Efficacy of 4-allylanisole-based products for protecting individual loblolly pines from *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae)

B.L. Strom, S.R. Clarke, and P.J. Shea

Abstract: We evaluated the effectiveness of 4-allylanisole (4AA) as a protective treatment for loblolly pines threatened by the southern pine beetle, *Dendroctonus frontalis* Zimmermann. Three products were evaluated in combination with two methods that promoted attack of trees by *D. frontalis*. One method used attractive semiochemicals and the other decreased host resistance, both of which are important scenarios for implementing protective treatments of individual trees. Each method promoted mass attack of unprotected control trees, thus providing a statistically verifiable challenge to the candidate protectants. In trees with increased susceptibility, mortality ranged from 63% (untreated) to 77% (4AA applied in paintball formulation), and two products appeared to alter the relative composition of scolytid species that attacked at two heights; however, tree mortality was unaffected. In trees challenged with semiochemical attractants, mortality ranged from 54% (4AA released from vials) to 82% (untreated and paintball application of 4AA). Although 4AA consistently reduces catch of *D. frontalis* in traps, it was not efficacious for protecting individual loblolly pines over a period of 30 or 60 days in this experiment.

Résumé : Nous avons évalué l'efficacité du 4-anisole d'allyle (4AA) pour protéger des pins à encens menacés par le dendroctone méridional du pin, *Dendroctonus frontalis* Zimmermann. Trois produits ont été évalués en combinaison avec deux méthodes favorisant l'attaque des arbres par *D. frontalis*. L'une des méthodes consistait à utiliser des composés semiochimiques d'attraction et l'autre, à diminuer la résistance de l'hôte. Toutes deux constituent des scénarios importants pour l'implantation de traitements visant la protection d'arbres individuels. Chacune d'elles a favorisé l'attaque massive d'arbres témoins non protégés, constituant de ce fait pour les produits de protection à l'étude une épreuve statistiquement vérifiable. Chez les arbres à susceptibilité accrue, la mortalité variait de 63 (arbres non traités) à 77 % (4AA appliqué via des balles de peinture), et deux produits semblaient modifier la composition relative des espèces de scolytidés s'attaquant à deux hauteurs; cependant, la mortalité des arbres est demeurée inchangée. Chez les arbres traités avec des composés semiochimiques d'attraction, la mortalité variait de 54 (émission de 4AA contenu dans des fioles) à 82 % (arbres non traités et application de 4AA via des balles de peinture). Bien que le 4AA ait invariablement réduit les prises de *D. frontalis* dans les pièges, il ne s'est pas montré efficace pour protéger les pins à encens individuels pendant des périodes de 30 et de 60 jours au cours de cette étude.

[Traduit par la Rédaction]

Introduction

In the southeastern U.S.A., the southern pine beetle, *Dendroctonus frontalis* Zimmermann, kills more loblolly pine, *Pinus taeda* L., than any other mortality agent in its range (Drooz 1985). Damage from *D. frontalis* exceeded $900 million in the 30 years from 1960 to 1990 and has worsened with successive outbreaks (Price et al. 1998). In addition to landscape-level mortality in forested areas, *D. frontalis* causes significant mortality of high-value pines, a phenomenon of increasing concern to homeowners and managers of urban forests, recreation areas, streamside management zones, and endangered species habitats (Thatcher et al. 1978; Cameron 1987; Hayes et al. 1996). Thus, the future need for tree protectants will be highly diverse. A recent example is provided by an outbreak of *D. frontalis* centered around Gainesville, Fla. (Alachua Co.). In just 18 months during 1994 and 1995, *D. frontalis* killed over 40 000 trees worth >$10 million on more than 600 properties (Hayes et al. 1996; J. Meeker, USDA For. Serv., Pineville, La., personal communication). The need for a variety of management tools to adequately address the wide range of landowner priorities and values is clearly evident.

Two main scenarios may be identified in which the protection of high-value, individual southern pines is needed: (*i*) trees near sources of *D. frontalis* aggregation semiochemicals (regardless of tree resistance) and (*ii*) weakened or stressed trees, including those struck by lightning (regard-

Received 25 February 2003. Accepted 24 September 2003. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 22 March 2004.

B.L. Strom.[1] USDA Forest Service, Southern Research Station, 2500 Shreveport Hwy., Pineville, LA 71360, U.S.A.
S.R. Clarke. USDA Forest Service, Region 8, Forest Health Protection, 701 N 1st Street, Lufkin, TX 75901, U.S.A.
P.J. Shea. USDA Forest Service, Pacific Southwest Research Station, 1107 Kennedy Place, Suite 8, Davis, CA 95616, U.S.A.

[1]Corresponding author (e-mail: brianstrom@fs.fed.us).

 doi: 10.1139/X03-236

Table 1. Tree (n = 120/district) and stand characteristics of experimental areas in two Ranger Districts (RD) in Alabama, U.S.A.

Characteristic	Bankhead RD	Oakmulgee RD
Diameter at breast height (cm)[a]	29.0±0.4	32.0±0.4
Tree height (m)	19.9±0.3	20.6±0.3
Height of lowest green branch (m)	11.0±0.3	10.0±0.3
Proportion of tree height occupied by live crown	0.46±0.01	0.52±0.01
Basal area (m^2/ha)		
Total	23.1±0.7	22.7±0.4
Pine	14.1±0.5	16.0±0.5

Note: Data are presented as mean±SE. No significant difference was found between Ranger Districts for any characteristic, $P > 0.05$, Kruskal–Wallis test, PROC NPAR1WAY, SAS Institute Inc., Cary, N.C.
[a]Breast height = 1.3 m.

less of *D. frontalis* population levels). Such weakened pines may be characterized by reduced flow of constitutive oleoresin (Hodges and Pickard 1971; Blanche et al. 1985), the only factor consistently equated with increased susceptibility to attack by *D. frontalis* (Hodges et al. 1979; Cook and Hain 1987; Strom et al. 2002). The protection of trees with low resistance offers a somewhat different challenge because they may also be colonized by secondary bark beetles, such as *Ips* spp. (e.g., Anderson and Anderson 1968; Flamm et al. 1993).

There are conventional chemical insecticides that are effective against *D. frontalis* (Hastings and Jones 1976; Billings 1980; Brady et al. 1980; Mizell et al. 1981; Berisford et al. 1982). However, because of environmental concerns with some compounds and a lack of effectiveness of others (e.g., Koerber 1976; Hastings and Coster 1981; Hastings et al. 2001), only lindane and chlorpyrifos (Cyren[R] 4E) are currently registered (by the U.S. Environmental Protection Agency (EPA)) and are effective against *D. frontalis*. Although both are effective in protecting trees from attack (Brady et al. 1980; Berisford et al. 1982), their use in forestry is restricted and neither is in production for forestry-labeled uses. It is noteworthy that permethrin (Astro[R]) and carbaryl (numerous formulations) are labeled for application against bark beetles in forestry, but neither is effective against *D. frontalis* (Hastings and Coster 1981; Hastings et al. 2001; C.W. Berisford, Department of Entomology, University of Georgia, Athens, Ga., unpublished data).

There are no prophylactic semiochemical-based treatments for individual trees currently labeled and demonstrated effective for use against *D. frontalis*. Both 3-methyl-2-cyclohexen-1-one (MCH) and verbenone are registered by the EPA as semiochemical antiaggregants; however, neither is labeled for protection of individual trees. Numerous compounds have antiaggregative activity against conifer-infesting bark beetles, including semiochemicals produced by conspecific and heterospecific beetles, and host and nonhost trees (Borden 1997). The activity of these antiaggregation compounds has been demonstrated predominantly by trapping studies in which the catch of a target species in attractive-baited traps is typically reduced by 40%–80% with the addition of an antiaggregant (e.g., Paine and Hanlon 1991; Salom et al. 1992; Hayes et al. 1994*a*). However, many promising antiaggregants have produced mixed results when applied in actual management settings (Shea et al. 1992; Borden 1993, 1997; Salom and Hobson 1995). Trapping studies, therefore, remain excellent first-step field bioassays for demonstrating activity of antiaggregants, but field experiments that test specific management objectives (e.g., a defined level of efficacy) must be completed before the effectiveness and utility of a potential treatment can be determined.

4-Allylanisole (4AA), a phenylpropanoid found in pine tissues, has been identified as an antiaggregant for *D. frontalis* (Hayes et al. 1994*a*, 1994*b*). Studies have demonstrated that 4AA reduces the number of *D. frontalis* caught in traps baited with aggregation semiochemicals by 35%–63% (Hayes et al. 1994*a*; Strom et al. 1999). In addition, 4AA has shown promise for protecting unattacked pines from *D. frontalis* (Hayes et al. 1994*a*, 1996; Strom et al. 1995). However, these studies were observational, not being designed for nor subjected to statistical analysis and rigorous interpretation. Our objective in this experiment was to follow up on previous observations by rigorously evaluating the efficacy of three 4AA products, currently under development, as protectants of individual pines that were demonstrably threatened by *D. frontalis*.

Materials and methods

Description of sites, trees, and stands

This study was conducted in similar forests in the Bankhead and Oakmulgee Ranger Districts (RD), Bankhead and Talladega National Forests, Ala., respectively (Table 1). Based on catches in baited funnel traps, both locations were believed to have sufficient populations of *D. frontalis* to reliably challenge experimental trees. Population levels subsequently were categorized as outbreak on the Bankhead RD and high on the Oakmulgee RD (Klepzig and Nettleton 1999).

Description of treatments

Initiation of beetle attack was promoted on apparently healthy loblolly pines by two methods. Attractant baiting employed a standard *D. frontalis* bait consisting of (±)-frontalin (100% chemical purity, Phero Tech, Inc., Delta, B.C.), the primary aggregation pheromone of *D. frontalis* (Kinzer et al. 1969), and steam-distilled pine turpentine (Chemcentral, Inc., Doraville, Ga.), consisting predominantly of (1*R*)-(+)-α-pinene (J.D. Reeve, Southern Illinois University, personal communication), a very active synergist to frontalin (Renwick and Vité 1969, 1970). Frontalin was

Table 2. Description of protective treatments, each with 4-allylanisole (4AA) as the active ingredient, evaluated for efficacy in preventing attack by *Dendroctonus frontalis* on loblolly pines in Alabama, U.S.A.

Paintball (Taensa, Inc., Fairfield, Conn.)	20 paintballs/tree applied evenly spaced from ground to base of crown. Each paintball contained 2.25 g of polymer (1.1 g active ingredient). Laboratory elution rate was ~140 mg/d each for ~8 d (L. Ingram, Mississippi State University, personal communication).
Sprayable (3M Canada Co., London, Ont.)	Microencapsulated 20% active ingredient concentrate mixed with water (1:8). Sprayed from ground to height of 8–10 m until bark saturation (~ 6 L/tree, 126 g active ingredient). Capsules ranged in size from 20 to 80 µm, with a mean of 40 µm. Elution rates are unknown, but previous work indicates activity for 3–4 weeks in the field.
Vial (Phero Tech, Inc., Delta, B.C.)	12 sealed vials attached on two sides of tree from ground to 5 m. Each vial contained 10.5 g active ingredient in a polymer formulation that eluted 50–150 mg of 4AA/d at 30 °C.

released at 5.2 mg/d from a packet with two Eppendorf tubes (laboratory release at 23 °C, Phero Tech, Inc.), and turpentine was released at 6–15 mL/d (field release, R. Billings, Texas Forest Service, personal communication) from 120-mL amber bottles (Scientific Specialties, Randallstown, Md.) with cotton wicks (Fisher Scientific Co., Pittsburgh, Pa.). Because placing attractants directly on trees has consistently overwhelmed antiaggregants (P.J. Shea, unpublished results), attractants were placed on stakes (approx. 1.5 m tall), 0.25–1.0 m from study trees.

The other method utilized infusions of sodium *N*-methyldithiocarbamate (MS) (Woodfume®; Osmose, Inc., Buffalo, N.Y.) plus dimethyl sulfoxide (DMSO) (MS + DMSO) applied into cuts made with a hatchet into the sapwood and spaced ~5 cm apart around the tree's circumference ~0.5 m above ground (Roton 1987). A cotton wick or cellulose sponge loaded with ~10 mL of MS + DMSO (mixed 4:1) was inserted into each cut. This method reduces resin yield to nearly zero after 1–2 weeks (B.L Strom, unpublished results) and causes pines to become highly susceptible to *D. frontalis* attack after 2–3 weeks (Roton 1987; Hayes et al. 1994*b*; Miller et al. 1995). Therefore, MS + DMSO infusion was done 1 week prior to all other treatments. This treatment widens the scope of evaluation by mimicking, in some respects, trees of low resistance, which are important potential targets for protection from attack by *D. frontalis* in the southeastern U.S.A. (Hayes et al. 1996).

The protective treatments consisted of three formulations of 4AA (Table 2). A polymer formulation, delivered in paintballs, was tested at the request of the manufacturer (Taensa, Inc., Fairfield, Conn.). Paintballs were applied from the ground to the base of the crown in a spiral pattern using a paintball gun following the manufacturer's recommendation. The duration of release of 4AA from paintballs in the field is unknown. The second product tested was a microencapsulated sprayable formulation (3M Canada Co., London, Ont.). It was obtained as a 20% liquid concentrate, mixed with water (J.L. Hayes 1998[2]), and sprayed onto the bole of trees using a 76-L hydraulic sprayer mounted on the back of a four-wheeled all terrain vehicle. Preliminary trials suggested that this treatment lasts 3–4 weeks in the field, so trees were resprayed at 30-d intervals, because this is a likely minimum interval for practical use. A different polymer formulation, delivered from within sealed vials, was included as a standard because its elution rate and >60-d effective duration had been previously determined (Phero Tech, Inc.; J.L. Hayes 1998[2]). Treatment with 12 vials per tree provided a total elution rate of ~1680 mg/d for the duration of the experiment, at least comparable to the rates reported as effective in previous studies (Hayes et al. 1994*a*; J.L. Hayes 1998[2]).

Treatments were installed during the weeks of 4 and 11 May 1999 on the Bankhead and Oakmulgee RDs, respectively, early enough to ensure that dispersing *D. frontalis* were present. In each District, 120 loblolly pines (>20 cm diameter at breast height (DBH)) were selected along roads with a minimum distance of 100 m between trees. The eight treatments were arranged in a 2 × 4 (2 challenging agents × 3 protective treatments plus unprotected control) factorial design. Each tree received a randomly assigned treatment, with treatments replicated 15 times in each RD.

Evaluation of treatments

All tested 4AA products were developed as treatments to prevent tree mortality from *D. frontalis*. Therefore, mortality of trees was our dependent variable and assumed if colonization occurred — this was characterized by numerous fresh pitch tubes on the bole, boring dust at the base of the tree, and when possible, crown fading. Successful colonization by *D. frontalis* assures the death of the host, but foliage may not fade for 2–6 weeks in the spring and early summer (Thatcher and Pickard 1964).

Trees were inspected one to two times weekly and, if successful attack had occurred, attractant baits were removed to limit the spread of infestations beyond the target tree. Out of concern for *D. frontalis* spot development, some target trees with numerous attacks had their attractive baits removed prior to successful beetle colonization. When this was discovered, baits were replaced (<1 week) or trees were excluded from analyses (n = 14). Although the study was designed to run at least 30 days, if a target tree was successfully colonized and the infestation was spreading, all attacked trees were felled to prevent further expansion of the infestation.

Efficacy was evaluated using a binomial statistical test with a priori parameters taken from previous work (Shea et

[2] J.L. Hayes. 1998. Progress report to the Forest Health Technology Enterprise Team, 12 February 1998. USDA Forest Sevice, Morgantown, W. Va.

Table 3. Experiment-wide results when 4-allylanisole (4AA) was employed as a protectant of individual loblolly pines treated with either of two methods to initiate attack by *Dendroctonus frontalis*.

Treatment	*n*	No. killed	% killed	95% C.L[a]	% with *D. frontalis*[b]
Semiochemical attractant with:					
No 4AA	28	23	82	64%–93%	—
4AA paintball	28	23	82	64%–93%	—
4AA vial	26	14	54	34%–73%	—
4AA spray	27	16	59	40%–78%	—
MS + DMSO with:[c]					
No 4AA	30	19	63	44%–80%	74
4AA paintball	30	23	77	58%–90%	65
4AA vial	29	21	72	54%–87%	33
4AA spray	28	20	71	52%–87%	40
Total	226	159	70	—	52

[a]Percentage of trees included in 95% confidence limit (C.L.) (or interval) for tree mortality.
[b]Mean number of trees with *D. frontalis* in at least two of four samples taken at 1.5 and 3 m on two sides of each tree (four samples per tree). Statistical analysis by *G* test produced a significant overall treatment effect ($G = 9.2$; critical value of $\chi^2 = 7.815$, degrees of freedom = 3, $\alpha = 0.05$), with the most homogeneous groups being (MS only, MS paintball) and (MS vial, MS spray). The sample size was 19–23 trees per treatment.
[c]Sodium *N*-methyldithiocarbamate (MS) + dimethyl sulfoxide (DMSO).

al. 1984; Haverty et al. 1996, 1998). This methodology requires that two criteria be met to demonstrate effective tree protection: (*i*) trees must be demonstrably challenged and (*ii*) trees must not die. To meet these criteria, at least 60% (18/30) of control trees (without 4AA, across districts) had to be mass attacked to assume a sufficient challenge of the study tree population. Once this criterion had been met, evaluation of efficacy proceeded. Treatments were considered efficacious if at least 80% (24/30) of treated trees were not successfully colonized and therefore survived. This evaluation provided a binomial statistical test with the following parameters: H_0: $P = 0.90$, H_1: $P = 0.70$, $\alpha \cong 0.05$ and power > 0.80 based on a sample size of 30–35 trees. That is, the null hypothesis (H_0) is that survival is ≥90%, while the alternative hypothesis (H_1) is that that survival is ≤70%. In our case, H_0 is rejected and treatments are considered inefficacious if at least 7 of 30 trees die. Alternatively, H_0 may not be rejected and treatments thus considered efficacious if 6 or fewer trees (of 30) die. Shea et al. (1984) provide more details of this method for binomial evaluation of treatment efficacy. Our evaluations were made at either 30 or 60 d post-treatment, depending on when the 60% mortality criterion for control trees was satisfied. Protection for <30 d was not considered to be operationally or commercially acceptable.

Because trees treated with MS + DMSO may be attacked by secondary bark beetles in addition to *D. frontalis* (a situation that also occurs with lightning-struck trees), these trees were sampled for the presence of *D. frontalis*. Bark samples were removed at 1.5 and 3 m on opposite sides of each moribund tree and inspected for *D. frontalis*. Treatment differences in the presence–absence of *D. frontalis* in bark samples were evaluated with *G* tests (Sokal and Rohlf 1995).

Results

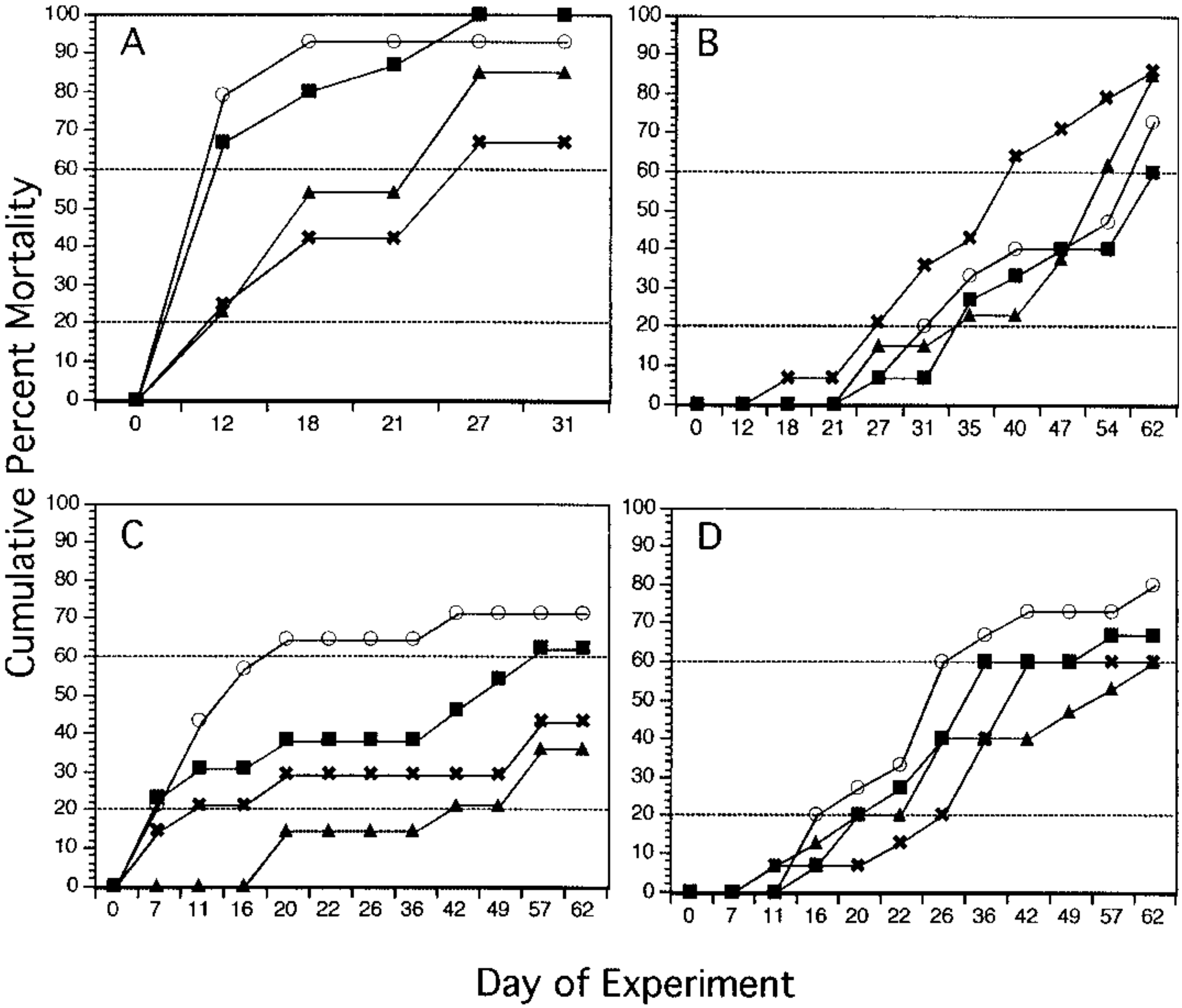
The 60% level of mortality was quickly reached in <30 d in the aggregation pheromone treatments on the Bankhead RD (Fig. 1A), so this experiment was evaluated after 30 d. The target mortality rate took longer to achieve in the MS + DMSO treatments on the Bankhead RD and in both challenge treatments on the Oakmulgee RD (Figs. 1B–1D), so these experiments were evaluated after 60 days.

Using our criteria, none of the 4AA treatments was efficacious in preventing tree mortality Figs. 1A–1D). The 20% mortality allowed for treatment efficacy was exceeded before or just slightly after the control-tree target mortality was reached in all cases, indicating that sufficient beetle pressure was present and that treatments were ineffective in the face of this pressure. Mortality of trees challenged with semiochemical attractants ranged from a high of 100% (Bankhead RD, control trees) to a low of 36% (Oakmulgee RD, 4AA spray). Mortality of trees treated with MS + DMSO ranged from a high of 86% (Bankhead RD, 4AA vial) to a low of 60% (Bankhead RD, control; Oakmulgee RD, 4AA spray).

Experiment-wide results were similar (Table 3). Across treatments, mortality was observed in 159 of 226 trees (70%). In treatments challenged by attractant semiochemicals, tree mortality was as follows: control trees, 82% (23/28); 4AA paintball, 82% (23/28); 4AA vial, 54% (14/26); 4AA spray, 59% (16/27). In trees challenged by MS + DMSO, the experiment-wide mortality was as follows: control trees, 63% (19/30); 4AA paintball, 77% (23/30); 4AA vial, 72% (21/29); 4AA spray, 71% (20/28).

Although 4AA treatments were not efficacious for tree protection, trees treated with MS + DMSO showed a significant effect of the 4AA treatments on the presence of *D. frontalis* (Table 3). Control trees had 74% of samples with *D. frontalis* present, 4AA paintball trees had 65%, 4AA vial trees had 33%, and 4AA spray trees had 40%. Control and paintball treatments separated statistically as one group, and the vial and spray trees separated as another group ($G = 9.2$; critical value of $\chi^2 = 7.815$, degrees of freedom = 3, $\alpha = 0.05$). Thus, the vial and sprayable 4AA treatments signifi-

Fig. 1. Cumulative percent mortality of loblolly pines baited with a standard *Dendroctonus frontalis* attractant (Fig. 1A, Bankhead Ranger District (RD); Fig. 1C, Oakmulgee RD) or treated with sodium *N*-methyldithiocarbamate (MS) and dimethyl sulfoxide (DMSO) (Fig. 1B, Bankhead RD; Fig. 1D, Oakmulgee RD) and treated with 4-allylanisole (4AA) in one of three formulations. Closed squares represent controls (no 4AA); open circles represent 4AA polymer formulation applied in paintballs; x's represent 4AA polymer formulation eluted from vials; closed triangles represent 4AA microencapsulated (sprayable) formulation. The dashed line at 60% cumulative mortality is the level of control tree mortality necessary for a valid test; the dashed line at 20% cumulative mortality is the maximum allowable mortality for treatments to be considered efficacious.



cantly reduced the presence of *D. frontalis* in trees challenged with MS + DMSO.

Discussion

This is the first study to evaluate the ability of 4AA products to protect individual loblolly pines from *D. frontalis* using an experimental design that was sufficient for statistical evaluation. We selected 4AA products for evaluation using two criteria. The vial treatment was selected because it was known to elute 4AA at or above rates previously considered effective for the duration of the experiment (Hayes et al. 1994*a*, 1996; J.L. Hayes 1998[2]). The paintball and sprayable formulations were selected because they were being considered for submission to EPA for registration as pesticides, although less is known about their elution properties. We created and evaluated trees likely to be attacked by *D. frontalis*, under two scenarios relevant to managers, for three reasons: (*i*) an adequate number of attacked control trees (60%) are needed to be confident that treatments are sufficiently challenged to demonstrate protection of trees from attack; (*ii*) protective treatments are most necessary and most likely to be applied when beetle pressure is high or when trees lack the capacity to resist attack and therefore should be tested under such conditions; and (*iii*) comparisons can be made with conventional chemical insecticides that are competing products and are known to be efficacious under severe pressure from *D. frontalis*. Under these conditions, none of the 4AA treatments that we applied provided effective protection.

Our procedures and efficacy criteria were less stringent than those used in many previous studies. We recognize that our allowable level of mortality for efficacy, set at 20%, may be higher than a typical homeowner or property manager would accept and is higher than that allowed in insecticide evaluations with *D. frontalis*. For example, Mizell et al. (1981) required 100% mortality of control trees against which fenitrothion could be evaluated as a tree protectant. We also did not place semiochemical baits directly on trees or at the height at which first *D. frontalis* attacks are concentrated (3–4 m; Coster et al. 1977; Dixon and Payne 1979). In previous studies, attractants were placed directly on trees or bolts, and the experiments were conducted in or near active infestations of *D. frontalis* (Brady et al. 1980; Mizell et al. 1981; Berisford et al. 1982). We selected less stringent criteria to follow established protocols for evaluating tree protectants against bark beetles (Shea et al. 1984; Haverty et al. 1996, 1998) and to increase the probability that potentially useful treatments (e.g., those that may be useful with additional "tweaking") would not be excluded from further consideration.

The relationship between trapping and tree protection studies with *D. frontalis* is unevaluated, and attempts with other scolytids to extrapolate results with traps to the protection of individual trees have met with mixed results (Borden 1997; P.J. Shea, USDA Forest Service, Davis, Calif., unpublished results). One obvious potential reason for this is that dissuading a portion (>35%) of the population of beetles is simply not good enough to provide long-term protection of a suitable resource. Previous studies have found that traps baited with an attractant and 4AA have caught 35%–63% of the number of *D. frontalis* as attractant-only traps (Hayes et al. 1994*a*; Strom et al. 1999). In this study, 82% of trees challenged with attractive semiochemicals and without 4AA were killed, while the best 4AA treatment saw 54% killed. A difference of 28% is less than the typical difference observed in trapping numbers and emphasizes the difference between evaluation techniques. Resource protection studies must be done to determine efficacy; it cannot be extrapolated from laboratory or trapping studies.

In experimental trees with reduced resistance (MS + DMSO trees), two of the 4AA products (the spray and vial treatments) decreased the number of bark samples in which *D. frontalis* was found, perhaps suggesting some level of deterrence. Despite this, the trees were killed by bark beetles. Though trapping studies have demonstrated that 4AA reduces catch to a variety of bark beetles (Hayes and Strom 1994; Joseph et al. 2001), Werner (1972) suggests that 4AA is attractive to *Ips grandicollis* (Eichhoff) males (the pioneering sex). Whether or not attraction of 4AA to less aggressive scolytids (like *I. grandicollis*) played a role in its failure to protect trees in this experiment was not evaluated, but remains a possibility. It is apparent, therefore, that the choice of tree protection method — even if efficacious, behaviorally based products are found for a particular species — must consider the evaluation of products under scenarios relevant to their use.

Acknowledgements

We thank personnel from the Bankhead and Oakmulgee Ranger Districts (USDA Forest Service, National Forests of Alabama), especially John Creed (Bankhead) and Joe Fowler (Oakmulgee) for their help and generosity with this study. Chris Steiner (USDA Forest Service, Southern Research Station) provided help with all aspects of the research. Billy Bruce and Roger Menard (USDA Forest Service, R8 Forest Health Protection) helped with fieldwork. Jim Baldwin (USDA Forest Service, Pacific Southwest Research Station) provided valuable statistical consultation. Taensa, Inc. (now Earth BioSciences, Inc.) provided partial funding. Useful comments on earlier drafts of the manuscript were provided by numerous reviewers.

References

Anderson, N.H., and Anderson, D.B. 1968. *Ips* bark beetle attacks and brood development on a lightning-struck pine in relation to its physiological decline. Fla. Entomol. **51**: 23–30.

Berisford, C.W., Turnbow, R.H., Jr., and Brady, U.E. 1982. Selective application of insecticides for prevention of southern pine beetle attack. J. Econ. Entomol. **75**: 458–461.

Billings, R.F. 1980. Direct control. *In* The southern pine beetle. *Edited by* R.C., Thatcher, J.L. Searcy, J.E. Coster, and G.D. Hertel. USDA For. Serv. Sci. Educ. Admin. Tech. Bull. 1631. pp. 178–192.

Blanche, C.A., Hodges, J.D., and Nebeker, T.E. 1985. Changes in bark beetle susceptibility indicators in a lightning-struck loblolly pine. Can. J. For. Res. **15**: 397–399.

Borden, J.H. 1993. Strategies and tactics for the use of semiochemicals against forest insect pests in North America. *In* Pest management: biologically based technologies. *Edited by* R.D. Lumsden and J.L. Vaughn. American Chemical Society, Washington, D.C. pp. 265–279.

Borden, J.H. 1997. Disruption of semiochemical-mediated aggregation in bark beetles. *In* Insect pheromone research, new directions. *Edited by* R.T. Carde and A.K. Minks. Chapman & Hall Inc., New York. pp. 421–438.

Brady, U.E., Berisford, C.W., Hall, T.L., and Hamilton, J.S. 1980. Efficacy and persistence of chlorpyrifos, chlorpyrifos-methyl, and lindane for preventive and remedial control of the southern pine beetle. J. Econ. Entomol. **73**: 639–641.

Cameron, R.S. 1987. Southern pine bark beetles in the urban environment. J. Arboric. **13**: 145–151.

Cook, S.P., and Hain, F.P. 1987. Susceptibility of trees to southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). Environ. Entomol. **16**: 9–14.

Coster, J.E., Payne, T.L., Hart, E.R., and Edson, L.J. 1977. Aggregation of the southern pine beetle in response to attractive host trees. Environ. Entomol. **6**: 725–731.

Dixon, W.N., and Payne, T.L. 1979. Sequence of arrival and spatial distribution of entomophagous and associate insects on southern pine beetle-infested trees. Tex. Agric. Exp. Stn. Bull. MP-1432.

Drooz, A. 1985. Insects of eastern forests. USDA For. Serv. Misc. Publ. 1426.

Flamm, R.O., Pulley, P.E., and Coulson, R.N. 1993. Colonization of disturbed trees by the southern pine bark beetle guild (Coleoptera: Scolytidae). Environ. Entomol. **22**: 62–70.

Hastings, F.L., and Coster, J.E. (*Editors*). 1981. Field and laboratory evaluations of insecticides for use against sourthern pine beetle. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SE-21.

Hastings, F.,L. and Jones, A.S. 1976. Contact toxicity of 29 insecticides to southern pine beetle adults. USDA For. Serv. Res. Note SE-245.

Hastings, F.L., Holsten, E.H., Shea, P.J., and Werner, R.A. 2001. Carbaryl: a review of its use against bark beetles in coniferous forests of North America. Environ. Entomol. **30**: 803–810.

Haverty, M.I., Shea, P.J., and Wenz, J.M. 1996. Metasystox-R, applied in Mauget injectors, ineffective in protecting individual ponderosa pines from western pine beetles. U.S. Dep. Agric. For. Serv. Pac. Southwest Res. Stn. Res. Note PSW-RN-420.

Haverty, M.I., Shea, P.J., Hoffman, J.T., Wenz, J.M., and Gibson, K.E. 1998. Effectiveness of esfenvalerate, cyfluthrin, and carbaryl in protecting individual lodgepole pines and ponderosa pines from attack by *Dendroctonus* spp. U.S. Dep. Agric. For. Serv. Pac. Southwest Res. Stn. Res. Pap. PSW-RP-237.

Hayes, J.L., and Strom, B.L. 1994. 4-Allylanisole as an inhibitor of bark beetle (Coleoptera: Scolytidae) aggregation. J. Econ. Entomol. **87**: 1586–1594.

Hayes, J.L., Strom, B.L., Roton, L.M., and Ingram, L.L., Jr. 1994*a*. Repellent properties of the host compound 4-allylanisole to the southern pine beetle. J. Chem. Ecol. **20**: 1595–1615.

Hayes, J.L., Ingram, L.L., Jr., Strom, B.L., Roton, L.M., Boyette, M.W., and Walsh, M.T. 1994*b*. Identification of a host compound and its practical applications: 4-allylanisole as a bark beetle repellent. *In* Proceedings of the 4th Southern Station Chemical Sciences Meeting, Starkville, Miss., 1–2 February 1994. *Edited by* J. Vozzo. U.S. Dep. Agric. For. Serv. South. For. Exp. Stn. Gen. Tech. Rep. SO-104. pp. 69–79.

Hayes, J.L., Meeker, J.R., Foltz, J.L., and Strom, B.L. 1996. Suppression of bark beetles and protection of pines in the urban environment: a case study. J. Arboric. **22**: 67–74.

Hodges, J.D., and Pickard, L.S. 1971. Lightning in the ecology of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). Can. Entomol. **103**: 44–51.

Hodges, J.D., Elam, W.W., Watson, W.F., and Nebeker, T.E. 1979. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks. Can. Entomol. **111**: 889–896.

Joseph, G., Kelsey, R.G., Peck, R.W., and Niwa, C.G. 2001. Response of some scolytids and their predators to ethanol and 4-allylanisole in pine forests of central Oregon. J. Chem. Ecol. **27**: 697–715.

Kinzer, G.W., Fentiman, A.F., Jr., Page, T.F., Jr., Foltz, R.L., Vité, J.P., and Pitman, G.B. 1969. Bark beetle attractants: identification, synthesis and field bioassay of a new compound isolated from *Dendroctonus*. Nature (London), **221**: 477–478.

Klepzip, K.D., and Nettleton, W.A. 1999. SPB Update [online]. USDA Forest Service, Southern Research Station, Research Work Unit 4501. Available from http://www.srs.fs.usda.gov/4501/june_99.htm [cited August 2003; updated December 2003].

Koerber, T.W. (*Compiler*). 1976. Lindane in forestry … a continuing controversy. Berkeley, CA. U.S. Dep. Agric. For. Serv. Pac. Southwest For. Range Exp. Stn. Gen. Tech. Rep. PSW-14.

Miller, M.C., Kinn, D.N., and Parresol, B.R. 1995. Effect of sodium *N*-methyldithiocarbamate with dimethyl-sulfoxide on southern pine beetle (Col., Scolytidae) development: results of initial field tests. J. Appl. Entomol. **119**: 55–61.

Mizell, R.F., III, Neel, W.W., and Lashomb, J.H. 1981. Field evaluation of fenitrothion for prevention of tree mortality from southern pine beetle attack. J. Econ. Entomol. **74**: 30–32.

Paine, T.D., and Hanlon, C.C. 1991. Response of *Dendroctonus brevicomis* and *Ips paraconfusus* (Coleoptera: Scolytidae) to combinations of synthetic pheromone attractants and inhibitors verbenone and ipsdienol. J. Chem. Ecol. **17**: 2163–2176.

Price, T.S., Doggett, C., Pye, J.M., and Smith, B. 1998. A history of southern pine beetle outbreaks in the southeastern United States. Georgia Forestry Commission, Atlanta, Ga.

Renwick, J.A.A., and Vité, J.P. 1969. Bark beetle attractants: mechanism of colonization by *Dendroctonus frontalis*. Nature (London), **224**: 1222–1223.

Renwick, J.A.A., and Vité, J.P. 1970. Systems of chemical communication in *Dendroctonus*. Contrib. Boyce Thompson Inst. **24**: 283–292.

Roton, L.M. 1987. Promising treatment for southern pine beetles. American Papermaker, **50**: 30–32.

Salom, S.M., Billings, R.F., Upton, W.W., Dalusky, M.J., Grosman, D.M., Payne, T.L., Berisford, C.W., and Shaver, T.N. 1992. Effect of verbenone enantiomers and racemic *endo*-brevicomin on response of *Dendroctonus frontalis* (Coleoptera: Scolytidae) to attractant-baited traps. Can. J. For. Res. **22**: 925–931.

Salom, S.M., and Hobson, K.R. (*Editors*). 1995. Application of semiochemicals for management of bark beetle infestations — proceedings of an informal conference. Annual Meeting of the Entomological Society of America, December 12–16, 1993, Indianapolis, Ind. U.S.D.A. For. Serv. Gen. Tech. Rep. INT-GTR-318.

Shea, P.J., Haverty, M.I., and Hall, R.C. 1984. Effectiveness of fenitrothion and permethrin for protecting ponderosa pine trees from attack by the western pine beetle. J. Ga. Entomol. Soc. **19**: 427–433.

Shea, P.J., McGregor, M.D., and Daterman, G.E. 1992. Aerial application of verbenone reduces attack of lodgepole pine by mountain pine beetle. Can. J. For. Res. **22**: 436–441.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. 3rd ed. W.H. Freeman and Co., New York.

Strom, B.L., Goyer, R.A., and Hayes, J.L. 1995. Naturally occurring compound can protect pines from the southern pine beetle. La. Agric. **38**: 5–7.

Strom, B.L., Roton, L.M., Goyer, R.A., and Meeker, J.R. 1999. Visual and semiochemical disruption of host finding in the southern pine beetle. Ecol. Appl. **9**: 1028–1038.

Strom, B.L., Goyer, R.A., Ingram, L.L., Jr., Boyd, G.D.L., and Lott, L.H. 2002. Oleoresin characteristics of progeny of loblolly pines that escaped attack by the southern pine beetle. For. Ecol. Manage. **158**: 169–178.

Thatcher, R.C., and Pickard, L.S. 1964. Seasonal variations in activity of the southern pine beetle in east Texas. J. Econ. Entomol. **57**(6): 840–842.

Thatcher, R.C., Coster, J.E., and Payne, T.L. 1978. Southern pine beetles can kill your ornamental pine. USDA Combined Forest Pest Research and Development Program, Southern Pine Beetle Handbook, Home and Garden Bulletin 226.

Werner, R.A. 1972. Aggregation behaviour of the beetle *Ips grandicollis* in response to host-produced attractants. J. Insect Physiol. **18**: 423–437.