Mechanisms of Resistance in *Eucalyptus* Against Larvae of the Eucalyptus Longhorned Borer (Coleoptera: Cerambycidae)

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ABSTRACT First instars of the eucalyptus longhorned borer, *Phoracantha semipunctata* (F.), were not capable of colonizing bark of vigorous standing trees of two *Eucalyptus* species. The lack of a kino gum reaction after the introduction of larvae into the bark of *E. grandis* Hill ex Maiden and *E. tereticornis* Small strongly indicates that this gum does not play an important role in the initial defense against borer attack. Larvae were also not able to colonize the bark of logs that were maintained at high moisture content but were able to colonize the bark of dry logs and artificially water-stressed trees that had reduced bark moisture content. We propose that bark moisture content plays a critical role in the resistance of eucalyptus trees against colonization by eucalyptus longhorned borer larvae.

KEY WORDS Insecta, *Phoracantha semipunctata*, *Eucalyptus*, plant resistance

ABIOTIC STRESS often renders plants more susceptible to feeding by phytophagous insects (Rhoades 1979, White 1984, Waring & Pitman 1985, Mattson & Haack 1987). Cambium feeders in particular appear to be strongly affected by host stress (Larsson 1989), probably because of their intimate association with host tissues. In its native Australia, the eucalyptus longhorned borer, *Phoracantha semipunctata* (F.), a cambium feeder, is a minor secondary pest that attacks severely stressed or dead eucalyptus trees (Duffy 1963, Pook & Forrester 1984). However, the insect often becomes a devastating pest when accidently introduced into other parts of the world where eucalyptus is planted as an exotic species as in South Africa (Drinkwater 1975, Ivory 1977), Israel (Bytinski-Salz & Neumark 1952), Tunisia (Chararas 1969), Spain (Gonzalez Tirado 1984), and Italy (Cavalcaselle 1980). In these situations, the beetle attacks and kills a much greater proportion of standing eucalyptus than is true in Australia, and it is well documented that drought stress predisposes trees to borer attack (Chararas 1969, Chararas et al. 1971, Drinkwater 1975, Ivory 1977, Scriven et al. 1986).

At present, the eucalyptus longhorned borer is an economically important pest in California that attacks many *Eucalyptus* species (Scriven et al. 1986). The biology of this species in southern California has been reviewed by Hanks et al. (1990). Females oviposit batches of up to 40 eggs in crevices and under loose bark with an average fecundity of 110 eggs per female. The eggs hatch after ≈5 d, and the first instars bore through the bark and then mine along the cambium, also consuming primary xylem on one side and phloem on the other. Larval development requires as little as 2.5 mo. Mature larvae bore into the sapwood, packing the opening to the surface with frass to construct a pupal cell. Pupation lasts ≈15 d. The nocturnal adults emerge from logs by chewing their way out of the pupal cell.

Adult borers are present continuously from early spring through September. The sexes mate on the host, and adult longevity is ≈1 mo. Development from egg to adult requires ≈3 mo during the summer, and there are apparently two asynchronous generations per year.

Eucalyptus species have been introduced into other countries for wood production and as landscape plants because of their rapid growth rate, tolerance of poor quality soils and drought, and because they are resistant to attack by most herbivores outside of Australia (Pryor 1976). Protection of the woody tissues is believed to be through the production of kino, a sticky gum that is an aqueous solution of polyphenolic compounds retained in veins or pockets under the bark (Tippett 1986). It has long been believed that kino flow prevents eucalyptus longhorned borer larvae from penetrating the tissues of healthy trees (Tooke 1935, Bytinski-Salz & Neumark 1952, Hardie 1974, Scriven et al. 1986). Drought stress reduces the production of kino and in this way is presumed to decrease the resistance to borer attack (Chararas 1969, Scriven et al. 1986). However, Chararas (1969) reported that water stress may more directly decrease resistance by reducing the turgidity of the bark, suggesting that sap flow in vigorous trees may prevent the larvae from entering the bark.

In this study, we contrast the relative importance of the kino reaction and bark moisture content on the ability of first-instar *P. semipunctata* to colonize the wood of two *Eucalyptus* species by artificially introducing larvae directly into the bark of standing trees subjected to two moisture treatments. The influence of bark moisture content on larval colonization was further examined by subjecting *Eucalyptus* logs to dry and watered treat-

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ments and determining the survivorship of larvae introduced into the logs.

Materials and Methods

Trials were conducted in 1990 in a research plantation of mixed eucalyptus species at the Moreno Valley field station of the University of California in Riverside County, Calif. All trees were 8 yr old and were planted 3 m apart. The plantation was flood-irrigated biweekly, and the natural incidence of eucalyptus longhorned borer attack was very low among standing trees.

Colonization of Living *E. grandis* Hill ex Maiden Trees by Eucalyptus Longhorned Borer. To document that larvae are not capable of colonizing healthy *E. grandis* trees, 20 first instars were introduced into incisions made in the bark of each of six living trees and in six 1-m-long logs of the same species that had been cut 2 d earlier. These introductions were conducted on 21 August 1990. Two weeks later the bark of trees and logs was dissected to determine the fate of the larvae and to evaluate the kino reaction.

In November 1990, three *E. grandis* trees were felled and cut into 1-m-long logs to study the change in bark moisture content in logs over time. Bark samples were taken before the trees were cut down, and from one log of each tree 1 d after felling.

Effect of *E. grandis* Log Moisture Content on Eucalyptus Longhorned Borer Colonization. To examine the influence of bark moisture content on colonization success, larvae were introduced into two groups of logs, one set that was maintained at high moisture content and a second set that was allowed to dry out naturally. Twelve logs (92.3 ± 3.1 cm long and 39.6 ± 4.4 cm in circumference) were cut from two *E. grandis* on 7 September 1990 and moved to a partially shaded shed on the Riverside campus. About 1 h after felling, six of these logs (which we will refer to as the watered logs) were randomly chosen and were placed standing in 72-liter plastic tubs filled with water to a depth of 10 cm. These logs were leaned against a 0.5-m-high table to keep them standing nearly upright and were interspersed with the six logs (referred to as the dry logs) that stood on the floor. On 9 September 1990, 2 d after felling, 20 first instars were introduced into incisions made in the bark of each log. On 24 October 1990, the logs were dissected to determine the fate of the larvae and to evaluate the kino reaction. At that time, we also removed a 10-cm-square sample of the bark of all logs for measurement of moisture content. Bark samples were also taken from three standing *E. grandis* trees to determine moisture content for comparative purposes.

Effect of Moisture Stress in *E. tereticornis* Small Trees on Eucalyptus Longhorned Borer Colonization. To determine if moisture stress renders standing trees more susceptible to borer colonization, we attempted to limit the water uptake of three *E. tereticornis* study trees by pruning the lateral roots with a backhoe, digging to a depth of 0.5 m at a distance of 0.2 m around all four sides of the bole. Five nontrenched control trees were separated from the trenched trees by at least one tree that was not included in the study. Root pruning was conducted on 20 June 1990. On 9 August, a strong wind left these root-pruned trees leaning at an angle of ≈70°; however, they maintained viable roots throughout the study.

To document the effect of root pruning, a moisture potential reading was taken of five leaves from each study tree with a pressure chamber (PMS Instrument Company, Corvallis, Ore.) on 13 September 1990. These readings were taken at ≈1400 hours (PST), at which time the ambient temperature was 37°C.

On 14 September 1990, 20 first instars were introduced into the bark of all study trees and into three *E. tereticornis* logs that had been cut 2 d earlier. On 25 October 1990, the bark of the study trees and logs was dissected to determine the fate of the larvae and evaluate the kino reaction. A 10-cm-square sample of the bark was also taken from all trees and logs for measurement of moisture content.

Rearing of Larvae and Introduction into Host Tissues. Adult beetles were reared from naturally infested logs and placed in glass aquaria in a 30°C growth chamber, where they were provided with sugar water and honey bee-collected pollen. Because the adult female borers prefer to oviposit under bark, a square of eucalyptus bark that was weighed down on a square of paper toweling was provided. Eggs laid on the paper toweling were collected on a daily basis and were kept in petri dishes until hatching in the same warm room. First instars were stored for a maximum of 2 d at 10°C in petri dishes.

To introduce the larvae into logs and trees, a shallow horizontal incision was cut in the bark with a razor blade at an angle nearly parallel to the bark surface and no more than 3 mm in depth. Incisions in standing trees were made ≈1.5 m from the ground. Five larvae were gently placed into each incision with a damp paint brush.

Determination of Larval Performance. The bark was stripped in the area of the incisions with a hammer and chisel until larval tunnels were encountered or the cambium layer was reached. In the former case, we followed the tunnel to confirm that the larvae were still alive.

Evaluation of Kino Reaction. Kino is very easy to identify by visual inspection because of its dark brown color (Wilkes 1986). The kino reaction of trees and logs was evaluated by the presence or absence of gum under the sites of larval introduction.

Measurement of Bark Moisture Content. Bark samples from trees and logs were placed in plastic bags and frozen on dry ice immediately after sampling. These bark samples were weighed in the

Table 1. Summary of Kruskal-Wallis analyses of percentage survivorship of first-instar eucalyptus longhorned borer introduced into trees and logs of two *Eucalyptus* species

Host species	Treatment	*n*	% Survivorship, $\bar{x}$ ± SEM	*P*
E. grandis	Trees	6	0	0.002
	Logs	6	31 ± 5.9	—
E. grandis	Watered logs	6	0	0.002
	Dry logs	6	39 ± 4.7	—
E. tereticornis	Control trees	5	0	0.04[a]
	Stressed trees	3	20 ± 12	—
	Logs	3	38 ± 1.7	—

[a] Test does not include logs.

Table 2. Summary of Kruskal-Wallis analyses of percentage bark moisture content versus log and tree treatments for two *Eucalyptus* species

Host species	Treatment	*n*	% Moisture $\bar{x}$ ± SEM	*P*
E. grandis	Watered logs	6	60 ± 1.3	0.0039
	Dry logs	6	18 ± 2.7	—
E. grandis	Watered logs[a]	6	60 ± 1.3	0.90
	Standing trees	3	60 ± 0.67	—
E. tereticornis	Control trees	5	58 ± 1.1	0.0253[b]
	Stressed trees	3	55 ± 0.73	—
	Logs	3	26 ± 3.4	—

[a] Same logs as used in the first experiment.
[b] Test does not include logs.

laboratory, freeze-dried, weighed again, and percentage moisture content was calculated using the equation [(wet weight − dry weight)/wet weight * 100].

Statistical Analysis. Differences among mean numbers of larvae colonizing and surviving in each treatment and among mean percentage moisture content of bark in each treatment were tested with a Kruskal-Wallis χ^2 approximation test (Proc NPAR1WAY, SAS Institute 1988).

Results

Colonization of Living *E. grandis* Trees by Eucalyptus Longhorned Borer. First-instar eucalyptus longhorned borer readily began feeding on bark tissue almost immediately after being introduced into bark incisions. An average of 31% of the introduced larvae colonized the *E. grandis* logs, whereas no larvae were found in the living trees (values significantly different; Kruskal-Wallis statistic = 9.47; df = 1,10; $P = 0.002$) (Table 1). There was no evidence that larvae had tunneled to any extent in the living trees, indicating that they had failed to penetrate the cambium and were killed very soon after introduction. There was also no evidence of a kino reaction under any of the bark incisions in the trees or logs.

The most conspicuous difference between tree and log tissues was the moisture content; tree tissues were turgid and green, but those of the logs were quite dry. Bark moisture content of three *E. grandis* trees was 60 ± 0.4% in standing trees compared with 51 ± 1.6% in logs from each tree only 1 d after felling (means significantly different; $F = 23.7$; df = 1, 4; $P = 0.0082$). Thus, at the time that we introduced the larvae into the study logs (2 d after felling), the moisture content of logs was undoubtedly substantially lower than that of standing trees.

Effect of *E. grandis* Log Moisture Content on Eucalyptus Longhorned Borer Colonization. An average of 39% of the larvae colonized and survived in the dry logs, whereas no larvae colonized the watered logs (values significantly different; Kruskal-Wallis statistic = 9.5; df = 1,10; $P = 0.002$) (Table 1). Larvae in the watered logs failed to enter the bark tissues, and there was no evidence of tunneling, again indicating that they died shortly after being introduced. The watered logs remained alive until the end of the study (47 d after the introduction of the larvae), with turgid green bark tissues and green branchlets sprouting along their sides. On the other hand, the tissues of the dry logs were brown and clearly dead. There were significant differences in the water content of the bark of dry logs and watered logs (Kruskal-Wallis statistic = 8.31; df = 1,10; $P = 0.0039$) (Table 2). However, the mean percentage moisture content of the watered logs was not significantly different from that of three standing *E. grandis* trees (Kruskal-Wallis statistic = 0.017; df = 1,7; $P = 0.90$) (Table 2).

Effect of Water Stress in Living *E. tereticornis* Trees on Eucalyptus Longhorned Borer Colonization. A mean of 38% of the introduced larvae colonized and survived in the logs, versus 20% in the root-pruned trees and zero in the control trees (Table 1). The difference between the means for the root-pruned and control trees was significant (Kruskal-Wallis statistic = 3.95; df = 1,6; $P = 0.04$) (Table 1). Among the control trees, an average of 46% of the incisions showed the formation of kino veins versus 29% in the stressed trees (means not significantly different; Kruskal-Wallis statistic = 1.91; df = 1,7; $P = 0.18$). Again, there was no indication that larvae had penetrated the bark of the control trees even in the absence of a kino reaction.

Leaves of root-pruned trees showed a moisture stress nearly 50% higher than that of the control trees (means significantly different; Kruskal-Wallis statistic = 5.0; df = 1,5; $P = 0.025$) (Fig. 1). The mean percentage water content of the bark of the root-pruned trees was also significantly lower than that of the control trees, whereas the water content of the logs was less than half that of the control trees (means for control and root-pruned trees significantly different; Kruskal-Wallis statistic = 5.0; df = 1,6; $P = 0.0253$) (Table 2). That we had successfully affected the resistance of the root-pruned trees to an ecologically significant degree was further demonstrated by the occurrence of natural oviposition by eucalyptus longhorned bor-

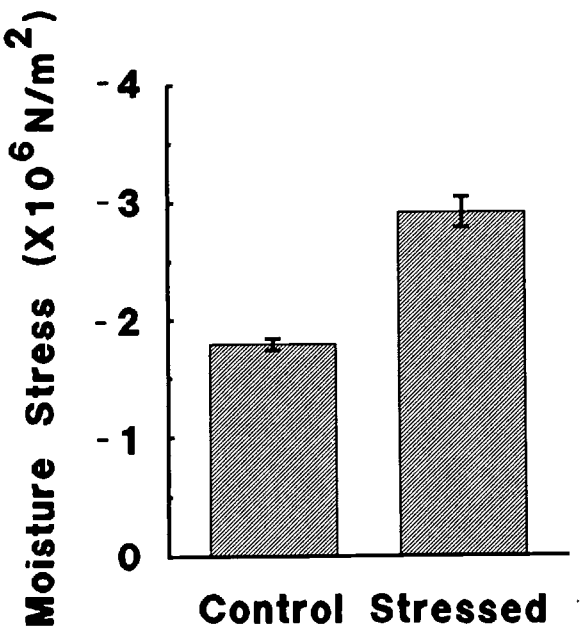

Fig. 1. Leaf moisture stress of three root-pruned ("stressed") trees and five control trees of *E. tereticornis*. Means and standard errors are presented.

ers on two of the stressed trees at the end of the season (November 1990); we found no such oviposition on any of the control trees.

Discussion

We have documented for two *Eucalyptus* species that first-instar eucalyptus longhorned borers are not capable of colonizing the bark and cambium of vigorous standing trees. Contrary to earlier convictions (Tooke 1935, Bytinski-Salz & Neumark 1952, Hardie 1974, Scriven et al. 1986), the absence of a kino reaction in bark incisions made in all standing *E. grandis* and in most of the standing *E. tereticornis* trees strongly indicates that kino did not play a great role in preventing colonization by first instars. The fact that no larvae succeeded in entering the bark of the watered logs (in which there was no indication of a kino reaction) further suggests that some other factor must be responsible for resistance against the borer.

The strength of the kino reaction in *Eucalyptus* trees varies both within species (Skene 1965, Doran 1975, Nelson & Hillis 1978, Nicholls & Matheson 1980) and between species (Nicholls & Griffin 1978; Wilkes 1985, 1986; Tippett 1986). Some *Eucalyptus* species completely lack the ability to produce kino (Nicholls & Pederick 1979). Thus, if kino were the only defence employed by *Eucalyptus* trees against the eucalyptus longhorned borer, the beetle would be expected to commonly attack at least some living trees in its native habitat, but this is not the case. Flows of kino are most often associated with any form of mechanical damage to the bark (Skene 1965, van der Sijde 1978, Old et al. 1986), and the importance of kino may lie in its acting as a barrier zone against invading microbes and fungi (Marks et al. 1981, Tippet et al. 1983, Wilkes 1985) and possibly in sealing bark injuries. Therefore, the occurrence of kino in association with eucalyptus longhorned borer galleries (Hardie 1974, Dale 1985) may be attributable to a later reaction to fungal invasion.

Skene (1965) has shown for *E. obliqua* that the initiation of the kino reaction required at least 2 wk. Because of this time delay, it would appear that kino is very unlikely to act as an initial defense against first instars boring into the bark.

First instars failed to penetrate the cambium of vigorous trees, indicating that the larvae were killed very early. However, they readily passed through the bark of logs or of trees with artificially limited water availability, both of which hosts differed from control trees most conspicuously in the reduced moisture content of their bark tissues. Larvae were not able to colonize *E. grandis* logs that differed from suitable host logs only by application of water that maintained bark moisture content at a level similar to that of the standing trees.

We cannot at this time rule out the possibility that the correlation between eucalyptus moisture stress and susceptibility to borer attack is attributable to other factors such as changes in chemical defenses with stress. However, because these larvae are completely surrounded by the host tissues, it appears that high moisture content in the bark may prevent their penetration by drowning them in situ. When dissecting the bark of vigorous trees, we found moisture content to be so high that it seemed unlikely that larvae tunneling through it would be able to breathe. Similarly, Powell (1982) observed that eucalyptus borer larvae were killed when logs became waterlogged after a heavy rain.

There is evidence for some bark beetles (Webb & Franklin 1978, Wagner et al. 1979, Miller & Berryman 1986) that bark and phloem moisture content alone may prevent colonization of healthy trees. There is also anecdotal evidence that strong sap flow can kill some cerambycid larvae (e.g., Peterson 1948). We propose that the mechanism by which water stress renders eucalyptus trees more suitable as hosts for eucalyptus longhorned borer is through reduction in bark moisture content.

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