3059.2011.02533.x

Rini, M. V., Hasan, S. N., Hidayat, K. F., & Aeny, T. N. (2022). Applications of arbuscular mycorrhiza fungi to improve growth of oil palm seedlings and disease resistance against *Ganoderma* sp. *Journal of Applied Agricultural Science and Technology, 6*(1), 31–40. https://doi.org/10.55043/jaast.v6i1.40

Rolph, H., Wijisekara, R., Lardner, R., Abdullah, F., Kirk, P. M., Holderness, M., & Flood, J. (2000). Molecular variation in *Ganoderma* isolates from oil palm, coconut, and betel nut. In J. Flood, P. D. Bridge, & M. Holderness (Eds.), Ganoderma *Diseases of Perennial Crops* (pp. 205–221). CABI. https://doi.org/10.1079/9780851993881.0205

Roslan, A., & Idris, A. S. (2012). Economic impact of *Ganoderma* incidence on Malaysian oil palm plantation – A case study in Johor. *Oil Palm Industry Economic Journal, 12*(1), 24–30.

Ryvarden, L. (1995). Can we trust morphology in *Ganoderma*? In P. K. Buchanan, R. S. Hseu, & J.

M. Moncalvo (Eds.), Ganoderma: *Systematics, Phytopathology and Pharmacology* (pp. 19–24). National Taiwan University, Taiwan.

Sanderson, F. R. (2005). An insight into spore dispersal of *Ganoderma boninense* on oil palm. *Mycopathologia, 159*, 139–141. https://doi.org/10.1007/s11046-004-4436-2

Sanderson, F. R., & Pilotti, C. A. (1997). *Ganoderma* basal stem rot: An enigma, or just time to rethink an old problem? *The Planter, 73*(858), 489–493.

Sanderson, F. R., & Pilotti, C. A. (1998). The implementation of a control strategy for basal stem rot of oil palm in Papua New Guinea and the Solomon Islands. In *Proceedings of the International Palm Oil Congress*. MPOB. Kuala Lumpur, Malaysia.

Sanderson, F. R., Pilotti, C. A., & Bridge, P. D. (2000). Basidiospores: Their influence on our thinking regarding a control strategy for basal stem rot of oil palm. In J. Flood, P. D. Bridge, & M. Holderness (Eds.), Ganoderma *Diseases of Perennial Crops* (pp. 113–120). CABI. Wallingford, UK. https://doi.org/10.1079/9780851993881.0113

Santoso, H., Gunawan, T., Jatmiko, R. H., Darmosarkoro, W., & Minasny, B. (2011). Mapping and identifying basal stem rot disease in oil palms in North Sumatra with QuickBird imagery. *Precise Agriculture, 12*, 233–248. https://doi.org/10.1007/s11119-010-9172-7

Santoso, H., Tani, H., & Wang, X. (2017). Random forest classification model of basal stem rot disease caused by *Ganoderma boninense* in oil palm plantations. *International Journal of Remote Sensing, 38*(16), 4683–4699. https://doi.org/10.1080/01431161.2017.1331474

Sariah, M., & Zakariah, H. (2000). The use of soil amendments for the control of basal stem rot of oil palm seedlings. In J. Flood, P. D. Bridge, & M. Holderness (Eds.), Ganoderma *Diseases of Perennial Crops* (pp. 89–99). CABI. Wallingford, UK. https://doi.org/10.1079/9780851993881.0089

Schoch, C. L., Seifert, K. A., Huhndorf, S., Robert, V., Spouge, J. L., Levesque, C. A., Chen, W., & Fungal Barcoding Consortium. (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for fungi. *Proceedings of the National Academy of Sciences, 109*, 6241–6246. https://doi.org/10.1073/pnas.1117018109

Schoch, C. L., Robbertse, B., Robert, V., Vu, D., Cardinali, G., Irinyi, L., Meyer, W., Nilsson, R. H., Hughes, K., Miller, A. N., & Kirk, P. M. (2014). Finding needles in haystacks: Linking scientific names, reference specimens, and molecular data for fungi. *Database: The Journal of Biological Databases and Curation, 2014*, bau061. https://doi.org/10.1093/database/bau061

Shafri, H. Z., Hamdan, N., & Izzuddin Anuar, M. I. (2012). Detection of stressed oil palms from an airborne sensor using optimized spectral indices. *International Journal of Remote Sensing, 33*, 4293–4311. https://doi.org/10.1080/01431161.2011.619208

Siddiqui, Y., Surendran, A., Paterson, R. R. M., Ali, A., & Ahmad, K. (2021). Current strategies and perspectives in detection and control of basal stem rot of oil palm. *Saudi Journal of Biological Sciences, 28*(5), 2840–2849. https://doi.org/10.1016/j.sjbs.2021.02.016

Simon, U. K., & Weiss, M. (2008). Intragenomic variation of fungal ribosomal genes is higher than previously thought. *Molecular Biology and Evolution, 25*, 2251–2254. https://doi.org/10.1093/molbev/msn188

Singh, G., Darus, A., & Sukaimi, J. (1991). *Ganoderma* the scourge of oil palm in the coastal area. In *Proceedings of* Ganoderma *Workshop* (pp. 7–35). PORIM, Kuala Lumpur, Malaysia.

Steyaert, R. L. (1975). The concept and circumscription of *Ganoderma tornatum*. *Transactions of the British Mycological Society, 65*, 451–467. https://doi.org/10.1016/S0007-1536(75)80043-X

Sundram, S., Meon, S., Seman, I. A., & Othman, R. (2015). Application of arbuscular mycorrhizal fungi with *Pseudomonas aeruginosa* UPMP3 reduces the development of *Ganoderma* basal stem rot in oil palm seedlings. *Mycorrhiza, 25*, 387–397. https://doi.org/10.1007/s00572-014-0620-5

Supramani, S., Rejab, N. A., Ilham, Z., Wan-Mohtar, W. A. A. Q. I., & Ghosh, S. (2022). Basal stem rot of oil palm incited by *Ganoderma* species: A review. *European Journal of Plant Pathology, 164*(1), 1–20. https://doi.org/10.1007/s10658-022-02546-2

Susanto, A., Sudharto, P. S., & Purba, R. Y. (2005). Enhancing biological control of basal stem rot disease (*Ganoderma boninense*) in oil palm plantations. *Mycopathologia, 159*, 153–157. https://doi.org/10.1007/s11046-004-4438-0

Tchoumi, J. M. T., Coetzee, M. P. A., Rajchenberg, M., & Roux, J. (2019). Taxonomy and species diversity of *Ganoderma* species in the Garden Route National Park of South Africa inferred from morphology and multilocus phylogenies. *Mycologia, 111*(5), 730–747. https://doi.org/10.1080/00275514.2019.1635387

Thompson, A. (1931). Stem rot of the oil palm in Malaya. *Bulletin of the Department of Agriculture, Straits Settlements and F.M.S. Science Series 6*.

Tisné, S., Pomiès, V., Riou, V., Syahputra, I., Cochard, B., & Denis, M. (2017). Identification of *Ganoderma* disease resistance loci using natural field infection of an oil palm multi-parental population. *Genes Genomes Genetics*, *7*(6), 1683–1692. https://doi.org/10.1534/g3.117.041764

Utomo, C., & Niepold, F. (2000a). Development of diagnostic methods for detecting *Ganoderma*-infected oil palms. *Journal of Phytopathology, 148*, 507–514. https://doi.org/10.1046/j.1439-0434.2000.00478.x

Utomo, C., & Niepold, F. (2000b). The development of diagnostic tools for *Ganoderma* in oil palm. In J. Flood, P. D. Bridge, & M. Holderness (Eds.), *Ganoderma Diseases of Perennial Crops* (pp. 235–247). CABI. Wallingford, UK. https://doi.org/10.1079/9780851993881.0235

Utomo, C., Werner, S., Niepold, F., & Deising, H. B. (2005). Identification of *Ganoderma*, the causal agent of basal stem rot disease in oil palm using a molecular method. *Mycopathologia, 159*, 159–170. https://doi.org/10.1007/s11046-004-4439-z

Virdiana, I., Flood, J., Sitepu, B., Hasan, Y., Aditya, R., & Nelson, S. (2012). Integrated disease management to reduce future *Ganoderma* infection during oil palm replanting. *The Planter, 88*, 383–393.

Virdiana, I., Rahmaningsih, M., Forster, B. P., & Flood, J. (2019). *Techniques in plantation science* (manual). CABI. Wallingford, UK. ISBN: 978-1-78924-1457.

Wang, D. M., & Yao, Y. J. (2005). Intrastrain internal transcribed spacer heterogeneity in *Ganoderma* species. *Canadian Journal of Microbiology, 51*(2), 113–121. https://doi.org/10.1139/w04-118

Widiastuti, H., & Tahardi, J. S. (1993). Effect of vesicular-arbuscular mycorrhizal inoculation on the growth and nutrient uptake of micropropagated oil palm. *Menara Perkebunan, 61*(3), 56–60.

Wening, S., Rahmadi, H. Y., Arif, M., Supena, N., Siregar, H. A., Prasetyo, A. E., & Purba, A. R. (2020). Construction of *Ganoderma* resistant oil palm planting material: Progress in IOPRI. In *Proceedings of the Sixth IOPRI-MPOB International Seminar: Current Approaches of Research and Management of Pests and* Ganoderma *Disease in Oil Palm for High Productivity* (pp. 54–66). IOPRI, Medan, Indonesia.

Wong, W. C., Tung, H. J., Nurul Fadhilah, M., Midot, F., Lau, S. Y. L., Melling, L., Astari, S., Hadziabdic, Đ., Trigiano, R. N., Goh, Y. K., & Goh, K. J. (2022). Evidence for high gene flow, nonrandom mating, and genetic bottlenecks of *Ganoderma boninense* infecting oil palm (*Elaeis guineensis* Jacq.) plantations in Malaysia and Indonesia. *Mycologia, 114*(6), 947–963. https://doi.org/10.1080/00275514.2022.2118512

Zakaria, L. (2023). Basal stem rot of oil palm: The pathogen, disease incidence, and control methods. *Plant Disease, 107*(3), 603–615. https://doi.org/10.1094/PDIS-02-22-0358-FE

Zhou, L.-W., Cao, Y., Wu, S.-H., Vlasák, J., Li, D.-W., Li, M.-J., & Dai, Y. C. (2015). Global diversity of the *Ganoderma lucidum* complex (*Ganodermataceae*, Polyporales) inferred from morphology and multilocus phylogeny. *Phytochemistry, 114*, 7–15. https://doi.org/10.1016/j.phytochem.2014.09.023