The occurrence of gummosis on invasive *Acacia decurrens* after Mount Merapi eruption in Yogyakarta, Indonesia

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**Abstract**

Gummosis on *Acacia decurrens*, an invasive tree species that was established in Merapi Volcano National Park (MVNP) after the eruption of the Mount Merapi volcano in 2010, was studied to i) identify the causal organism of the disease, ii) analyze the disease symptoms, iii) understand the spatio-temporal distribution of gummosis in the tree population and iv) examine how the disease affects the anatomy of tree wood. Pathological, morphological and molecular assessments were used in this study. *Ceratocystis fimbriata* was found associated with gummosis in the affected trees. The disease spread was probably aided by an ambrosia beetle, *Euwallacea* sp., which bores holes in the stem. The number of parenchyma cells in infected stems was significantly higher than in healthy stems, which apparently facilitated water and nutrition transport within trees, helping them to grow normally despite serious gummosis. The disease is noted to spread from the base of the trees, where the ambrosia beetle bores holes first, to the upper part. The management of invasion by *A. decurrens* in the MVNP area poses a serious challenge due its success as an invader in the volcano-impacted area and the threat of the gummosis pathogen spreading to other species, both of which will affect the regeneration and establishment of native species and recovery of the ecosystem.

**Key words:** spatio-temporal, ambrosia beetle, *Ceratocystis fimbriata*, invasive tree, parenchyma cells

**Introduction**

Large, but infrequent, volcanic eruptions, such as the 2010 eruption of Mount (Gunung) Merapi in Yogyakarta, Indonesia, caused significant changes in ecosystem composition and vegetation structure in areas surrounding the volcano (MVNP 2012, *unpublished data*). Similar ecological impacts were observed in Washington, USA when Mount St. Helens erupted in 1980. The eruption of Mount St. Helens produced a complex of disturbance agents, such as pyroclastic flow, debris avalanche, mud flow, ash deposits, blow downs, and several other agents which interacted at specific sites, exacerbating the degree of damage and delay in recovery (Adams et al. 1987; Dale et al. 1998; Franklin et al. 1985; del Moral 1993). Additionally, combinations of post-disturbance site characteristics
influenced the composition of the biota. The pyroclastic flow from Mount
Merapi destroyed all flora and fauna that it contacted in the area
surrounding the volcano.

In a period of two years following the 2010 eruption, *Acacia decurrens*
(Wendl.) Willd. (green wattle) was the first tree species to appear, establish,
and dominate large areas impacted by the pyroclastic flow. Data collected
by Merapi Volcano National Park (MVNP) in 2012 showed that the density
of *A. decurrens* averaged 16167 seedlings ha\(^{-1}\) and 11814 saplings ha\(^{-1}\) at
the sites (MVNP 2012, *unpublished data*). Native to Australia, *A. decurrens* is
introduced and grown in plantations in several countries in the tropics
and subtropics. It is an important invasive species especially in Africa and
Oceania, where it spreads rapidly via seed and root suckers (CABI 2018).
The tree can invade grasslands, roadsides, savannah and riverine habitats,
developing dense thickets impacting on native biodiversity and obstructing
water flow (Boucher 1978). The rapid establishment of *A. decurrens* in the
MVNP area poses a serious threat since it will affect the recuperation of
ecosystems and regeneration of native flora impacted by the volcanic eruption.

A preliminary survey conducted in 2014 by MVNP on the health of
*A. decurrens* stands showed that ambrosia beetles (Coleoptera: Curculionidae:
Scolytinae), bagworms (Lepidoptera: Psychidae), *Ceratocystis* sp.,
*Uromycladium falcatarium* Doungsa-ard, McTaggart & R.G. Shivas and
*Ganoderma* sp. occurred in the stands. Rahayu et al. (2015) reported that
over 50% of *A. decurrens* stands in the region showed gummosis and
symptoms of stem canker associated with *Ceratocystis* sp. However, these
symptoms were not visible on trees within the area around Mount Merapi
before eruption. Gummosis of *A. decurrens* and *Acacia mearnsii* caused by
*Ceratocystis fimbriata* Ellis and Halst. was recorded from Brazil and South
Africa, respectively, by Ribeiro et al. (1988) and Morris et al. (1993). The
symptoms described on *A. mearnsii* were similar to those observed on
*A. decurrens* in MVNP. The genus Ceratocystis includes some well-known
pathogens of trees responsible for a wide range of diseases including stem
cankers, vascular wilts and root diseases (Kile 1993). For example, *C. fimbriata*
is known to cause diseases of several vegetable crops, fruit trees and forest
trees (Johnson et al. 2005). Another species of *Ceratocystis*, *C. albifundus*
M.J. Wingf., de Beer & M.J. Morris occurs on *Acacia mearnsii* plantations in
southern and eastern Africa, causing gum exudation, wood-discoloration,
stem cankers, rapid wilting and tree death (Morris et al. 1993; Roux et al.
1999). It is also reported by Kile (1993) that wounds on trees are a predisposing
factor for *C. fimbriata sensu lato* to cause infection. These wounds can result
from wind and hail damage, growth cracks, insect and animal damage as
well as activities such as grafting and pruning.

Recent studies have shown that artificially induced wounds on trees
incited infection by *Ceratocystis* spp. (Barnes et al. 2003; Roux et al. 2004;
Rodas et al. 2008). Success of infection was dependent on different physical
and environmental factors. For example, *C. fimbriata* can infect their hosts when viable fungal propagules are deposited onto bark wounds (DeVay et al. 1968). Other *Ceratocystis* spp., such as *Bretziella fagacearum* (formerly *Ceratocystis fagacearum*), can only infect if viable fungal propagules are deposited onto freshly exposed wood of the host (Kuntz and Drake 1957). Temporal factors also affect the success of infection by *Ceratocystis* spp. For example, Kuntz and Drake (1957) showed that *B. fagacearum* could not cause infection when wounds were older than 24 h. Variations in temperature and relative humidity have also been shown to influence germination of spores and infection by *Ceratocystis* spp. (Cole and Fergus 1956). Based on the foregoing evidences, we hypothesized that tree wounds caused by insects could be one of the reasons for the occurrence of gummosis on *A. decurrens* in the Mount Merapi region and that the spread of the disease may have been assisted by the dominance (monoculture) of *A. decurrens* trees in the MVNP area.

According to Harrington (2007), *Ceratocystis* infections induce sapwood discoloration because the pathogen attacks living parenchyma cells. Harrington (2013) also noted that the discoloration is caused by a combination of host response chemicals and the pigmentation of the spores and hyphae of the *Ceratocystis*. Fungal spores will rapidly germinate and colonize the xylem and phloem (Johnson et al. 2005), absorbing nutrients from the xylem parenchyma (Mace et al. 1981). Once the hyphae are present in the vascular cylinder, the pathogen will move systematically into the cambium and inner bark; killing these tissues causes a canker. Prior to our current analysis, no study of the wood anatomy of *A. decurrens* in the Mount Merapi area had been conducted. Because of its status as a dominant invader after the 2010 eruption and its association with gummosis disease, we deemed it necessary to assess the anatomy of infected *A. decurrens* wood to help specify the causal pathogen.

Against this background, the present study was aimed at i) confirming *Ceratocystis* sp. as the pathogen associated with the gummosis disease, ii) examining the disease symptoms and predisposing factors for infection, iii) understanding the spatio-temporal distribution of gummosis in the tree population and iv) assessing the anatomy of the infected wood. This information would help to develop methods to manage *A. decurrens* and control the spread of the gummosis pathogen to native plants.

**Materials and methods**

*Location and tree material*

The study was conducted at Merapi Volcano National Park (MVNP), which is located in two Indonesian provinces (Yogyakarta and Central Java Provinces) and with geographic coordinates between 110°15′–110°37′30″E and 07°22′30″–07°52′30″S, within an 8.4 ha restoration plot. The study area
was affected by pyroclastic flow from the Merapi eruption in November 2010. The entire site became barren and covered by sand and dust. The first species that emerged at the site, about one year after eruption, was *Acacia decurrens*. Subsequently, this species dominated the area. The stands of *A. decurrens* were approximately four years old when the study was conducted in 2015.

**Isolation of the causal organism, identification and characterization**

Ten *A. decurrens* trees were selected purposively from all trees in the study area (Figure 1) with new gummosis symptoms (i.e., with at least three gummoses on the stem). Furthermore, three or more discolored wood and bark samples at least 3 × 3 cm in size were drawn from the leading edge of the gummosis (after clearing the gummosis with a sharp knife). These excised sections were then wrapped separately in newspaper to maintain moisture. All 30 wood and bark samples were then transferred to the laboratory for further processing. In order to secure the freshness of the samples, baiting processes were performed immediately in the laboratory. Carrot slices were used as a bait to isolate *Ceratocystis* from the diseased samples (Moller and de Vay 1968). Isolations from stem samples and pathogenicity tests were conducted using standard methodology (Waller et al. 2002; Rahayu et al. 2015). All isolates were maintained on potato dextrose agar (PDA) in the laboratory of Forest Health and Protection, Faculty of Forestry, University Gadjah Mada, Indonesia. Morphological characteristics of the isolates were studied to identify the species.
In order to identify the species of *Ceratocystis* associated with the gummosis disease, DNA extraction from the fungus isolate (collected in 2015) and amplification of rDNA ITS were conducted in 2018 in the Molecular Genetics Laboratory, Ministry of Environment and Forestry, Yogyakarta. Sequencing of ITS fragments was conducted in 1st Base Singapore. DNA was extracted using SDS buffer (200 mM Tris HCl pH 8.5; 250 mM NaCl; 25 mM EDTA and 0.5% SDS) (Raeder and Broda 1985) as modified by Glen et al. (2002). The primer pairs used to amplify the rDNA ITS are ITS4 (TCC TCC GCT TAT TGA TAT GC) (White et al. 1990) and ITS1-F (CTT GGT CAT TTA GAG GAA GTA A) (Gardes and Bruns 1993). DNA sequence chromatograms were viewed in Chromas version 2.6.5 (Technelysium Pty Ltd) software and edited to remove poor quality sequences at each end. Searching of the public DNA database GenBank (Benson et al. 2017) was conducted to retrieved sequences of high similarity using BLAST (Basic Local Alignment Search Tool) (Altschul et al. 1997). Phylogenetic analysis to confirm the identification of the isolates was conducted using Mega7 (Kumar et al. 2016). Sequences were aligned using Clustal W (Larkin et al. 2007) in BioEdit 7.0.9.0 (Hall 1999) with full multiple alignments prior to phylogenetic analysis. The phylogenetic tree was constructed using the Maximum Likelihood method based on the Tamura-Nei model (Figure 4; Tamura and Nei 1993).

**Assessment of gummosis symptoms**

To analyze disease incidence and intensity, a 10 m wide transect was laid along a river at the study site and nine 100 × 10 m rectangular plots were marked to record observations. Each plot contained 6–10 trees and the total number of trees measured was 79. The first rectangular plot was 10 m away from the boundary of the restoration plot and the distance between each rectangular plot was a minimum of 20 m. The symptoms of gummosis were evaluated on each tree by marking three segments on the stem, viz.: 1) lower stem (L) which includes the base of the stem up to 130 cm in height (the height at which diameter breast high, or dbh, is measured); 2) upper stem (U), the area between 130 cm to the base of the first branch; and 3) stem covered by the crown (S) (Figure 2). Based on preliminary survey in 2015, we found many bark beetles associated with gummosis symptoms on the stems. In turn, any small pinholes of bark beetles and the associated galleries were observed on gummosis portions of the diseased trees. The beetle most often found associated with gummosis symptom was then identified up to genera using an online bark beetle identification resources link (http://www.ambrosiasymbiosis.org/resources/) provided by Jiri Hulcr (University of Florida, USA).

The number of wounds with new or old gummosis in each stem segment was recorded. Disease severity was calculated based on the number of wounds with gummosis occurring on each tree. The progress of gummosis...
Figure 2. Segments of a tree identified for assessing gummosis.

along the stem was made by observing the number of gummoses on each segment of individual stems. Number of wounds with gummosis in each tree segment (L, U, and S), and distance between asymptomatic and symptomatic trees were recorded bimonthly between February and August 2015. The geographical position of each tree was marked with GPS Garmin 64s and the nearest distance from a focal tree to each of those trees was measured using proximity tools in Arc GIS version 10.1 software.

Mean disease severity (%) of individual trees was calculated using the following formula (Cooke 1998):

\[
\text{Mean Disease Severity} (\%) \text{ on individual trees (Eq. 1)} = \frac{(z_1 + z_2 + z_3)}{3} \times 100\%
\]

Disease incidence was calculated based on the number of trees showing gummosis out of total number of trees observed.

\[
\text{Disease incidence (DI) (Eq. 2)} = \frac{n}{N} \times 100\%
\]
Where
\[ n = \text{Number of trees with new (oozing at the time of observation) or old gummosis} \]
\[ N = \text{Total number of trees assessed} \]
\[ z_1 = \text{Number of gummosis on the lower stem} \]
\[ z_2 = \text{Number of gummosis on the upper stem} \]
\[ z_3 = \text{Number of gummosis on the stem covered by crown} \]

"3" represents 3 segments of the stem observed for gummosis

The horizontal pattern of distribution was determined by measuring the shortest distance between trees with gummosis symptoms. These distances were then grouped for each measurement occasion.

**Anatomy of gummosis affected stem**

To analyze changes in anatomy of the wood, 1 cm³ cuboid wood samples were cut from 10 trees selected randomly from all diseased (i.e., newly symptomatic) trees as well as 10 trees selected randomly from all healthy (i.e., asymptomatic) trees. Wood samples close to the infected area were collected from the diseased trees and those from healthy trees were collected from stems with similar diameter and at the same height. Transverse, radial and tangential sections of the stem (10–15 μm thick) were cut using a sledge microtome. The sections were soaked in lactophenol cotton blue for 1 hr, washed in distilled water, dried and a drop of xylol was added. The sections were then gently warmed to remove water and xylol and mounted on slides using Canada balsam or Entellan. The sections were observed under a light microscope (BX51, Olympus Corporation, Japan), photographed using a digital camera (DP 70, Olympus Corporation, Japan) and the dimensions of fibers and parenchyma cells were measured using the digital images.

**Analysis of data**

Qualitative data such as identification and characterization of the causal agent associated with gummosis were described on a qualitative scale. Quantitative data such as severity and incidence of gummosis, percentage of fiber and parenchyma cells of infected and healthy wood as well as temporal trend of gummosis severity were analyzed using Excel 2013 software. To identify the effect of distance on disease spread, we classified the distances of individual trees from the focal tree into 5 m classes (0–5, 5–10, 10–15, …, > 50 m). Number and proportion of symptomatic and asymptomatic trees were calculated and projected into histograms.

**Results**

**Characterization and identification of the pathogen associated with gummosis**

The cultures from gummosis-affected wood yielded two types of Ceratocystis isolates (UGM AD 1 and UGM AD 2). Mature ascomata were produced in
Gummosis on invasive *Acacia decurrens* after Mount Merapi eruption

Rahayu et al. (2021), *Management of Biological Invasions* 12(4): 886–900, https://doi.org/10.3391/mbi.2021.12.4.08

**Figure 3.** Diagnostic features of the *Ceratocystis* complex from *A. decurrens* trees at Merapi Volcano National Park: a) globose ascomata with long neck; b) divergent ostiolar hyphae; c) hat-shaped ascospores oozing from the ostiole; d) chlamydospores; e) cylindrical conidia and barrel-shaped conidia. Scale bars a = 90 μm; d–e = 10 μm; b, c, f, g, h = 5 μm. Photomicrographs by Sri Rahayu.

**Figure 4.** Molecular phylogenetic analysis of *Ceratocystis* spp. including two isolates from *A. decurrens* (UGM-AD1 and UGM-AD7).

culture during a 2-week incubation on PDA. The ascomata had black, globose to sub globose bases (Figure 3a) and long necks with ostiolar divergent hyphae (Figure 3b) exuding hat-shaped ascospores from their tips (Figure 3c). Ascomata varied in size, the neck and base were 0.2–1.3 and 0.2–0.6 mm long, respectively. Chlamydospores and both barrel-shaped and cylindrical conidia were produced in culture. (Figure 3d, e). Based on ITS sequence BLAST on the GenBank database (https://blast.ncbi.nlm.nih.gov), all two isolates showed the closest similarity to *Ceratocystis fimbriata* (Figure 4). Molecular analysis involved 15 nucleotide sequences with *Ceratocystis fimbriatomima* (MH863157) as an out group. There was a total of 172 positions in the final dataset.
Symptoms of gummosis

Gummosis is evidenced by exudation of resin or gum from the wood, which gets deposited on tree bark. The gum is produced in response to wounds on the stem due to insect attack, infection by plant pathogens or physical injury. On *A. decurrens* at MVNP, gum exudation was mainly due to wounds made by insects, as indicated by boring dust and pitch tubes occurring outside the bark (Figure 5a) and characteristic galleries under the bark. Our observations showed that most of the holes in the bark were caused by ambrosia beetles (e.g. *Euwallacea* sp.) which can bore into the xylem of the diseased trunk producing copious amounts of frass (Figure 5b). Additionally, all the bore holes we examined were affected by *C. fimbriata* and the disease was found progressing upwards on the stem. Ambrosia beetles are known vectors of *Ceratocystis* diseases and the spread of gummosis was apparently due to feeding of the beetles on the stem. More bore holes occurred on woody or older stems, whereas only limited holes were present on young branches (Figure 6).

Occurrence of symptoms of gummosis on *A. decurrens*

The first survey (Feb. 2015) indicated the presence of gummosis on 80% of the trees surveyed. By Aug. 2015 (fourth survey), all the trees (100%) were found affected, which indicated a 20% increase in incidence in six months. In terms of the occurrence of gummosis on different segments of the stem, the highest incidence was on the lower stem (L) compared to the upper part...
Figure 7. a) The incidence of gummosis on acacia trees assessed bimonthly at MVNP and b) severity of gummosis on different segments of the stem during the assessment period in 2015.

U and stem covered by crown (S) (Figure 7a, b). Over time, the mean severity of gummosis tended to increase from the bottom to the top of the tree which indicated that the bark beetles were settled, increased in number and actively moved from the lower part to the upper part of the stem.

Spatio-temporal distribution of gummosis

Measurement of the nearest distance among symptomatic trees was used as a variable to assess disease spread given that Ceratocystis and other disease-inducing agents had spread from tree to tree via active movement of the insect vector or passive movement of the wind. Based on the number of trees that showed gummosis at distances ranging from 1 m to > 50 m, it was interpreted that inoculum was prevalent within 1 to 5 m of healthy trees. The highest number of trees with incidence of gummosis was observed at 5 m but decreased thereafter without a definite pattern with increasing distance (Figure 8a). The highest percentage of gummosis incidence followed the same pattern (Figure 8b).

Anatomy of the infected stem

The percentage of parenchyma cells in infected wood was higher and significantly different (P < 0.05) than in healthy wood (Figure 9), as also shown qualitatively in Figure 10. However, the percentage of fiber cells, fiber diameter and fiber length were higher in healthy wood than in infected wood, although statistically they did not show a significant difference (Figure 11).
Gummosis on invasive *Acacia decurrens* after Mount Merapi eruption

Rahayu et al. (2021), *Management of Biological Invasions* 12(4): 886–900, https://doi.org/10.3391/mbi.2021.12.4.08  896

**Figure 9.** The proportion of parenchyma cells in healthy and infected *Acacia decurrens* trees.

**Figure 10.** The parenchyma cells pictured in a) healthy wood; b) infected wood of *Acacia decurrens* trees. Photomicrographs by Januar Mahmud.

**Figure 11.** a) Percentage occurrence of fiber; b) fiber diameter; and c) fiber length of healthy and infected wood of 4-year-old *A. decurrens* trees at MVNP.

**Discussion**

The occurrence and spread of *A. decurrens* as an invasive species in all ecosystems in MNVP after the eruption of Mount Merapi have been documented by several researchers (Lymberty et al. 2014; Okoli et al. 2017). However, the ecological impact of the species on the unique successional processes in the post-eruption ecosystems around Mount Merapi is only poorly known. The pathways of invasion, and factors influencing the invasion success and spread of *A. decurrens* in the MNVP area as well as its impact on native species merit further investigation.
It is apparent from the current study that the fungal pathogen *Ceratocystis fimbriata* is associated with gummosis in *A. decurrens* in MNVP. Based on our observations in the field, we hypothesize that stem holes bored by ambrosia beetles (e.g. *Euwallacea* sp.) facilitated infection by *C. fimbriata*. The beetles may have acted as a vector for the spread of the disease since trees without stem holes were free from *Ceratocystis* infection. As already discussed, *C. fimbriata* is a pathogen of several crop plants and it is widely distributed in the tropics and subtropics (Johnson et al. 2005). It has been recorded on *A. decurrens* in Brazil (Ribeiro et al. 1988). The occurrence of the pathogen on *A. decurrens* in MNVP poses a threat to several crop plants in Indonesia.

In MNVP, although most trees displayed severe gummosis, with 3 to 30 wounds per individual, the trees appeared healthy, with straight stems, green canopy, and good performance in terms of height and diameter. The normal diameter of 5-yr-old healthy *A. decurrens* in South Africa ranged from 9.2 to 9.6 cm (Okoli et al. 2017), while in MVNP the mean diameter of 4-yr-old gummosis affected trees was already 9.3 cm. This suggests that the gummosis had no meaningful adverse effect on the growth of *A. decurrens* in MNVP.

The increased number of parenchyma cells in the infected wood and the healthy growth of trees despite gummosis indicate that the parenchyma cells aid in storage, conversion, and active transport of nutrients in the gummosis-affected trees (Schwarze et al. 2004). In addition, parenchyma cells can also maintain meristematic activity such as wound healing and regeneration of young cells. However, strength properties of infected trees in MNVP are significantly poor compared to healthy trees since the infection affects fiber quality (Crawford et al. 2017). Ribeiro et al. (1988) reported that *A. decurrens* trees affected by *C. fimbriata* in the Capão Bonito region of Brazil exhibited wilting, branch drying, wood splitting and gum exudation that resulted in tree mortality. Nevertheless, trees infected by *C. fimbriata* in MNVP appeared generally healthy, even though strength properties were affected. A possible explanation for the robust growth of gummosis-affected trees in MNVP may be that the *C. fimbriata* strain that affected trees in MNVP is less virulent than the strain that affected the trees in Brazil. Also, the genetic base of the trees may be different between the locations.

The vertical position of gummosis symptoms, which were abundant on the lower part of the stem and comparatively less on the upper part of the stem and stem surrounded by the crown, indicates that wound formation and subsequent infection by *Ceratocystis* typically was initiated from the lower part of the trees. This observation appears to support our hypothesis that ambrosia beetles (e.g., *Euwallacea* sp.), which bore into the xylem of trees, can serve as vectors for *Ceratocystis* spp. (Somasekhara 1999). The frass which clings close to the holes or accumulate on the bark and/or at the base of the tree may also help spread of the pathogen (Paine et al. 1997; Six 2003; Harrington 2005).
According to Jakle et al. (2011) and Lieutier (2004), bark beetles generally oviposit at a location about 90 cm above ground (on pine trees), supporting the idea that boring by beetles tends to occur near the bottom of trees or the lower part of the stem. Also, bark beetles locate mates and attract or repel other individuals of the same species by emitting species-specific pheromones (Sanborn 1996). However, according to Harrington (2005), those insects generally do not attack healthy trees and are not expected to be a common vector. Regardless, the spatial distribution of the trees with gummosis would tend to be clustered, due to the boring beetle occurring on the trees around the infected trees. We did not find clear evidence of clustering, and we cannot say definitively that the trees with gummosis were infected due to the presence of wounds caused by either ambrosia beetles or stressful environmental conditions. The stress caused by the pyroclastic flow could be another reason for the susceptibility of the trees to Ceratocystis.

Although the occurrence of gummosis does not significantly impact growth of the invasive A. decurrens at MVNP, the fungal inoculum of C. fimbriata associated with the gummosis poses a threat to other plants within successional processes of the recovering ecosystem. It appears that the tolerance of A. decurrens to C. fimbriata may allow it to compete more successfully as an invasive species within the MVNP ecosystem.

To conclude, the challenges here are complex, on the one hand the growth and spread of A. decurrens is to be managed and on the other, growth of native species needs to be promoted in the MVNP area by protecting them from the invasive plant and the pathogen that occurs on it. Considering the highly successful establishment and spread of A. decurrens, attempts to manage it and reclaim the land in the MVNP area for regeneration of native species will be an onerous task unless supported by the Government, land managers and the public, alike.

Conclusion

Ceratocystis fimbriata was found associated with gummosis on Acacia decurrens trees that invaded MVNP ecosystems following eruption of the volcano Mount Merapi in Indonesia. The incidence of gummosis on the trees tended to increase over time with most symptoms located on the lower part of the stem. It is hypothesized that the holes bored on the stem of the trees by ambrosia beetles and subsequent infection by C. fimbriata were the main reasons for the occurrence and severity of the disease. Also, the dominance of the species in the region and the probability of the beetle acting as a vector caused the spread of the disease. Though the infection did not significantly affect the growth of the trees, management of invasion and spread by A. decurrens poses a serious challenge to all concerned due to the unparalleled invasion success of the species and the threat from its gummosis pathogen C. fimbriata to native species.
Acknowledgements

We thank the Ministry of Higher Education Indonesia and the Educational Development Fund Universitas Gadjah Mada year 2017 for financial support. Dr. Istiana Prihatini is thanked for kindly sharing part of the laboratory work with the lead author. Thanks are also for Dr. Ned B. Klopfenstein, and Phill Cannon, Research Plant Pathologists, Forest Service, Rocky Mountain Research Station, USA for advice and helpful suggestions, and for Frank H. Koch and Catherine Jarnevich for their excellent reviews.

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