

## RESISTANCE OF *Tectona grandis* TO CERATOCYSTIS WILT

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### ABSTRACT

*Tectona grandis* (teak) is a tree species highly appreciated for its high-quality hardwood and versatile industrial applications. Despite clonal teak plantations showing several advantages, such as reduced rotation time and increased wood volume production, the genetic uniformity of plantations makes them more susceptible to diseases. Ceratocystis wilt caused by *Ceratocystis manginecans* has been the most prevalent disease on teak plantations, reducing tree growth rate, and wood quality and value. Planting resistant genotypes is the most effective measure to mitigate losses caused by the disease. Thus, this work aimed to assess the resistance to Ceratocystis

wilt of twelve teak clones commercially planted in Brazil, as well as the inheritance of resistance in teak open-pollinated families. Five teak clones exhibited resistance to *Ceratocystis* wilt, and all investigated open-pollinated teak families segregated resistance. The findings support the interpretation that resistance to *Ceratocystis* wilt in teak is a quantitative trait with additive gene effects in determining this trait. The information obtained in this work is an important contribution to directing the efforts of teak breeding programs in the attempt to reduce the losses caused by *Ceratocystis* wilt.

**Keywords:** *Ceratocystis fimbriata*. Genetic variability. Inheritance. Open pollination. Phenotyping. Teak.

## 1. INTRODUCTION

*Tectona grandis* (teak) is a wood diploid species of the Lamiaceae family, deciduous, and predominantly cross-pollinated (Kaosa-Ard 1989; Li et al. 2016). Pollination is primarily carried out by insects, especially bees, which tend to forage on the same tree or neighboring trees. However, the species exhibits an extremely high rate of self-incompatibility (96-100%), so self-pollinated flowers rarely develop into fruit (Hedegart, 1973; Kaosa-Ard 1989). Its wood has a golden-brown color that is highly sought after by industry for manufacturing luxurious furniture, decorative objects (such as doors, frames, and floors), and shipbuilding, making it one of the most valuable hardwoods (Kollert et al. 2024; Midgley et al. 2015). In Brazil, it is estimated that 76,000 ha are planted with teak (IBA 2023). It is an attractive country for teak plantations due to the favorable climate conditions, know-how in forestry management, and large-scale land availability (Takizawa 2022).

The yearly worldwide demand for teak wood is estimated at around 30 million m<sup>3</sup>. However, approximately 2.0-2.5 million m<sup>3</sup> of teak roundwood are harvested annually from natural and planted forests (Midgley et al. 2015), resulting in a substantial supply deficit. Such a gap between production and demand highlights the

need for expansion in the cultivation area and an increase in productivity for this forestry species. Nonetheless, the expansion in planted areas of this species along with factors such as intensive soil preparation, soil heterogeneity in the planting areas, genetic uniformity of planted teak trees, and inadequate implementation of disease management practices in teak plantations, as well as climate fluctuations have favored an increase in the incidence and severity of abiotic and biotic stresses (Alfenas et al. 2023). Among these stresses, Ceratocystis wilt, caused by *Ceratocystis manginecans*, is the most significant biotic disease affecting teak plantations in Brazil.

The taxonomic position of the *Ceratocystis* species has undergone significant study and frequent revisions over the years. *C. fimbriata* is currently recognized as a clonal lineage restricted to sweet potato (Harrington et al. 2023; Marincowitz et al. 2020). The interfertile taxa *C. manginecans*, *C. eucalypticola*, *C. mangivora*, and *C. mangicola* form the *C. manginecans* complex (Harrington et al. 2023) and are also interfertile with *C. fimbriata*. Because of this, some authors have treated them as *C. fimbriata* sensu lato (Valdetaro 2019; Fernandes et al. 2022, 2024). However, using both names concurrently can lead to confusion. As recommended by Lynn et al. (2025), the taxonomy proposed by Harrington et al. (2023) represents the least disruptive approach. Therefore, this study follows the taxonomic proposal by Harrington et al. (2023).

Ceratocystis wilt was first reported in teak in 2009 in Brazil (Firmino et al. 2012) and in 2020 in Ecuador (Belezaca-Pinargote et al. 2020). Since then, several field outbreaks have been reported by farmers, resulting in an approximately 30% reduction in the volumetric growth rate of infected trees and thereby compromising both teak wood yield and quality. In highly susceptible clones and under favorable environmental conditions, the disease can lead to tree mortality (Alfenas, RF, unpublished data). The

significant increase in disease incidence prompted the demand for more effective control strategies.

In teak plantations, infections by soilborne *Ceratocystis* spores are frequently observed, but pruning tools are a common management practice considered one of the main modes of spreading the pathogen in the plantations (Alfenas et al. 2023). The pathogen penetrates and colonizes the plant vascular system, causing mainly wilting and wood darkening. The colonization of the xylem and phloem vessels by the fungus, along with the accumulation of tyloses, blocks the transport of water and nutrients, leading to wilting and eventual death of the infected trees (Alfenas et al. 2023; Silva et al. 2018). The use of resistant genotypes is the most favorable method to control *Ceratocystis* wilt. Selection of resistant genotypes has been conducted for *Eucalyptus* spp. (Guimarães et al. 2010; Oliveira et al. 2015; Zauza et al. 2004), *Mangifera indica* (Arriel et al. 2016; Guimarães et al. 2021), *Actinidia* spp. (Oliveira et al. 2020), *Acacia mangium* (Brawner et al. 2015), and *Gmelina arborea* (Méndez-Álvarez et al. 2023). However, for teak, there are few studies on the resistance of *Ceratocystis* wilt (Alfenas et al. 2023; Oliveira et al. 2021).

Field observations indicate intraspecific variability of *T. grandis* for resistance to *Ceratocystis* wilt among seed-originated trees and clonal teak genotypes introduced into Brazil (Alfenas 2017). Therefore, the evaluation of resistance in a larger number of clones and the determination of heritability are essential to understand the genetic basis of resistance in teak genotypes. Inoculation under controlled conditions serves as a valuable tool in this investigation. It is already an established method for evaluating this disease in forest species (Oliveira et al. 2015; Arriel et al. 2016). Thus, the objective of this work was to assess the resistance of commercial teak clones and

assess the inheritance of resistance in open-pollinated families to *Ceratocystis* wilt through inoculations under controlled conditions.

## **2. MATERIAL AND METHODS**

### **2.1 Growth and maintenance of commercial teak clones**

Twelve commercial teak clones available in Mato Grosso and provided by a local forestry company were micropropagated in January 2019 and transplanted into 3.5 L pots containing a substrate with pine bark and carbonized rice husk in a 1:1 ratio supplemented with 3 kg of Basacote Mini 6M (13% N, 6% P<sub>2</sub>O<sub>5</sub>, 16% K<sub>2</sub>O) per m<sup>3</sup> of substrate. They were kept for 60 days in the greenhouse (28 °C ± 5 °C), with irrigation three times a day until inoculation. Daily fertilizations were carried out with a nutrient solution.

### **2.2 Seed collection of open-pollinated trees and growth of their derived plants**

Based on the variability in resistance to *Ceratocystis* wilt observed among field-evaluated clones, as well as the results from resistance assays conducted with commercial materials, we selected progenies derived from crosses involving clones A3, C1, C5, and E4 for further evaluation. These clones were growing in five-year-old intercropped rows. For the formation of open-pollinated progeny families, we assume that mixed plantations, where different clones are grown side by side, provide pollinators with consistent access to genetically distinct trees. Because self-pollination in teak is largely ineffective, most of the fruit produced in these environments is expected to result from cross-pollination among clones. In contrast, monoclonal stands contain only a single genotype, and the absence of alternative pollen sources increases the relative frequency of self-pollination, which nevertheless remains inefficient and results in considerably lower fruit yield.

Based on these assumptions, fruit collections were carried out to obtain the open-pollinated families used in this study. The first fruit collection occurred in August 2019 in São José dos Quatro Marcos, Mato Grosso, Brazil (15°37'17" S, 58°10'35" W), where open-pollinated fruits were obtained from the clones A3 and C1. Seeds collected from A3 constituted family F1, while those from C1 formed family F2. Additionally, seeds were collected from a monoclonal plantation of clone A3, generating family F3. In July 2020, fruits were collected from trees of clone C5, growing in a mixed teak compartment containing clones A3 and C5, producing seeds from C5 mother trees (family F4). Finally, in another mixed plantation containing clones A3, C5, and E4, fruits were collected from C5 mother trees, yielding family F5 (Table 1).

Because the crosses occurred under open-pollination conditions, all individuals within families were considered half-sibs. Microsatellite markers CIRAD3TeakA11, CIRAD3TeakB02, CIRAD1TeakB03, CIRAD2TeakB07, CIRAD2TeakC03, and CIRAD3TeakF01, developed by Verhaegen et al. (2005), were used for genotyping to confirm the identity of the mother trees. The procedures for PCR amplifications, capillary electrophoresis on an automated sequencer, and loci analysis during genotyping were as described by Queiroz et al. (2023). The molecular profile of the teak mother trees was analyzed and compared with the PROTECA company database to verify their genetic identity.

The collected fruits were sun-dried to facilitate pericarp removal. Subsequently, the pericarp was removed, and the seeds were placed in mesh bags and subjected to running tap water for 24 h to break dormancy. The seeds were then sown on a moistened sand bed for germination. For the first six days, the moistened sand bed was covered with black plastic to increase the temperature and relative humidity while reducing light intensity. Subsequently, after removing the plastic cover, the moistened

sand bed was irrigated twice a day for 15 days until the seeds began to germinate. The germinated seeds were transplanted into 55 cm<sup>3</sup> pot cells containing a substrate with pine bark and carbonized rice husk in a 1:1 ratio, supplemented with 3 kg of Basacote Mini 6M per m<sup>3</sup> substrate, and kept for 60 days under greenhouse conditions (28 °C ± 5 °C). Fertilizations were carried out daily with a nutrient solution. Rooted seedlings were transplanted into 3.5 L pots containing the same substrate, fertilized as previously described, and kept for 60 days under greenhouse conditions (28 °C ± 5 °C) with irrigation three times a day until inoculation.

### 2.3 Pathogen inoculation and resistance assessment

The *C. manginecans* isolate LPF2199 was obtained in 2016 from a diseased teak tree in a commercial plantation located in the municipality of São José dos Quatro Marcos in Mato Grosso state, Brazil. This fungal isolate belongs to the Culture Collection of the Laboratory of Forest Pathology / Bioagro of the Universidade Federal de Viçosa, Minas Gerais, Brazil. In an unpublished study conducted by our research, eight *C. manginecans* isolates obtained from teak were evaluated in a phenotyping assay to assess their aggressiveness. Within this set, LPF2199 consistently ranked among the most aggressive isolates. The isolate was grown on potato-dextrose-agar (PDA) medium at 25 ± 2 °C with a 12 h photoperiod under 20 µmol/m<sup>2</sup>/s for 15 days. The inoculation was performed by making a wound at the base of the plant stem using a disinfected 5-mm-diameter cork borer (Figures 1A and 1B) and placing a mycelium plug from the 15-day-old culture of the fungal isolate on the wound (Figure 1C). The inoculation site was wrapped with a wet cotton plug and parafilm to reduce desiccation and contamination (Figure 1D).

Using this method, ten plants of each of the twelve commercial teak clones were inoculated with isolate LPF2199 using the method described above. In addition, a total

of 82, 60, 70, 131, and 124 plants of open-pollinated families F1, F2, F3, F4, and F5, respectively, were inoculated with the same isolate, including ten plants of the resistant clone A3 and ten plants of the susceptible clone C1 as controls. The inoculated plants were kept in a greenhouse ( $28^{\circ}\text{C} \pm 5^{\circ}\text{C}$ ) in a completely randomized design, applying irrigation three times a day.

Disease assessments of the inoculated plants were conducted weekly for up to 90 days after inoculation (DAI). Lesion size and plant height were measured, and disease severity (lesion size/plant height) was calculated and expressed as a percentage. For wilted plants, disease severity was 100%. The pathogen was re-isolated from the infected plants, and the carrot bait method (Moller and Devay 1968) was used to confirm the infection by *C. manginecans*.

## 2.4 Statistical analysis

Statistical analyses were conducted in the R environment v. 4.1.3 (R Core Team, 2023). The Scott-Knott test ( $p \leq 0.05$ ) was used to group the clones and open-pollinated families using the “easyanova” package (Arnhold, 2016). Based on this grouping, the clones were classified as either resistant or susceptible to diseases.

For the open-pollinated families, plants were classified as resistant when their disease severity values were equal to or lower than the mean disease severity observed in the resistant control clone (A3); conversely, plants with severity values higher than this threshold were considered susceptible. Additionally, the “lme4” package (Bates et al. 2015) was used to estimate variance components and genotypic values through a mixed-effects linear regression model, employing Restricted Maximum Likelihood/Best Linear Unbiased Prediction (REML/BLUP) methods (Henderson, 1975; Patterson and Thompson, 1971), according to the following equation 1:

$$y = X\beta + Zu + e \quad (1)$$

In which,  $y$  is the vector of observations (severity);  $\beta$  is the vector of unknown fixed effect parameters;  $u$  is the vector of unknown random effect parameters;  $X$  is the known design incidence matrix, where  $X$  relates  $y$  to  $\beta$ ; and  $Z$  is the known design incidence matrix, where  $Z$  relates  $y$  to  $u$ . The mother trees  $X$  and  $Z$  consist of 1's and 0's, whereas  $e$  refers to the random effect associated with unobservable errors. The genetic parameters were estimated according to Resende et al. (2007, 2014), considering the disease severity.

### 3. RESULTS

#### 3.1 Resistance of commercial teak clones to *Ceratocystis* wilt

The commercial teak clones were categorized into two distinct groups by the Scott-Knott test based on comparisons of disease severity means (Table 2). Clones A12, C1, C7, C16-1, C16-2, D19, and E4 were classified as susceptible (group a). Lesion size in these clones varied from 15.5 to 27.7 cm, and disease severity ranged from 51.5 to 87.7%. In contrast, clones A3, A8, B1, C5, and T4 were considered resistant (group b), with lesion size varying from 11.9 to 19.1 cm and disease severity from 22.8 to 34.9%. External wilting symptoms were readily visible in the most susceptible clones starting at 18 DAI (Figure 2A-B). Internal dark lesions in the longitudinal and radial direction of the stem were also observed at 90 DAI (Figure 2C-D). By the end of the assay, plant wilting reached up to 80% in susceptible clones (Table 2) while the most resistant clones did not wilt. The pathogen was re-isolated from all inoculated teak clones exhibiting disease symptoms, and its growth on carrot slices (Figure 2E), as well as its perithecia and ascospores (Figure 2F), were typical of *C. manginecans*.

### 3.2 Resistance to *Ceratocystis* wilt in open-pollinated families

The progenies in families obtained by open pollination varied in resistance (Table 3). The families showed significant differences in their response to inoculation with *C. manginecans* and were separated into four distinct groups by the Scott-Knott test based on disease severity. Clone C1, used as a susceptible control, showed the largest means of lesion size and disease severity (12.7 cm and 17.7%, respectively) and formed group a. The families F1 and F2 formed group b with lesion sizes of 10.4 and 8.5 cm and mean disease severity of 11.4 and 12.5%, respectively. The family F3, together with clone A3 (resistant control), formed group c, with mean lesion sizes of 9.0 and 8.9 cm and disease severity of 8.7 and 8.8%, respectively. Finally, families F4 and F5 formed group d with the lowest mean lesion sizes (5.4 and 4.5 cm, respectively) and mean disease severity (6.3 and 4.8%, respectively). In general, the means of lesion size and disease severity decreased from F1 to F5. Wilting was observed only in families F1 and F2, being 1 and 3% of the total plants evaluated, respectively. Re-isolation of the pathogen and its growth characteristics on carrot baits confirmed the infection by *C. manginecans*.

### 3.3 Inheritance of resistance in open-pollinated families

All families exhibited segregation for resistance, with a high prevalence of resistant genotypes, especially in families F4 and F5 (Figure 3). Genetic parameters and variance components of teak resistance to *C. manginecans* were estimated for open-pollinated families (Table 4). The results indicated values of total genetic variance among half-sib families ( $V_g$ ), additive genetic effects ( $V_a$ ), environmental variance ( $V_e$ ), and individual phenotypic variance ( $V_p$ ) of 6.05, 24.21, 19.59, and 25.64, respectively. The resistance trait showed high heritability ( $h^2 = 94.40$ ). However, there was considerable environmental variability ( $CV_e = 63.32$ ) relative to

genotype variation ( $CV_g = 35.19$ ) with a relative coefficient of variation ( $CV_g/CV_e$ ) of 0.56, suggesting environmental factors significantly influenced the expression of resistance. The accuracy of genotype selection was high (0.99), indicating the reliability of the selection processes.

#### **4. DISCUSSION**

This study aimed to elucidate the resistance to *Ceratocystis* wilt in commercial teak clones and the inheritance of resistance in open-pollinated families. The results of the present study revealed that five clones planted in Brazil exhibit resistance to *Ceratocystis* wilt. Among these, one clone was Brazilian provenanced, whereas the others were from the Solomon Islands, Malaysia, and Tanzania; notably, no wilting was observed in these clones at 90 days after inoculation (DAI). The different geographic origins of these clones suggest the existence of genetic variability among them. Similarly, Oliveira et al. (2021) reported that resistance to this disease was identified in only a few of the evaluated teak clones. Due to the limited number of resistant genotypes, the introduction of new genetic materials into teak plantations is crucial to broadening the genetic base of this species in Brazil. Such a strategy is essential to mitigate the risks associated with establishing genetically uniform populations, in which susceptible clones could dominate. This concern has already been addressed in a study by Queiroz et al. (2023), who, upon evaluating teak clones planted in Brazil, demonstrated that despite the high genetic diversity detected through microsatellite markers, a significant proportion of these clones originated from trees with recent shared ancestry. These findings indicate that the selection of elite clones in breeding programs frequently occurs within the same families, thereby contributing to the narrowing of genetic diversity.

It is important to highlight the inherent challenges associated with performing controlled crosses in teak. The reproductive biology of the species, characterized by a high dependence on natural cross-pollination, asynchronous flowering among individuals, a long vegetative period before flowering, and low seed production per tree (Kaosa-Ard et al. 1998), hinders the implementation of controlled pollination protocols. Due to these limitations, genetic studies and breeding programs in teak often rely on open-pollinated progenies or use clonal tests as a substitute for progeny tests. In this context, the present study investigated plants from families derived through natural open-pollinated crosses, which revealed segregation for resistance to *Ceratocystis* wilt among the progenies. Notably, the F4 and F5 families, derived from clone C5 as mother trees, exhibited the highest levels of resistance. These findings not only demonstrate that clone C5 exhibits strong general combining ability (GCA) (Dudley 1997), making it a valuable parent in breeding programs, but also reinforce that this clone has potential for commercial cultivation due to its disease resistance.

The high narrow-sense heritability observed in the progenies indicates a strong additive genetic component. However, the considerable environmental variance suggests that resistance expression is still heavily influenced by environmental factors (Resende 2007). Together, these findings support the interpretation that resistance to *Ceratocystis* wilt in teak is a quantitative trait, as previously reported in other pathosystems involving *Ceratocystis* and various plant species, such as *Eucalyptus* spp. (Rosado et al. 2010), *Acacia mangium* (Brawner et al. 2015), *Mangifera indica* (Arriel et al. 2016), and *Actinidia deliciosa* (Oliveira et al. 2020).

The high additive genetic variance reinforces the role of additive gene effects in determining this trait, aligning with Rosado et al. (2010), who reported strong additive genetic control of disease resistance in *Eucalyptus* spp. In the case of *Eucalyptus*, the

use of families derived from interspecific crosses contributed to greater genetic diversity, increasing the frequency of resistance alleles and resulting in higher heritability estimates. In contrast, for teak, the assumption of true half-sib relatedness among individuals in open-pollinated families is likely inaccurate, potentially inflating estimates of additive variance. Nonetheless, the results indicate that selection among mother trees can still lead to substantial genetic gains in resistance, demonstrating the effectiveness of current screening methods for identifying superior genotypes.

The relatively low broad-sense heritability observed suggests a limited total genetic contribution to resistance, likely due to environmental effects or a narrow genetic base in the studied population. Therefore, further studies under diverse environmental conditions are necessary to validate the stability of this inheritance pattern and to confirm the robustness of resistance to *Ceratocystis* wilt in teak.

Some level of specificity has been observed in the interactions between *Ceratocystis* isolates and distinct genotypes of the same host (Alexandre et al. unpublished; Oliveira et al. 2020; Guimarães et al. 2021). This level of specificity of the interactions can negatively impact the durability of resistance and increase the risk of the fungus evolving to produce additional virulence factors in specific pathogen populations (Cowger et al. 2000). Hence, the resistance of the teak genotypes evaluated may depend on the physiological specialization of the pathogen population tested. In this study, only one virulent *C. manginecans* isolate was inoculated into healthy teak plants, limiting to draw clear conclusions on the effectiveness of the resistance against naturally occurring populations. To select teak genotypes likely exhibiting more durable resistance under field conditions, it is necessary to investigate larger and more genetically diverse panels of both teak plants and fungal isolates. Despite this limitation, the findings of this study represent an important step toward

strengthening teak breeding efforts. Through rigorous screening, the study revealed genetic variability and heritability for resistance among clones and open-pollinated progenies, enabling the selection of promising resistant genotypes for incorporation into breeding programs and their adoption in large-scale commercial plantations.

## **ACKNOWLEDGEMENT**

The authors are grateful to Aleffe Leite, Beatriz Feltrin Magosso, Gustavo Felizardo, and Márcia Jantsch for assistance in data collection

## **FUNDING INFORMATION**

This study received support from Proteca and Clonar companies, which provided plant material and access to greenhouse facilities. The scholarships granted by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) were essential for the development of this research.

## **CONFLICT OF INTEREST STATEMENT**

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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## TABLES

**Table 1.** Origin of *Tectona grandis* seed families from open-pollinated crosses

| Family | Mother trees | Crossing environment      | Possible pollen sources    |
|--------|--------------|---------------------------|----------------------------|
| F1     | A3           | Open-pollinated (A3 x C1) | C1                         |
| F2     | C1           | Open-pollinated (C1 x A3) | A3                         |
| F3     | A3           | Monoclonal (A3 x A3)      | A3 (self or cross with A3) |
| F4     | C5           | Open-pollinated (C5 x A3) | A3                         |
| F5     | C5           | Mixed stand (C5 x A3, E4) | A3 or E4                   |

**Table 2.** Response to *Ceratocystis manginecans* of commercial *Tectona grandis* clones at 90 days after inoculation

| Clone | Provenance     | Wilted plants (%) | Lesion size (cm) | Disease severity (%) <sup>a</sup> | Category <sup>c</sup> |
|-------|----------------|-------------------|------------------|-----------------------------------|-----------------------|
| A3    | Solomon Island | 0                 | 16.0 (3.2)       | 34.9 (10.4) <sup>b</sup> b        | R                     |
| A8    | Solomon Island | 0                 | 18.7 (3.0)       | 22.8 (9.8) b                      | R                     |
| A12   | Solomon Island | 30                | 24.8 (2.9)       | 51.5 (9.3) a                      | S                     |
| B1    | Brazil         | 0                 | 16.8 (2.9)       | 28.6 (9.3) b                      | R                     |
| C1    | Malaysia       | 60                | 26.6 (2.9)       | 72.0 (9.3) a                      | S                     |
| C5    | Malaysia       | 0                 | 11.9 (3.1)       | 25.3 (9.8) b                      | R                     |
| C7    | Malaysia       | 60                | 15.5 (2.9)       | 69.8 (9.3) a                      | S                     |
| C16-1 | Malaysia       | 80                | 27.7 (2.9)       | 87.7 (9.3) a                      | S                     |
| C16-2 | Malaysia       | 70                | 17.2 (3.1)       | 81.0 (9.8) a                      | S                     |
| D19   | India          | 40                | 18.8 (3.1)       | 61.2 (9.8) a                      | S                     |
| E4    | Indonesia      | 40                | 21.2 (2.9)       | 55.4 (9.3) a                      | S                     |
| T4    | Tanzania       | 0                 | 19.1 (2.9)       | 29.4 (9.3) b                      | R                     |

<sup>a</sup> Means with the same letter within the column are not significantly different, at a 5% level by the Scott-Knott test.

<sup>b</sup> Values in parentheses indicate standard errors.

<sup>c</sup> R, resistant; S, susceptible.

**Table 3.** Number of *Tectona grandis* genotypes in families obtained by open pollination and their reactions to *Ceratocystis manginecans* at 90 days after inoculation

| Family         | Crossing<br>(♀ x ♂) <sup>a</sup> | No. of<br>genotypes | Wilted<br>plants (%) | Lesion size<br>(cm) | Disease<br>severity (%) <sup>b</sup> |
|----------------|----------------------------------|---------------------|----------------------|---------------------|--------------------------------------|
| F1             | A3 x C1                          | 82                  | 1                    | 10.4 (0.5)          | 11.4 (0.9) <sup>c</sup> b            |
| F2             | C1 x A3                          | 60                  | 3                    | 8.5 (0.6)           | 12.5 (1.1) b                         |
| F3             | A3 x A3                          | 70                  | 0                    | 9.0 (0.6)           | 8.7 (1.0) c                          |
| F4             | C5 x A3                          | 131                 | 0                    | 5.4 (0.4)           | 6.3 (0.7) d                          |
| F5             | C5 x A3, E4                      | 124                 | 0                    | 4.5 (0.4)           | 4.8 (0.8) d                          |
| <b>Control</b> |                                  |                     |                      |                     |                                      |
| A3             |                                  |                     | 0                    | 8.9 (1.0)           | 8.8 (1.9) c                          |
| C1             |                                  |                     | 0                    | 12.7 (1.0)          | 17.7 (1.9) a                         |

<sup>a</sup> The open-pollinated families were formed by crossing the mother trees (♀) with likely fathers (♂).

<sup>b</sup> Means with the same letter within the column are not significantly different, at a 5% level by the Scott-Knott test.

<sup>c</sup> Values in parentheses indicate standard errors.

**Table 4.** Estimates of genetic parameters and variance components for the resistance of open-pollinated *Tectona grandis* families to *Ceratocystis manginecans* based on disease severity

| <b>Genetic parameters</b>                                | <b>Values</b> |
|----------------------------------------------------------|---------------|
| Total genetic variance among half-sib families ( $V_g$ ) | 6.05          |
| Additive genetic variance ( $V_a$ )                      | 24.21         |
| Environmental variance ( $V_e$ )                         | 19.59         |
| Individual phenotypic variance ( $V_p$ )                 | 25.64         |
| Heritability in the broad-sense ( $h_g^2\%$ )            | 23.60         |
| Heritability in the narrow-sense ( $h_a^2\%$ )           | 94.40         |
| Coefficient of genotype variation ( $CV_g\%$ )           | 35.19         |
| Coefficient of environmental variation ( $CV_e\%$ )      | 63.32         |
| Coefficient of relative variation ( $CV_g/CV_e$ )        | 0.56          |
| Accuracy                                                 | 0.99          |
| Mean                                                     | 6.99          |
| <i>SE</i> : Standard error of prediction                 | 0.32          |

## FIGURES

**Figure 1.** Inoculation of *Ceratocystis manginecans* on teak. (A, B) wounding of the stem, (C) deposition of a mycelium plug in the wound, (D) wrapping of the inoculum with cotton and parafilm.

**Figure 2.** Symptoms of *Ceratocystis* wilt in susceptible teak clones inoculated under controlled conditions and re-isolation of the pathogen. (A) wilted plant, (B) darkening of the outer stem tissue, (C) radial darkening of the internal stem tissue, (D) internal darkening of the stem in a longitudinal section, (E) pathogen recovered from infected tissue growing on carrot discs, (F) perithecia and ascospore mass typical of *Ceratocystis manginecans*.

**Figure 3.** Frequency distribution of disease severity (lesion size/plant height) in plants of five *Tectona grandis* families (F1, F2, F3, F4, and F5) obtained by open pollination at 90 days after inoculation with *Ceratocystis manginecans*. Genotypes showing disease severity values equal to or less than the mean value of the resistant control (8.81) of the resistant control (clone A3) were classified as resistant (orange), while those with values above this threshold were classified as susceptible (light pink).