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VERIFICATION OF TOLERANCE TO INFECTION BY *CERATOCYSTIS MANGINECANS* IN CLONES OF *ACACIA MANGIUM*

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Ceratocystis canker and wilt disease has had a devastating impact on plantations of *Acacia mangium* in Sabah, Malaysia effectively resulting in its discontinuation in the region. The immediate future of industrial tree plantations in Malaysia relies on alternative species, such as *Eucalyptus pellita*, which are suited to the environment and market opportunities. However, identifying *A. mangium* planting stock with high levels of tolerance to *Ceratocystis manginecans* provides substantial opportunities for its large scale planting and sustainability in the future. The aim of this study was to verify tolerance to *C. manginecans* in over 100 putatively tolerant *A. mangium* clones selected from a family screening trial consisting of 100 wild families. Selections from the family screening trial were based on either short-lesion length measured six weeks after inoculation or survival 12 months post inoculation. Six clonal trials were established under field conditions over two years with more than five ramets of most clones tested in at least two separate trials. The trees were inoculated with *C. manginecans* 12 months after trial establishment, and assessments of crown health and survival as well as the presence or absence of sunken bark, gummosis or stem borer infestation were carried out 12 months post inoculation. Narrow-sense heritability estimates were moderate for external variables and for crown health (0.14–0.24) and survival (0.14–0.22). Genetic correlation estimates between trials were generally high, indicating that assessments were repeatable across trials. Correlations between traits used to assess damage following inoculation indicated that different traits may be used to identify clones that tolerate infection. The accuracy of the screening showed that resistant clones can be identified and used to produce *A. mangium* tolerant to infection by *C. manginecans*.

Key words: *Acacia mangium*, *Ceratocystis manginecans*, disease resistance, inoculations, resistant clones

INTRODUCTION

Ceratocystis canker and wilt disease (CCWD) caused by *Ceratocystis manginecans* is a serious disease affecting *Acacia mangium* in South East Asia, particularly in advanced rotation plantations established in the wet tropics. The first symptoms of infection in *A. mangium* are bark lesions and blackened streaks in the cambium followed by cankers and wilting (Tarigan et al. 2011a, Wingfield et al. 2023) with infected trees typically escaping detection until the disease is well advanced. Infection requires wounds and occurs via entry points to the vascular tissue created by animal damage or singling and pruning, with boring insects such as nitidulid beetles thought to be a primary vector for transmission among trees (Appel et al. 1990, Tarigan et al. 2011b, Brawner et al. 2015, Nastution et al. 2019).

The disease was first identified in *A. mangium* plantations in Sumatra, Indonesia in 2003 (Wingfield et al. 2023) and became increasingly prevalent in subsequent years. Tarigan et al. (2011a) described the disease and conducted the first pathogenicity trials with *Ceratocystis* on *A. mangium*, linking the disease to the decline of *A. mangium* plantations in Indonesia. It was thought that a significant proportion of the 2,000,000 ha of tropical *Acacias* planted in SEA at that time was not commercially viable due to the combined impacts of root rot disease and CCWD (Mohammed et al. 2014, Harwood & Nambiar 2014, Lee 2018, Wingfield et al. 2023). Indonesia was a case in point where *A. mangium* plantations in Sumatra were deemed unviable, while more recently developed plantations in areas such as

Kalimantan were deteriorating rapidly (Harwood & Nambiar 2014).

Similar symptoms of disease were reported in Malaysia where *A. mangium* had been extensively planted as the forestry industry transitioned away from natural, mixed-tropical hardwood forests (Lee 2018). In 2011, large scale plantation health surveys began in one of the largest estates of *A. mangium* in Sabah managed by Sabah Softwoods Berhad in response to increasing reports of diseased trees. In 2012, isolates were collected from infected trees and sequenced at Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa, confirming the presence of *C. manginecans* in Malaysia for the first time (Barnes et al. 2023, Wingfield et al. 2023). The official plantation area of *A. mangium* in Sabah in 2018 was approximately 50,000 ha (Sabah Forestry Dept. 2019), although based on what had been witnessed elsewhere and on field observations, a significant proportion of the trees in the estate were already severely infected with *C. manginecans*.

Plantations of *A. mangium* in much of the wet tropics have largely been replaced with *Eucalyptus pellita* (Brawner et al. 2010, Nambiar et al. 2018), which has shown excellent growth potential and suitability for production of solid wood products (Japarudin et al. 2020, Japarudin et al. 2021) and pulpwood (Amorim et al. 2021). However, *A. mangium* remains a desired and potentially important industrial tree plantation species given its consistent superior performance in early evaluation trials, early canopy closure, tolerance of compacted soils and ability to grow on a diverse range of sites (Nambiar et al. 2018, Nurudin et al. 2013). Therefore, Sabah Softwoods Berhad (one of the first companies in Sabah to plant *A. mangium*) undertook to develop an inoculation programme to screen a large number of trees from many families to identify tolerant individuals. Although including tolerant individuals in breeding programmes is a goal of many organisations, Brawner et al. (2015) found that heritability estimates for traits used to evaluate disease tolerance that were reliant on natural infection were close to zero, and that low heritability of lesion length following controlled inoculation would make the development of tolerant populations difficult. Thus, improving the accuracy of the screening systems used to assess disease resistance would have a direct impact on the level of improvement.

Although it may be difficult to develop *Ceratocystis*-resistant pure *A. mangium* breeding populations, interspecific hybrids with *A. auriculiformis* for example, and backcrosses with more tolerant *A. mangium* parents, could provide *Acacia* germplasm for reforestation in the wet tropics. *Acacia auriculiformis* has shown a range of genetic tolerance and amenability to screening and repropagation for the deployment of tolerant clones following screening (Kein et al. 2017, Chi et al. 2019, Brawner et al. 2020). Clonal propagation of interspecific hybrids (*A. mangium* × *A. auriculiformis*) will capture complementary traits from additive and non-additive genetic effects. A reduction in the impact of physiological aging has made the *Acacia* hybrids a better option for deployment compared with tolerant *A. mangium* clones. The identification of disease-resistant *A. mangium* individuals, which could be used as parents in a clonal seed orchard or as parents for the production of *Acacia* hybrids, is required to implement these strategies. This study reports on the culmination of a large and long-term inoculation programme derived from clones selected in a pedigreed progeny trial, and the verification of tolerance in subsequent clonal screening trials.

MATERIALS AND METHODS

Inoculum

Cultures were isolated from symptomatic trees, displaying typical symptoms of canker and wilt disease. Sporulation of the fungus was induced using carrot baiting of wood samples (Moller & DeVay 1968) and single ascospore masses were transferred onto malt extract agar (MEA; 20 g malt extract, 20 g Biolab agar per 1L water), supplemented with 100 mg l^{-1} streptomycin sulphate. Each isolate was identified and verified based on DNA sequence data with known cultures of this fungus (Tarigan et al. 2010, Barnes et al. 2023, Wingfield et al. 2023). Pathogenicity of isolates was tested in preliminary trials and a single isolate was then used in a trial conducted between April and October 2014, the results of which were presented by Brawner et al. (2015). This isolate (T75) was used in all subsequent inoculations, after first being passed through an inoculated tree and re-isolated to verify pathogen aggressiveness. These re-isolated cultures are

maintained in the culture collection, CMW, of the Forestry and Agricultural Biotechnology Institute (FABI), South Africa.

Family screening

Two progeny trials were conducted in Sabah between 2013 and 2014, following initial screening trials in 2012. Each of the trials included 2000 trees from 100 families replicated in 20 single-tree plots in a randomised block design. The results from the inoculation of the trials are not reported here; the method of inoculation and selection of putative tolerant individuals from one of these trials is described by Wingfield et al. (2023) and further detail is provided here for completeness.

Trees in family screening trial (104C) were inoculated in replicates 1-7, 8-14 and 15-20 at six, 12 and 18 months of age respectively, each time using rejuvenated cultures of isolate T75. Most trees in the trial died after inoculation. The surviving trees were inspected six months after inoculation and the first round of selections of 89 trees was made based on the length of the lesion at the inoculation site. It was, however, found that trees could effectively be assessed based on mortality, and subsequent evaluations assessed survival 12 months post inoculation. In this way, 143 trees were selected for verification of tolerance. From both selections, 179 trees were successfully captured as grafts for inclusion in the clonal verification trials.

Screening of a clonal seed orchard

A total of 900 trees of nine ramets from 100 clones were established in a clonal seed orchard in January 2012 and inoculated in August 2015. The clones were selected from two diverse progeny-within-provenance trials established in 1996 and 1997 and propagated along with other selections from the breeding programme for the establishment of the clonal seed orchard. Eighteen months after inoculation, only 100 ramets from eight clones remained alive across the nine replicates. These eight clones were recaptured as grafts and included in the clonal verification trials. Some of the seed for the family screening trials described above were collected from this clonal seed orchard.

Clonal verification

One hundred and eighty-seven individuals were selected from family screening trial 104C and the Clonal Seed Orchard for verification of tolerance in replicated clonal trials. The selections from trial 104C represented 86 open-pollinated families. Six trials (Table 1) were established over the course of two years between November 2014 and December 2016 at Brumas forestry camp, Tawau, Sabah. Trial design and planting density changed over the course of the trials, reflecting evolving methodologies over time. Initially, stocking was very high because the trials were planned to run no longer than 12 months. As

Table 1 Description of clonal trials used to verify tolerance to *Ceratocystis* canker and wilt disease in *Acacia mangium* clones

Trial	Block	Planting date	Number of clones	Number of families	Clone souce	Design	Replicates	Stocking (stem ha^{-1})	Inoculation date	Inoculum
CS1	105B	Nov-14	15	15	104C	Single tree	20	4444	Jan-16	T75C
CS2	105B	Aug-15	31	29	104C	Single tree	20	1600	Nov-16	T75D
CS3	94G	Nov-15	49	37	104C	Single tree	15	1111	Jan-17	T75D
CS4	94G	Apr-16	30	27	104C	3-tree line	5	1111	May-17	T75F
CS5	94G	May-16	46	34	104C	3-tree line	5	1111	May-17	T75F
CS6	92H	Dec-16	55	37	104C	3-tree line	5	1111	Apr-18	T75G

selections moved away from assessment of lesion length in the relatively short-term to longer-term tree survival, spacing between the trees was increased to accommodate tree growth. Table 1 provides details of the trial design.

Tree inoculation and assessment of tolerance

Inoculations were performed on trees aged approximately 12 months. An 8 mm diameter wound was created on each tree 1 m above the ground using a sterilised hole punch. Mycelial plugs (8 mm diameter) were excised from margins of actively growing cultures and placed into the wounds with the mycelium facing inwards. The wound was covered and protected by replacing the bark and wrapping it with plastic wrap.

The degree of infection resulting from the inoculations was measured 12 months post inoculation by scoring binomially for sunken bark associated with the inoculation points, presence of borers and gummosis in the area of inoculation as well as tree survival. In addition, an assessment of the health of the crown of living trees was on a scale of '1' to '4', with '1' being very unhealthy and '4' for a completely healthy crown.

Statistical analysis

Assessment data were used to estimate the heritability of traits using a linear mixed model fit with Asreml (Gilmour et al. 2015) within the R environment (R Development Core Team 2013). Models for traits with a binomial distribution were fit with a generalised linear mixed model including a logit link function, and a general linear mixed model for normally distributed traits. Each trial was analysed separately using a model that included a fixed effect for replications and a random effect for clones with the residuals from each ramet providing an estimate of error variance. For all generalised linear mixed models, the error variance was fixed at one and the variance of the logit link function was included in the estimate of phenotypic variance.

Data from the assessment of all inoculation studies were analysed to produce across-site heritability and genetic correlation estimates. The complete linear model included fixed effects for trial and replication within trial with a random effect included for clones. A separate error variance was estimated for each trial for the normally distributed diameter and crown health assessments. Taylor series approximations were used to estimate standard errors of genetic parameters while Wald F-tests were used to determine the significance of including fixed effects in the mixed model. Heritability (h^2) or clonal repeatability estimates from the generalised linear model of binomial data were calculated where the error variance was fixed at one and the variance of the link function was π 2/3.

RESULTS

A total of 2411 trees were inoculated but 70 were excluded from the across-site analysis as negative controls or were stunted from the outset. The summary statistics for the combined verification trials are presented in Table 2 while mean and standard error for all tolerance indices within each trial is provided in Table 3.

Survival and crown health were significantly different among trials ($p < 0.001$) and inoculated trees ($p < 0.01$) when the data were combined to test control versus inoculated ones. There were no statistically significant differences between control and inoculated trees for borer, sunken bark and gummosis, although differences among

Table 2 Combined summary statistics for the clonal verification trials, CS1–CS6

Variable	*n*	mean	sd	min	max
Height (m)	478	9.61	1.857	1.5	13.6
DBH (cm)	701	9.871	2.909	2.1	19.7
Survival (0–1)	2341	0.668	0.471	0	1
Crown health (1–4)	2341	1.809	1.529	0	4
Borer (0–1)	2341	0.562	0.496	0	1
Gummosis (0–1)	2341	0.529	0.499	0	1
Sunken bark (0–1)	2341	0.754	0.431	0	1

Table 3 Mean and standard error of all tolerance indices across six clonal verification trials

	CS1	CS2	CS3	CS4	CS5	CS6
Survival (0–1)	0.66 (0.03)	0.66 (0.03)	0.58 (0.02)	0.66 (0.02)	0.64 (0.02)	0.83 (0.02)
Crown health (1–4)	2.57 (0.12)	1.58 (0.07)	1.57 (0.07)	1.58 (0.07)	1.49 (0.06)	2.49 (0.07)
Borer (0–1)	0.69 (0.03)	0.51 (0.03)	0.93 (0.01)	0.52 (0.02)	0.54 (0.02)	0.16 (0.02)
Gummosis (0–1)	0.69 (0.03)	0.5 (0.03)	0.28 (0.02)	0.58 (0.02)	0.56 (0.02)	0.65 (0.02)
Sunken bark (0–1)	0.07 (0.02)	0.51 (0.03)	0.94 (0.01)	0.94 (0.01)	0.93 (0.01)	0.7 (0.02)

Table 4 Mean survival and standard error of re-inoculated clones selected on short lesion length, survival, or combination of short lesion length and survival

Trial	Selection Criteria		
	Lesion only	Lesion + Survival	Survival only
CS1	0.66 (0.10)	0.65 (0.13)	-
CS2	0.66 (0.15)	0.73 (0.12)	-
CS3	0.54 (0.17)	0.70 (0.12)	-
CS4	-	0.59 (0.06)	0.63 (0.05)
CS5	-	-	0.66 (0.06)
CS6	-	-	0.64 (0.07)

Table 5 Heritability estimates and correlation for *Ceratocystis* tolerance indices across six clonal disease-tolerance verification trials

Trial	Survival	Crown health	Borer	Gummosis	Sunken bark
CS1	0.07 (0.047)	0.10 (0.055)	0.06 (0.045)	0.057 (0.042)	0.00 (0.000)
CS2	0.07 (0.045)	0.12 (0.054)	0.03 (0.030)	0.05 (0.037)	0.07 (0.044)
CS3	0.14 (0.044)	0.11 (0.04)	0.02 (0.023)	0.05 (0.031)	0.02 (0.021)
CS4	0.14 (0.048)	0.14 (0.046)	0.17 (0.053)	0.14 (0.047)	0.02 (0.024)
CS5	0.10 (0.0351)	0.23 (0.051)	0.23 (0.051)	0.21 (0.049)	0.05 (0.029)
CS6	0.22 (0.061)	0.24 (0.061)	0.21 (0.058)	0.05 (0.038)	0.06 (0.038)
rg	0.82 (0.228)	0.83 (0.186)	0.58 (0.331)	0.76 (0.283)	0.99 (0.000)

rg = genetics correlations of heritability estimates

trials were significant for these traits and for replications within trials for borer ($p < 0.001$) and gummosis ($p < 0.001$).

In the initial phases of this study, the family selection trial was based on trees having a short lesion length. These selections were tested in CS1, CS2 and CS3 with 12, 23, and 40 based on lesion length alone and 3, 7 and 9 clones respectively, selected using both lesion length and survival. Thereafter, CS4 – CS6 tested selections of survival and lesion length (CS4 only) or survival only (CS5 & CS6). There was no difference in mean survival of clones selected for either short lesion length or survival only or both traits (Table 4). A direct comparison of clones selected on lesion length alone or survival alone was not possible.

Heritability estimates

Heritability estimates for assessments of tolerance (Table 5) typically increase from the previous in each subsequent clonal trial, with a notable exception of sunken bark. This improvement is attributed to greater genetic variation in trials with more clones or more accurate phenotyping. The modest number of clones in CS1 (15) for instance, likely contributed to the low heritability estimates while increasing heritability of crown health over

time indicates improvements in phenotyping with practice, although this pattern differed for each trait; for example, heritability for survival in CS2 and CS5 was the same or close to CS1 despite having more clones. This would not be attributable to improvement in phenotyping, thereby indicating that survival was affected by other factors. However, genetic correlations of heritability estimates (rg) were high for crown health, survival and sunken bark, indicating high repeatability when the same clones are evaluated in different screening trials. Although this demonstrates that crown health and survival can be reliable indicators of tolerance in screening for CCWD, it is of little value for sunken bark due to their extremely low heritability. The low and consistent heritability of sunken bark indicates either significant environment effect or inability to adequately capture differences in this characteristic, or both.

Breeding value correlations

Estimating trial-trial correlations for all pairs led to an unstable model and hence, a common correlation model was fitted to calculate correlations among breeding values which approximates genetic correlations (Figure 1). It was found that an increased borer incidence correlated with lower survival and higher survival correlated with healthier crowns, as might be expected. Higher prevalence of gummosis was associated with fewer observations of borer attack, healthier crowns and better survival, which may be explained as a response to infection. All correlations were statistically significant with the exception of sunken bark with crown health and survival, although significance of correlations between sunken bark and borer or gummosis was low.

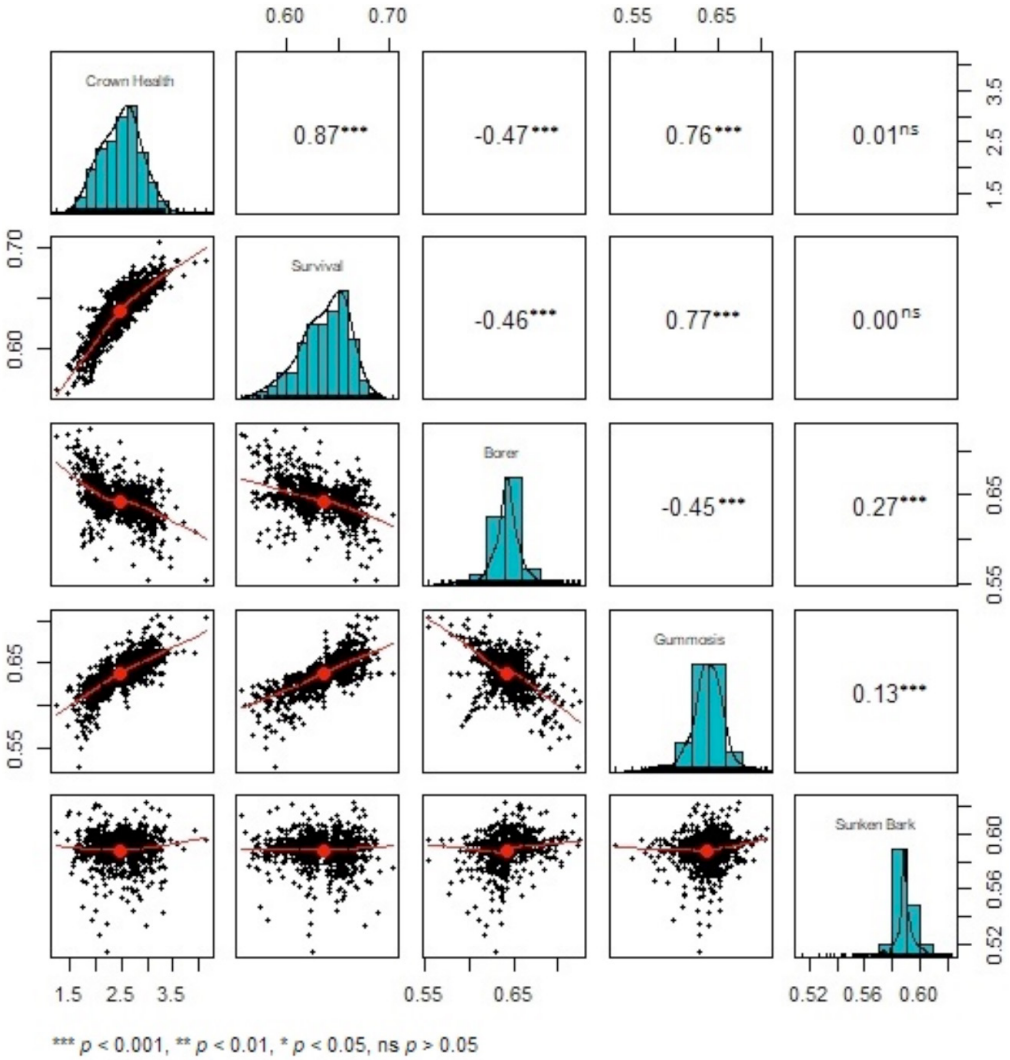

Figure 1 Breeding value correlations and significance of differences for *Ceratocystis* tolerance indices across six clonal disease-tolerance verification trials

DISCUSSION

A total of 187 clones captured from trees surviving large-scale inoculation trials, including 2000 trees representing 100 families, were tested for tolerance to infection by *C. manginecans*. The trees that survived re-inoculation confirmed the tolerance observed in the preliminary family screening trials and on-ground selections were made from these, amounting to 50 clones that displayed strong evidence of disease tolerance. Post-hoc analysis of the trial can now be used to cross-reference breeding values for survival and crown health with these selections.

Heritability estimates for all tolerance indices ranged from low to moderate but were generally higher than previously reported when CCWD first emerged as a problem in Sabah. Brawner et al. (2015) found heritability values of 0.43–0.25, 0.001–0.003, 0.001 for crown health, borer and gummosis respectively. The exception was sunken bark associated with the points of inoculation, earlier study showed had relatively high heritability in one trial ($h^2 = 0.12$), but this trait was of little value in these trials. Heritability estimates from that study showed tree survival and crown health were the most useful criteria to assess tolerance to infection by *C. manginecans*. The correlation between these traits was expectedly strongly positive as healthy crowns would be more conducive to survival. Most heritability estimates typically increased from the previous in each subsequent clonal trial, demonstrating improvements in phenotyping and providing confidence in the assessment protocols and repeatability of the results. The overall improvement in estimates found in this study are likely derived from an improved screening methodology.

Genetic correlations among assessment traits were generally high and statistically significant. There was a significant positive correlation between crown health, survival and gummosis in inoculated trees. The persistence of a healthy crown has been reported with other symptoms used to assess the severity of infection, including gummosis (Brawner et al. 2017). As such, gummosis is seen as a positive response by the tree to infection and may relate to the presence of antifungal compounds induced by *C. manginecans* (Trang et al. 2018).

The clonal verification study reported here was designed on the understanding that test trees require a well-developed vascular system to screen a vascular wilt pathogen, as shown by Wingfield et al. (2022). This requires established trees under field conditions, which involves considerable effort and time. Rapid screening using young plants or plant parts would shorten the time needed for such studies; for example, Brawner et al. (2020) used inoculations of small plants and phyllodes of *A. auriculiformis* to show moderate heritability estimates for disease tolerance. Importantly, and as pointed out by Brawner et al. (2020), those studies will require field-level verification. It should also be noted that *A. auriculiformis* has a substantially higher level of tolerance to infection by *C. manginencans* than does *A. mangium*, and this could also influence the results of artificial inoculations.

Recently, field trials were established to verify tolerance of *A. mangium* clones that survived nursery screening trials (Brawner et al. 2022). Although most trees developed wilt symptoms, and many died, four clones developed significantly smaller lesions and 100% of the ramets inoculated survived.

The possibility of developing *Ceratocystis*-tolerant breeding populations is limited by the likelihood of identifying its tolerance at the family level (Roux et al. 1999, Brawner et al. 2015, Brawner et al. 2020). Although tolerant *A. mangium* individuals are relatively rare as shown in the family screening trials (Brawner et al. 2015, Wingfield et al. 2023), the current study used heritability estimates and breeding value predictions to verify on-ground selections of tolerant *A. mangium* parents. Breeding strategies integrate adaptive traits and utilise favourable propagation traits of hybrids of these clones with *A. auriculiformis* to provide tolerance in progeny to *C. manginecans*. These clones can then be redeployed into industrial tree plantations in the wet tropics that were once populated with *A. mangium*.

CONCLUSION

This clonal verification study showed that survival and persistence of a healthy crown after inoculation with *Ceratocystis* canker and wilt disease was heritable and repeatable across trials. Post-hoc analysis and prediction of breeding values verified on-ground selection of 50 clones that were deemed to be disease-tolerant and will be established in seed orchards and hybridised with *A. auriculiformis*. *Acacia mangium* is no longer

part of the industrial tree plantation landscape in much of Sabah, Malaysia due to the *Ceratocystis* canker and wilt disease. The study contributes to the future development of seed and hybrid clones with heightened tolerance to *C. manginecans*.

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