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Susceptibility of Honeylocust Cultivars to *Thyronectria austro-americana* and Response of *Agrilus* Borers and Bagworms to Infected and Non-infected Trees[1]

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Abstract

Six cultivars of honeylocust, *Gleditsia triacanthos* L., were inoculated with the canker fungus *Thyronectria austro-americana* to test the hypothesis that trees stressed by *Thyronectria* are rendered more attractive to wood borers, or more suitable as hosts for the bagworm, *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae). Relative susceptibility of cultivars to the fungus, and seasonal flight activity of associated borers were also monitored. Cultivars 'Sunburst,' 'Shademaster,' and 'Rubylace' developed the largest cankers; 'Imperial' was variable, and 'Skyline' and 'Trueshade' were somewhat less susceptible. Adults of four species of *Agrilus* borers (Coleoptera: Buprestidae) were abundant on honeylocust. Beetles were active from late May until August. Adult borers were attracted equally to infected and non-infected trees, but borers apparently failed to colonize trees of either type. Levels of soluble protein were higher in foliage of diseased trees, but growth and survival of bagworms were similar for both treatments. This study did not support a close relationship between *Thyronectria* canker disease of honeylocust and predisposition to wood borers, at least on relatively vigorous hosts.

Index words: Buprestidae, *Gleditsia triacanthos, Thyridopteryx ephemeraeformis*, resistance, plant stress, canker fungus, *Thyronectria austro-americana.*

Species used in this study: Honeylocust (*Gleditsia triacanthos* L.).

Significance to the Nursery Industry

Thyronectria canker disease of honeylocust causes significant losses of nursery and landscape trees. Honeylocust is also susceptible to injury from flatheaded wood borers (*Agrilus* spp.) and bagworms, and it has been suggested that these pests and other insects may preferentially attack trees that are stressed by disease, drought, or other factors. We evaluated relative susceptibility of six honeylocust cultivars to Thyronectria canker, and monitored the seasonal flight activity of associated wood borers in Kentucky. We also tested the hypothesis that infection with Thyronectria predisposes trees to attack by borers or bagworms. Cultivars 'Sunburst,' 'Shademaster,' and 'Rubylace' developed the largest Thyronectria cankers, 'Imperial' was intermediate, and 'Skyline' and 'Trueshade' were somewhat less susceptible. Four species of *Agrilus* borers were attracted to honeylocust. Adults were active from late May until August, but most abundant in June and July. Trees inoculated with Thyronectria did not attract more borers than non-infected trees, nor were they more suitable for growth or survival of bagworms. Borers failed to infest either infected or non-infected trees in this study. These results suggest that alleviation of tree stress may encourage remission of Thyronectria canker symptoms and discourage colonization by borers.

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Introduction

Honeylocust (*Gleditsia triacanthos* L.), has become a popular landscape and shade tree since the development of thornless and fruitless cultivars in the 1950s (25). Endemic to the eastern United States, honeylocust is regarded as relatively pest free in its natural habitat, but suffers severe disease and insect problems in urban settings (13, 22).

Thyronectria canker, caused by the fungus *Thyronectria austro-americana* (Spegazzini) Seeler (Hypocreales: Hypocreaceae), has been associated with widespread decline and mortality of honeylocust (4, 11). This aggressive pathogen causes elongate, sunken bark lesions on trunks and branches, often followed by girdling, wilting, and death of infected limbs (4, 11). Environmental stresses are thought to predispose trees to infection, and wounds caused by pruning, sunscald, or insects are apparently necessary for entry of the fungus (4). Honeylocust cultivars differ in susceptibility to *T. austro-americana*, although ranking of particular cultivars has varied somewhat in different geographic regions (12, 17).

Honeylocusts are also attacked by insect pests, including the honeylocust plant bug, *Diaphnocorus chlorionis* (Say), bagworm, *Thyridopteryx ephemeraeformis* (Haworth), mimosa webworm, *Homadaula anisocentra* Meyrick, and others (13). Three species of wood-boring *Agrilus* beetles (Coleoptera: Buprestidae) are known to colonize honeylocust as larvae (9, 10), but information about their seasonal flight activity is limited.

Outbreaks of phytophagous insects often follow periods of biotic or environmental stress (16, 24). Many wood borers, including *Agrilus* spp., selectively attack and colonize trees that have been weakened by drought, defoliation, or other stress (2, 5, 15, 18). Attraction of borers to diseased trees has been shown in several studies (6, 7, 21, 23). Increased susceptibility of stressed trees has been attributed to improved quality of plant tissues as a resource for herbivores, either through increased concentrations of limiting nutrients, especially soluble protein (24), or by decreases in chemical defenses (19). However, the mechanisms by which stress may affect plant suitability for wood-boring or foliar-feeding insects are poorly understood.

Emergence holes or larval galleries made by *Agrilus* spp. are often associated with Thyronectria cankers (4, 14, author's observations); however, whether or not infection by *T. austro-americana* predisposes honeylocust to attack by borers or other insects is not known. We tested the hypothesis that *Agrilus* wood borers are attracted to and selectively colonize Thyronectria-infected trees, and compared growth and survival of the bagworm, a foliar-feeding caterpillar, on infected and non-infected trees. We also compared susceptibility of six honeylocust cultivars to *T. austro-americana*, and determined seasonal flight activity of *Agrilus* wood borers associated with honeylocust in central Kentucky.

Materials and Methods

Susceptibility of cultivars to Thyronectria canker. Twenty trees [1.5-2.1m (5-7 ft) tall, 2.5-3.5 cm (1-1.4 in) diam] of each of six honeylocust cultivars, 'Skyline,' 'True-shade,' 'Shademaster,' 'Imperial,' 'Rubylace,' and 'Sunburst,' were obtained from J. F. Schmidt & Son Co., Boring, OR. The trees were planted on March 14, 1988 at the corporate office grounds of Ashland Oil, Inc. in Lexington, KY. Soil type was a silty clay loam (38% clay, 50% silt, 12% sand) with pH = 5.54. Trees were planted on 4.6 m (15 ft) centers in a randomized complete block with 10 replications and duplicate trees of each cultivar within each block. An isolate of *T. austro-americana* was obtained from naturally infected honeylocust saplings in Lexington. Inoculum was produced by growing the fungus on potato dextrose agar in petri dishes at 24°C (75°F) for 7 to 10 days. One tree of each cultivar within each block was randomly selected for inoculation. Tree stems were inoculated on the northeast side at 1.0 m (3.3 ft) height by placing fungal-agar plugs into 9 mm diam (0.35 in) cork borer wounds, one wound per tree, on June 1, 1988. Wounds were made up to the depth of the vascular cambium. The control treatment consisted of sterile agar plugs placed into similar wounds on other trees. The inoculation sites were wrapped with tape to prevent drying. The tape was removed after 2 weeks. Trees were thoroughly watered [4 liters/tree (1 gal/tree)] on June 8 and July 8. Manual control of weeds was the only other tree maintenance activity applied to the plot.

Length and width of cankers were measured and the number of conidial stromata counted in January and September 1989, 7 and 15 months after inoculation. Size of cankers was estimated as the area of an ellipse of equivalent length and width. Wound closure (width of callus tissue measured from edge of wound) and tree diameter [0.7 m (28 in) height] were also determined after 7 months. Data from infected trees were analyzed by two-way analysis of variance (ANOVA) for effects of cultivar and replicate, and means were separated by Fisher's least significant difference (LSD) test at $P = 0.05$.

Attraction of borers to infected vs. non-infected trees. To test the hypothesis that adult Buprestidae would be differentially attracted to diseased trees, a second planting was established so that capture of females on sticky traps would not interfere with potential egg-laying and colonization of trees in the main plot. Ten additional trees of each of the four cultivars 'Skyline,' 'True-shade,' 'Shademaster,' and 'Sunburst,' were planted in a block adjacent to the main study site. Source and size of trees, spacing, planting date, and experimental design were the same as for the main study site. Half of the trees were inoculated with *T. austro-americana* on June 1, 1988 in the manner described before.

Beetles attracted to the trees were trapped on 0.95 liter [1 qt], cylindrical cardboard cartons [10.2 cm (4 in) diam, 25 cm (10 in) height] covered with brown contact paper and coated with Tree Tangletrap (Tree Tangletrap Co., Grand Rapids, MI). The cartons were split lengthwise and fitted around the trunk of each tree just above the site of inoculation. There were three trapping periods: May 30 to June 29, June 30 to July 27, and July 28 to September 19, 1989. Fresh traps were used for each interval. Old traps were taken to the laboratory and examined for adult buprestids. Beetles were cleaned in hexane to remove the adhesive and preserved in 75% ethanol for later identification to species. Beetle counts were subjected to square-root transformation, and then numbers of beetles of each species and total buprestids captured were analyzed by repeated measures ANOVA for main effects of cultivar, disease, and date.

Growth and survival of bagworms on infected vs. control trees. Bags containing overwintering bagworm egg masses were collected from junipers in Lexington in early May 1989. Egg masses were held outdoors in a screened cage until the larvae began to emerge on May 21. Newly-hatched bagworms were placed in plastic jelly cups (15 larvae/cup) with six honeylocust leaflets. Cups containing 3-day-old larvae were taken to the main study site on May 24. A bag [15 x 28 cm (6 x 11 in)] constructed from fine organdy mesh was placed over one shoot on the south side of each infected and non-infected tree of two cultivars, 'Shademaster' and 'Sunburst.' A cup with bagworms was placed on the foliage within each bag, and the bag was then sealed around the base of the shoot with a wire twist-tie. Initial weights of 20 additional bagworms from the same cohort were recorded. Cages with bagworms were left in the field for 14 days. The shoots were then harvested, the bags opened, and surviving bagworms were counted, sorted by larval instar on the basis of head capsule measurements, and weighed.

Samples of foliage were collected at the beginning of the experiment from each tree upon which bagworms were caged. Leaves were frozen on dry ice, lyophilized, and ground in a Wiley mill to pass a 40-mesh screen. Leaf powder was extracted with 200 nM PO_4 buffer, pH 7.0, and soluble protein in the supernatant was determined colorimetrically (3) using D-ribulose 1,5-diphosphate carboxylase from spinach as standard. Larval weights, percent survival, and soluble protein content of foliage were analyzed by ANOVA for main effects and interaction of cultivar and *Thyronectria* infection. Within each cultivar, differences be-

tween infected and non-infected trees were analyzed by Tukey's test at $\alpha = 0.05$.

Final Harvest. All 120 trees in the main site were felled in November 1990, 29 months after inoculation. The trees were cut into 1 m (3 ft) sections and taken to the laboratory where they were measured, examined for emergence holes of borers, and dissected. Height, trunk diameter, and total length (cm) of living and dead branches were determined for each tree. Area (cm^2) of cankers was determined for infected trees as before. Depth of cankers was determined by measuring discoloration of sapwood in cross sections taken through the point of inoculation. Healing of original inoculation wounds was visually estimated (100% = complete closure with callus). After being examined for borer exit holes, all trunk sections and woody branches were split and examined for borer larvae. Tree growth parameters and borer counts were analyzed by ANOVA for main effects and interaction of cultivar and *Thyronectria* infection.

Flight phenology of adult borers attracted to honeylocust in the landscape. Seasonal flight activity of adult Buprestidae attracted to honeylocust was monitored in 1989 and 1990 on 11 trees in Lexington. Trees were grouped at four sites, two on the University of Kentucky campus and two in other institutional landscapes. Tree diameter ranged from 5 to 20 cm (2-8 in); most of the trees selected for monitoring showed symptoms of Thyronectria canker. Beetles attracted to the trees were trapped on polyethylene bands [20 cm (8 in) wide] stapled around each tree at 1 to 1.5 m (3.3-5 ft) height and coated with Tree Tangletrap. Sticky traps were examined weekly from May 15 to September 20, 1989, and from May 11 to August 31, 1990. Adhesive was renewed as needed. Specimens were cleaned in hexane and preserved in ethanol until they could be identified. Voucher specimens are deposited in the University of Kentucky Insect Collection.

Results and Discussion

Susceptibility of cultivars to Thyronectria canker. All inoculations with *T. austro-americana* were successful and resulted in formation of characteristic Thyronectria cankers. The causal fungus was isolated from several cankers and its identity confirmed 15 months later. Seven months after inoculation there were significant differences among cultivars for canker area ($P = 0.047$) and average distance between the two farthest removed stromata within cankers ($P = 0.003$, Table 1). Cultivars 'Shademaster,' 'Sunburst,' and 'Rubylace' produced relatively large cankers with greater spread of conidial stromata from the site of inoculation wound than occurred on 'Skyline,' 'Imperial,' or Trueshade.' Rate of closure of cork borer wounds in control (non-infested) trees also varied ($P = 0.06$), with 'Sunburst' forming less callus than most other cultivars. None of the Thyronectria-infected trees formed callus in the inoculation wound. Differences in canker area among cultivars also approached significance ($P = 0.08$) after 15 months, with 'Sunburst' and 'Rubylace' producing the largest cankers and 'Skyline' and 'Trueshade' having somewhat smaller cankers (Table 1). Number of conidial stromata per canker did not differ among cultivars, nor did trunk diameter differ between infected and non-infected trees on either date.

Attraction of borers to infected vs. control trees. A total of 310 adult buprestids was captured on the sticky traps during the experimental period (May 30 to September 19). Four species were represented: *Agrilus egeniformis* Champlain and Knull (45.2% of total), *A. cladrastis* Knull (28.7%), *A. fallax* Say (24.2%), and *A. difficilis* Gory (1.9%). Capture rates of individual borer species did not differ significantly among cultivars, or between infected and non-infected trees, within any sample interval. Beetle counts were therefore pooled across species and sample dates and totals were analyzed for main effects of cultivar and *Thyronectria* infection. There was again no difference in numbers of adult borers captured among the different cultivars ($P = 0.51$), and no evidence that beetles were differentially attracted to infected trees ($P = 0.23$; Fig. 1).

Growth and survival of bagworms on infected vs. control trees. Soluble nitrogen content of foliage was higher for infected trees than for non-infected trees (ANOVA, $P = 0.04$), and higher for 'Sunburst' than for 'Shademaster' ($P < 0.001$). Analyzed separately by cultivar, the difference in soluble protein between infected and non-infected trees was significant for 'Sunburst,' but not for 'Shademaster' (Table 2). Elevated levels of soluble protein in foliage of diseased trees is consistent with predictions of plant stress theory (24). However, growth or survival of bagworms did not differ significantly between the two cultivars, or between infected and non-infected trees (Table 2).

Final Harvest. There was less difference among cultivars in expression of *Thyronectria* canker after 29 months. Mean area of primary cankers ranged from 19.1 cm^2 (3 in^2) for 'Rubylace' to 12.4 cm^2 (1.9 in^2) for 'Skyline,' but did not differ among cultivars ($P = 0.40$). Depth of primary cankers

Table 1. Canker formation on six honeylocust cultivars inoculated in June 1988 with *Thyronectria austro-americana*.

	7 months after inoculation				15 months after inoculation	
Cultivar	Canker area (cm^2)[z]	Conidial stromata/canker	Max. distance between stromata (cm)[y]	Callus (mm)[x]	Canker area (cm^2)	Conidial stromata/canker
Shademaster	7.4 ± 1.8a	27.4 ± 6.4a	4.1 ± 1.0a	1.7 ± 0.3ab	9.7 ± 2.7abc	14.3 ± 3.9a
Sunburst	7.2 ± 0.9ab	32.3 ± 4.2a	4.3 ± 0.4a	1.0 ± 0.3b	12.9 ± 2.8a	17.0 ± 2.5a
Rubylace	7.3 ± 0.9ab	25.4 ± 4.9a	4.6 ± 0.5a	1.4 ± 0.3ab	10.9 ± 0.7ab	9.8 ± 2.3a
Skyline	4.9 ± 0.6abc	19.5 ± 4.0a	2.4 ± 0.2b	1.8 ± 0.5a	4.2 ± 0.8c	10.7 ± 1.8a
Imperial	4.6 ± 1.0bc	22.0 ± 6.5a	2.7 ± 0.4b	1.8 ± 0.3a	10.1 ± 3.9abc	11.1 ± 3.6a
Trueshade	4.0 ± 0.3c	17.5 ± 2.3a	2.4 ± 0.2b	1.8 ± 0.3a	5.5 ± 0.7bc	10.7 ± 1.3a

[z]Within columns, means (±SE) not followed by the same letter differ significantly (LSD test following ANOVA, $P < 0.05$).

[y]Distance between the two farthest removed stromata.

[x]Callus formation in uninoculated wounds. Callus was not produced in inoculated wounds.

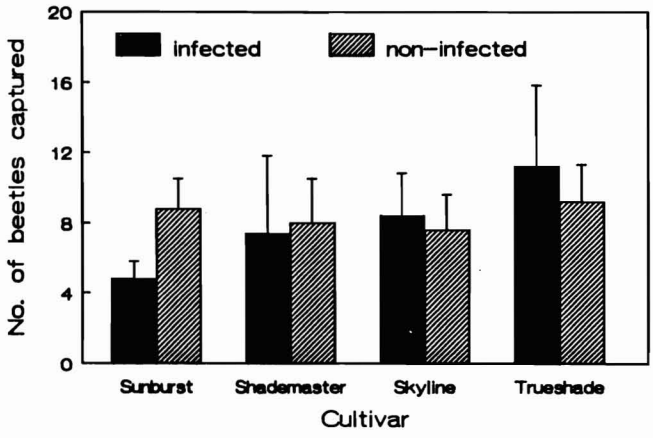

Fig. 1. Attraction of adult *Agrilus* spp. to Thyronectria-infected vs. non-infected honeylocust cultivars. Bars represent means (+ SE).

differed significantly among cultivars (P = 0.04), averaging 11.4 mm (0.45 in) on 'Rubylace,' followed by 'Shademaster' [9.8 mm (0.39 in)], 'Skyline' [9.5 mm (0.37 in)], 'Sunburst' [9.0 mm (0.35 in)], 'Trueshade' [7.9 mm (0.31 in)], and 'Imperial' [7.3 mm (0.29 in)]. Two trees each of 'Rubylace,' 'Sunburst,' and 'Skyline' developed additional cankers; these were absent on the other cultivars. Infected and non-infected trees did not differ significantly in height, trunk diameter, or total length of living or dead branches. Closure of the inoculation wound also did not differ among cultivars although, as expected, average wound closure was much greater for non-infected trees than for those inoculated with Thyronectria (80.4% vs. 24.8%, respectively; P < 0.0001). Remarkably, in spite of our capture of numerous *Agrilus* adults on sticky traps in the adjacent plot, we found a total of only 10 emergence holes made by wood borers (three on infected, seven on non-infected trees) and recovered no borer larvae from trees of either treatment. Borers thus failed to colonize the trees in numbers sufficient to support meaningful statistical analysis.

Flight phenology of adult borers attracted to honeylocust in the landscape. A total of 507 adult buprestids representing eight species was captured on sticky traps on honeylocusts in the landscape in 1989. *Agrilus egeniformis* was the most abundant species (39.4% of total), followed by *A. fallax* (26.2%), *A. cladrastis* (25.0%), *A. difficilis* (8.1%), *A. obsoletoguttatus* Gory (< 1%), *Chrysobothris adelpha* Gemminger and Harold (< 1%), *Anthaxia viridifrons* Gory (< 1 %) and *Actenodes davidi* Nelson (< 1%). Flight activity of the four most abundant species began in late May or early June, with sustained flight from late June until late July or August (Fig. 2). First captures of *A. difficilis, A. egeniformis,* and *A. fallax* were about two weeks earlier in 1990, but their general flight patterns were similar to 1989 (Fig. 3).

Agrilus egeniformis and *A. fallax* are relatively small species that preferentially attack branches and twigs of honeylocust (9), while *A. difficilis*, a larger species, attacks the main branches and trunk (1). *Agrilus difficilis* colonizes both large and small trees, reportedly favoring those under stress (1). Only *A. difficilis* has been regarded as a pest of honeylocust (1, 13). Adults of these same three species, together with *A. pseudofallax* Frost, were the most abundant buprestids collected from honeylocust foliage in northern Ohio (8). *Agrilus pseudofallax* was not collected in our study, whereas *A. cladrastis* was abundant in our samples but was not collected by Herms *et al.* (8). To our knowledge, neither of these species has been confirmed to colonize honeylocust as larvae although, like *A. difficilis*, the adults feed upon the foliage (authors' observations).

Information on the flight activity of adult buprestids is sparse. Herms *et al.* (8) reported seasonal abundance of pooled *Agrilus* spp. adults within honeylocust canopies, but did not separate individual species. Beetles were present from early June until August, with the greatest numbers collected in late June and July. In another Ohio study (1), emergence of *A. difficilis* from honeylocust began as early as June 5 and was completed as late as July 22, with female beetles living for an average of 48 days. These observations are consistent with the species' prolonged flight period in Kentucky (Figs. 2, 3).

In summary, this study suggests that cultivars 'Sunburst,' 'Rubylace,' and 'Shademaster' are particularly susceptible to *T. austro-americana*, while 'Skyline' and 'Trueshade' are somewhat less susceptible in Kentucky. Size of cankers on 'Imperial' was inconsistent between the 7 and 15 month evaluations. For unknown reasons, about half of the 'Imperial' trees showed leader dieback during the first summer after planting. This condition was not associated with Thyronectria, but it may have affected normal expression of canker symptoms. In earlier studies, Thyronectria cankers were most frequent on 'Sunburst,' less frequent on 'Skyline,' and least frequent on 'Imperial' and 'Shademaster' in Illinois (17), and 'Sunburst' was found to be more susceptible than 'Skyline' or 'Imperial' in Colorado (12). Reasons for variation in cultivar resistance in different locations warrant further study. None of the cultivars that have been evaluated are completely resistant to Thyronectria canker.

Table 2. Development and survival of newly-emerged bagworms on non-infected honeylocust cultivars or trees infected with *Thyronectria austro-americana* and soluble protein content of corresponding leaves.[z]

Cultivar treatment	Mean larval wt (mg)[y]	% Survival	Distribution of instars (%)			Soluble protein (μg/g dry wt)
			1st	2nd	3rd	
Sunburst						
Infected	2.6 ± 0.1	81.7 ± 9.4	0	90	10	150.1 ± 11.3*
Non-infected	2.9 ± 0.4	76.0 ± 8.8	7.8	90.2	2	127.2 ± 9.3
Shademaster						
Infected	2.5 ± 0.2	94.1 ± 2.3	0	100	0	98.2 ± 6.7
Non-infected	2.8 ± 0.1	88.2 ± 4.0	4.2	94.8	1.0	91.7 ± 5.1

[z]Bagworms were confined on the trees on May 24 and evaluated after 14 days.

[y]Within cultivars, an asterisk denotes that the mean for infected trees differs significantly from the corresponding mean for non-infected trees (ANOVA, P < 0.05).

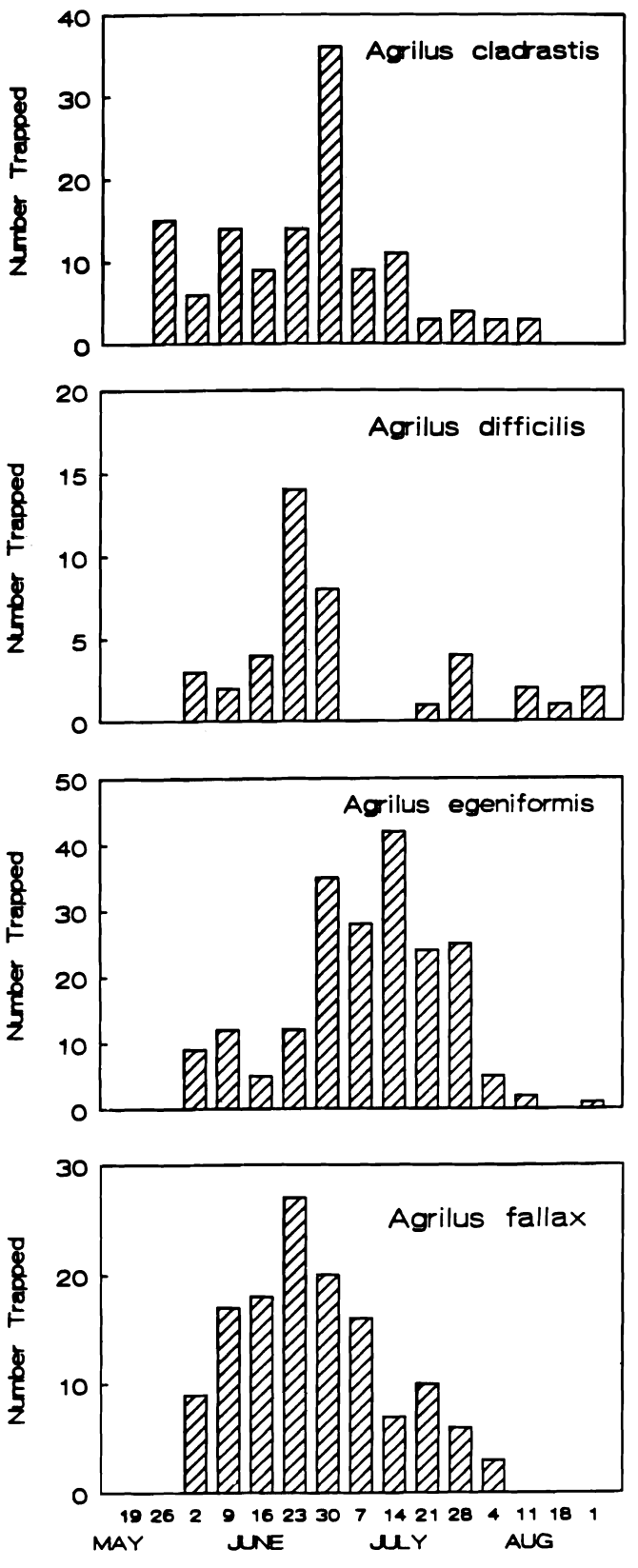

Fig. 2. Seasonal capture rates of adult *Agrilus* spp. on sticky band traps on honeylocust trees in the landscape, Lexington, KY, 1989.

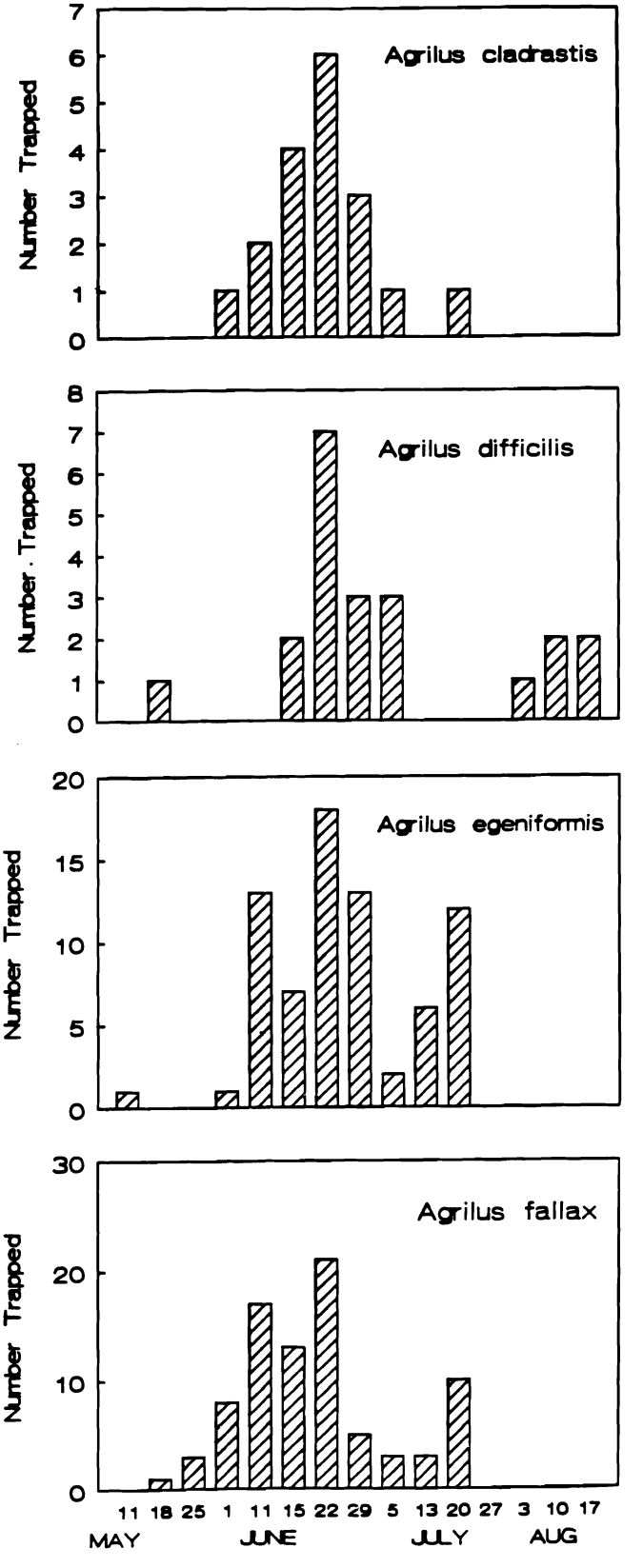

Fig 3. Seasonal capture of adult *Agrilus* spp. on sticky band traps on honeylocust trees in the landscape, Lexington, KY, 1990.

This study also shows that infection with *T. austro-americana* does not necessarily predispose honeylocust to attack by *Agrilus* wood borers. This fails to account for the observation that borer emergence holes, especially those made by *A. difficilis*, are often associated with trunk cankers (4, 14, authors' observations). Knowledge of host associations of *Agrilus* with honeylocust are based mostly on work by Hespenheide (9, 10), in which beetles were reared from dead or dying branches of severely stressed trees. Although data are lacking, *A. difficilis* also reportedly favors stressed hosts (1). *Agrilus* adults that are attracted to vigorous or moderately-stressed honeylocusts for feeding may fail to oviposit upon or the larvae may not colonize such hosts. There was severe drought in Lexington during the summer of 1988, especially in June when only 1.55 cm (0.61 in) of rain fell, the least amount in over 30 years. In contrast, rainfall from May to August was higher than normal in both 1989 and 1990. Average summer temperatures were much higher in 1988 (2-3°F above normal) than in 1989 or 1990. After the first summer, alleviation of weather-related stress appeared to favor recovery of trees from Thyronectria canker. Jacobi (12) using mechanical girdling to induce stress found that stressed trees had larger cankers following spring, but not fall inoculations. Formation of callus tissue in inoculation wounds and compartmentalization of cankers were evident by the final harvest. These responses to infection are typical for vigorously growing trees (20). Infected trees in our study may not have been sufficiently stressed by Thyronectria to allow colonization by borer larvae.

Interactions between tree vigor, *T. austro-americana*, and *Agrilus* spp. warrant further study, as does the suggestion (4) that adult borers may passively transmit the fungal pathogen or create wounds that provide infection courts for the fungus. By girdling trunks and branches, severe cankering of stressed trees could alter nutritional or defensive characteristics of subcortical tissues, rendering them more vulnerable to colonization by borers. Alternatively, the observed co-occurrence of borers and Thbyronectria cankers may be correlative, both agents acting as independent, opportunistic invaders of weakened or declining hosts.

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