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Dutch elm disease pathogen transmission by the banded elm bark beetle *Scolytus schevyrewi*

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Summary

Dutch Elm Disease (DED) is a vascular wilt disease of *Ulmus* species (elms) incited in North America primarily by the exotic fungus *Ophiostoma novo-ulmi.* The pathogen is transmitted via root grafts and elm bark beetle vectors, including the native North American elm bark beetle, *Hylurgopinus rufipes* and the exotic smaller European elm bark beetle, *Scolytus multistriatus*. The banded elm bark beetle, *Scolytus schevyrewi,* is an exotic Asian bark beetle that is now apparently the dominant elm bark beetle in the Rocky Mountain region of the USA. It is not known if *S. schevyrewi* will have an equivalent vector competence or if management recommendations need to be updated. Thus the study objectives were to: (i) determine the type and size of wounds made by adult *S. schevyrewi* on branches of *Ulmus americana* and (ii) determine if adult *S. schevyrewi* can transfer the pathogen to American elms during maturation feeding. To determine the DED vectoring capability of *S. schevyrewi*, newly emerged adults were infested with spores of *Ophiostoma novo-ulmi* and then placed with either *in-vivo* or *in-vitro* branches of American elm trees. The inoculation of trees via feeding wounds was successful 30% of the time for *in-vivo* trials and 33% for *in-vitro* trials. Although the infection rate of DED has declined in Colorado over the past 10 years, the disease is still present in urban elms. While it appears that *S. schevyrewi* is another vector of the DED pathogens, it appears that *S. schevyrewi* is no more efficient than *S. multistriatus*. Thus, management programs that remove elm bark beetle breeding sites, rapidly remove DED-infected elms and include the planting of DED-resistant elms should continue to be effective management tactics.

1 Introduction

Dutch Elm Disease (DED) is a vascular wilt disease of *Ulmus* species (elms) incited by the exotic fungi *Ophiostoma ulmi* (Buisman) Nannf. and *O. novo-ulmi* Braiser. These pathogens move among trees via elm bark beetle vectors and by root grafts (Lanier 1981; Peacock 1981; Webber and Gibbs 1989; Vega 2005). In North America, two beetle species from the subfamily Scolytinae in the family Curculionidae are the two confirmed vectors of the DED fungi: *Hylurgopinus rufipes* Eich., the native North American elm bark beetle, and *Scolytus multistriatus*., the smaller European elm bark beetle which is an introduced species (Collins et al. 1936; Parker et al. 1941, 1947; Sinclair 1978; Holmes 1980; Lanier 1981; Stipes 1981; Faccoli 2001). The relatively recent introduction to North America of an Asian species, *Scolytus schevyrewi*, Curculionidae, subfamily Scolytinae, the banded elm bark beetle, probably occurred in the decade prior to its detection in 2003 in Colorado and Utah (Negron et al. 2005). The presence of this Asian species of elm bark beetle raised the question of whether or not *S. schevyrewi* can also vector the DED pathogens.

In North America, it is common for healthy elm trees to be inoculated with the DED pathogen via wounds made by adult elm bark beetles. Feeding wounds on branches are the most common method of inoculation. Some infections may also take place by wounding during breeding activities (Sinclair 1978). Sinclair (1978) noted that feeding wound depth is important in estimating the probability of infection because deeper wounds are potentially more conducive to infection. Radial penetration during adult *S. multistriatus* feeding activity is usually between 2 mm and 4 mm. Spring and early summer are when adults of elm bark beetles are active (Sinclair 1978).

The relative effectiveness of elm bark beetles as vectors of the DED pathogen in North America is currently not known. Researchers working in Spain noted a difference in the number of beetles infested with fungal spores among three species of elm bark beetles. They found 6% of *Scolytus kirschi*, 64% of *S. multistriatus* and 98% of *S. scolytus* were carrying spores (Webber 1990). Although the number of spores per insect varied greatly H, *S. multistriatus* and *S. scolytus* had consistently carried more spores than *S. kirschi*. This research did not assess the insect's effectiveness in vectoring.

Adult *S. schevyrewi* were first identified in North America in Aurora, Colorado and Ogden, Utah, in 2003 in a joint USDA Forest Service and USDA APHIS-PPQ Rapid Detection and Response Pilot Project (Negron et al. 2005). By the spring of 2010, *S. schevyrewi* was found in traps baited with an attractant which contained pheromones of *S. multistriatus* and 2-methyl -3-buten-2-ol and noted in association with declining and dying elm trees in over 28 states (Lee et al. 2009; National Agricultural Pest Information System (NAPIS) 2010). In the Rocky Mountain region of the U.S.A., *S. schevyrewi* has outcompeted *S. multistriatus* and made up 68 to 90% of the beetles trapped in Nevada, Wyoming, Utah and Colorado (Lee et al. 2009). In its native Asia, *S. schevyrewi* is reported as a pest of members of several plant genera including *Ulmus*, *Salix*, *Caragana, Malus*, *Prunus, Pyrus* and *Elaeagnus* but is not known as a vector of DED (Wang 1992). In North America, *S. schevyrewi* was only found in association with elms in the field and in laboratory studies (Lee et al. 2011). Both *S. multistriatus* and *S. schevyrewi* conduct maturation feeding in twig crotches after emerging from pupal chambers (Negron et al. 2005). Recent studies indicate that *S. schevyrewi* apparently have a competitive advantage over *S. multistriatus* in host colonization because *S. schevyrewi* is strongly attracted to host elm volatiles, while *S. multistriatus* is only moderately attracted to host

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volatiles, but strongly to female-derived pheromones (Lee et al. 2010). Additionally, *S. schevyrewi* was a stronger interspecific competitor than *S. multistriatus* in controlled breeding trials, resulting in fewer *S. multistriatus* progeny and four times the number of *S. schevyrewi* progeny compared with *S. multistriatus* when both were raised on the same logs (Lee and Seybold 2010).

Due to biological and feeding similarities shared by *S. schevyrewi* and *S. multistriatus*, urban foresters in the USA. are concerned that adult beetles may vector the DED pathogen (Negron et al. 2005). The potential for *S. schevyrewi* to vector the DED pathogen is apparently high because *O. novo-ulmi* was found with relatively equal frequency, 46 and 42%, respectively on *S. schevyrewi* and *S. multistriatus* adults emerging from diseased American elms (*Ulmus americana*) in Colorado (Jacobi et al. 2007). However, the efficiency of *S. schevyrewi* in wounding twigs during maturation feeding and depositing *O. novo-ulmi* spores is not known. The ability of the pathogen to remain on adult *S. schevyrewi* through maturation feeding and then be vectored to healthy uninfected elms during egg laying is assumed to occur, but there is no documented evidence for this proposition.

It is not known if *S. schevyrewi* will have an equivalent or better vector competence for the DED pathogens when compared to *S. multistriatus*, and if DED management recommendations will need to be modified. Thus, the objectives of our study were to (i) determine the type and size of wounds made by adult *S. schevyrewi* on branches of *Ulmus americana* (to see if they are deep enough for the fungus to reach the xylem) and (ii) determine if adult *S. schevyrewi* can transfer the pathogen to American elms during maturation feeding.

2 Materials and methods

2.1 Fungal sources

The fungal isolates of *O. novo-ulmi* were obtained from infested adult *S. schevyrewi* collected in 2004 from DED-positive American elm trees in Fort Collins and Denver, Colorado. The beetles were crushed and placed in Petri dishes containing amended elm sapwood agar (CSESA) (200 ppm cycloheximide, 100 ppm streptomycin sulphate, 2.5% American elm sawdust, 3.0% agar) (Jacobi et al. 2007). The plated beetles were incubated under laboratory lighting at 21C for up to 4 weeks and examined periodically with a dissecting microscope for the presence of the synnematal state of *O. novo-ulmi*. Pure cultures of *O. novo-ulmi* were derived from these cultures.

2.2 Beetle sources

Siberian elm trees (*Ulmus pumila* L.), not infested with DED pathogen, were harvested in Fort Collins in May 2006 and April 2007. Branches and/or stems, 10–45 cm in diameter, were cut into 40 cm long sections, and the cut ends were sealed with hot paraffin. Equal numbers of stem sections were placed at four locations in Fort Collins (where *S. schevyrewi* adults had previously been trapped) for 3 weeks to allow natural colonization by the beetles to occur. Infested branch and stem sections were collected and placed in plastic rearing containers. Adult beetles began emerging from collected sections within 4–6 weeks. All beetles were identified to species to assure that only *S. schevyrewi* was used in vectoring experiments.

2.3 Infesting beetles

To determine the DED vectoring capability of *S. schevyrewi*, newly emerged adults were infested with spores of *O. novo-ulmi*. The spores were produced by growing the fungus on CSESA for 7–28 days in Petri dishes at 21 C under laboratory lighting (Jacobi et al. 2007). Insects were gently tumbled on the fungal cultures, and afterwards, the beetles were placed either in fabric cages secured over branches of American elm trees growing in the field, or in plastic rearing containers along with excised American elm branches in a laboratory setting with constant 21°C and laboratory lighting.

2.4 Experimental elms

The 20 American elms used in the study comprised the following trees. Five trees were 5-year-old clonal offspring from a selected tree on the Colorado State University campus. These trees were 3–4 m tall and 4–6 cm in diameter at 1.3 m (d.b.h.) at the time they were planted at Colorado State University's Agricultural Research, Development, & Education Centre (ARDEC) in May 2006. Ten additional elms used were 10-year-old clonal elms (selection number 502) from the Wisconsin breeding program. These trees were planted at ARDEC in 1996 and measured 5–6 m tall and 8–12 cm d.b.h. in 2007. The remaining five elms were naturalized American elms in a riparian area of Lee Martinez Park, Fort Collins, Colorado. These naturalized elms were 4–6 m tall and 8–14 cm d.b.h. at the time of inoculation. Branch samples for *in-vitro* tests were collected from one American elm tree on the Colorado State University campus.

2.5 *In-vivo* trials

Newly emerged *S. schevyrewi* adults were collected from rearing cages and stored at 5°C in sterile Petri dishes before their use within 24 h in inoculation trials. Groups of 10–20 *S. schevyrewi* adults were put into Petri dishes containing *O. novo-ulmi* growing on CSESA. The beetles were allowed to move around or were rolled in the cultures for 20–60 min to

infest the beetles with spores of the fungus. We did not assess the number of spores on a beetle although this technique has been effectively used in previous inoculation tests (Parker et al. 1941; Faccoli and Battisti 1997). Infested beetles were placed into fabric cages (30 × 75 cm) constructed of sheer polyester fabric just prior to each cage being tied around the selected branches of the previously mentioned elm trees. On average, 47 beetles were placed in each fabric cage, and the cages were left in place for an average of 57 days.

Thirteen *in-vivo* inoculation trials were conducted in July of 2006 and between May and August of 2007. Inoculations in 2006 (trials 1–5) used the five clonal American elms propagated from a select tree on the Colorado State University campus. Beetles infested with spores of *O. novo-ulmi* were introduced to one cage per tree on each of five different dates between the 5th and 24th of July 2006. Inoculation trials in 2007 (trials 6–13) used the five clonal American elms from Colorado State University tree growing at ARDEC, two to five of the ten trees from the Wisconsin breeding program growing at ARDEC, and the five naturalized American elms growing in Lee Martinez Park (Table 2). Caged branches were harvested 4–8 weeks after the beetles were introduced into the cages, except at Lee Martinez Park where branches were harvested 1 year after inoculation (August 21, 2008) to allow time for the fungus to colonize branches and cause foliar wilting. The number and size of branch crotches, the number and location of feeding wounds and the depth and dimensions of feeding wounds were measured. We could account for all the insects at the end of the trial, and they were dead. Each twig section containing a *S. schevyrewi* feeding wound was cut into three sections: (i) 10 mm distal to the wound, (ii) the feeding wound and (iii) 10 mm proximal to the wound. The xylem tissue associated with each of the three sections was placed on an amended water agar medium (CSWA) (200 ppm cycloheximide, 100 ppm streptomycin sulphate, 3.0% agar) incubated at 21 C under laboratory lighting and examined every 5 days for synemma of *O. novo-ulmi*.

2.6 *In-vitro* trials

Two *in-vitro* inoculation trials were initiated in August of 2006, using eight branches, 10–20 mm in diameter, from an American elm tree located on the Colorado State University campus. Each of the eight branches was cut into three 20 cm sections. Branch ends were not sealed with paraffin for this short trial. The three branch sections were placed in a plastic container (30 cm × 25 cm × 15 cm), with plastic lids with screens to provide ventilation. Rearing boxes were kept at 21 C under laboratory lighting, and damp paper towels were placed in the bottom of each box and replaced every 3 days to maintain a suitable environment for the beetles. For each of the eight branches in the first trial, 30 adult *S. schevyrewi* beetles were exposed to *O. novo-ulmi* as described previously and then placed in the plastic rearing container. For the second trial, 50 beetles were placed in each plastic rearing container. The number of feeding wounds, and their size and type, were recorded in each trial after 5–9 days. Tissue from all feeding wounds was placed on CSWA as previously described.

3 Results

3.1 Wound sites

In the *in-vivo* inoculation trials, *S. schevyrewi* maturation feeding wounds occurred primarily at branch crotches and rarely on sections of branch tissue between crotches. There were many branch crotches available for the beetles to feed on with an average of two large side branches (>3 mm) and 41 small side branches (1–3 mm) per branch. Feeding wounds were normally rounded or elongated. Feeding wounds at branch crotches ranged from 0.5 to 2 mm deep (average 1.3 mm), and all wounds etched the xylem (Table 1).

The observed number of feeding wounds, 57 in all the *in-vivo* trials and 18 wounds in the *in-vitro* trials, was low (Table 2). The number of wounds per introduced beetle was 0.023 in the *in-vivo* trials and 0.046 in the *in-vitro* trials. Wounds occurred most commonly at branch crotches of large side branches, and all wounds were on twigs at least 5 mm in diameter. There was no relationship (equal success) between the type of feeding wound (round *vs.* elongated) and isolation of *O. novo-ulmi,* so isolation results are combined for both wound types in Table 2.

3.2 Inoculations

The inoculation of *O. novo-ulmi* into feeding wounds by *S. schevyrewi* was successful in both the 2006 and 2007 *in-vivo* (30%) and *in-vitro* (33%) trials (Table 2, *in-vitro* data not shown). The growth of the fungus away from the wound was

Table 1. Size of feeding wounds made by adult *Scolytus schevyrewi* beetles at branch crotches of field-grown American elm trees (*Ulmus americana*), Fort Collins, Colorado 2006.

	Length (mm)	Width (mm)	Depth (mm)	Main branch Dia (mm)	Side branch Dia (mm)
Minimum	4.0	1.0	0.5	4.0	3.0
Maximum	12.0	3.0	2.0	10.0	5.0
Range	4.0–12.0	1.0–3.0	0.5–2.0	4.0–10.0	3.0–5.0
Average	7.0	2.0	1.3	6.2	3.6

Wounds n = 13.

Table 2. Inoculations with *Ophiostoma novo-ulmi* by adult *Scolytus schevyrewi* beetles on field-grown American elm trees (*Ulmus americana*) in Fort Collins, Colorado, 2006–2007.

Trial[1]	Date	Exposure to beetles (days)	Trial initiation to isolation (days)	Beetles per branch	Number of feeding wounds (% beetles producing wounds)	Positive isolation[2]		
						Distal	Wound	Proximal
1	7/5/2006	9	49	46	15 (33)	4	9	2
2	7/13/2006	10	55	45	0 (0)	0	0	0
3	7/14/2006	63	30	60	3 (5)	0	0	0
4	7/18/2006	59	59	75	5 (7)	0	3	0
5	7/24/2006	43	43	50	0 (0)	0	0	0
6	5/16/2007	20	64	28	1(1)	0	1	0
7	5/22/2007	22	62	30	6(4)	1	1	0
8	6/13/2007	90	90	41	2 (1)	0	1	0
9	6/19/2007	49	49	14	3 (4)	0	0	0
10	6/26/2007	77	77	60	2 (4)	0	0	0
11	7/17/2007	56	56	35	2 (2)	0	1	0
12	7/24/2007	49	49	31	3 (2)	0	1	0
13	8/7/2007	66	371	50	8 (6)	0	0	0
Means		47	57(trial 1–12)	43	(5.1%)	10%	30%	4%

[1]Trials 1–5 were completed on one branch on each of five American elms propagated from an elm at the Colorado State University campus and planted at the Agricultural Research, Demonstration and Education Centre (ARDEC), Colorado State University, Fort Collins, Colorado. Trials 6–7 were completed at ARDEC on one branch on each of the five Colorado State University clonal elms. Trials 8–12 were completed on 10 clonal trees of American elm selection 502 from the Wisconsin breeding program, with one branch on each of four trees for trial 8, on one branch on each of five trees for trial 9, on one branch on each of two trees for trial 10, on one branch on each of three trees for trial 11 and on one branch on each of four trees for trial 12. Trial 13 was completed on one branch of each of five naturalized American elms at Lee Martinez Park, Fort Collins, Colorado.

[2]Wounds include round and elongated wounds at branch crotches. All wounds at branch crotches were at side branches larger than 3 mm. Over all trials, two elongated wounds occurred on the branch stem, and the fungus was not isolated from these two wounds. Isolations were attempted from xylem tissue at each wound and 10 mm distal and proximal of the wound.

less common, with 10% distal and 4% proximal isolations successful. All but two of the *in-vivo* trials had branches wounded by the beetles.

In field inoculations of naturalized American elms at Lee Martinez Park, the branches were left attached for a year to allow enough time for the fungus to cause foliar wilting. None of the branches on the elms at Lee Martinez Park displayed foliar wilting or discoloration of vascular tissue distal or proximal to any of the feeding wounds. Additionally, the fungus was not isolated from the feeding wounds, and 50% of the wounds were partially callused over 12 months after beetle infestation (Table 2, trial 13).

The *in-vitro* inoculation trials yielded 18 wounds with eight at branch crotches and 10 elsewhere on the branch, resulting in 33% positive isolations from the wounds. Even though the proportion of wounds infected was relatively high based on recovery of the fungus by culturing, the number of wounds was low given to the number of beetles introduced to the branches. The fungus was isolated from xylem tissues of four branch sections distal and two branch sections proximal to wounds.

4 Discussion

Our studies confirmed that artificially infested adult *S. schevyrewi* beetles can: (i) produce maturation feeding wounds that scar the xylem tissue, (ii) carry the Dutch elm disease pathogen to healthy American elm trees and (iii) inoculate the wound. However, extensive colonization by the pathogen up or down the branches, or wilting of leaves was not observed in either *in-vivo* or in- vitro inoculation trials. The numbers of *S. schevyrewi* feeding wounds in the *in-vivo* trials and in the *in-vitro* trials were low with 0.023–0.046 wounds per beetle.

The locations of *S. schevyrewi* maturation feeding wounds at branch crotches of both small (1–3 mm) and larger (>3 mm) side branches were similar to those produced by *S. multistriatus* (Rabaglia and Lanier 1984). The low rates of transmission observed in our study are similar to those reported for *S. multistriatus* (Collins et al. 1936; Parker et al. 1941, 1947; Webber and Brasier 1984; Faccoli and Battisti 1997). The original DED transmission work in New York State, U.S.A. by Parker et al. (1941) found 13.3% success in infecting elms via naturally or artificially infested *S. multistriatus* adults, and 3.3% of feeding wound scars were infected with the fungus. Webber (1990) suggested that there would have to be at least 1000 spores present on beetles to ensure successful infection and noted that most beetles do not carry this high spore load. We do not know the spore loads on beetles here but suspect them to be high because they were exposed to a high density of spores when rolled over the cultures.

The low rate of wounding (0–33%) and low rate of isolation of *O. novo-ulmi* from a wound, and the tissues distal and proximal to the wound (4–30%) suggest that the vector relationship between *S. schevyrewi* and *O. novo-ulmi* exists, but

S. schevyrewi may not be very efficient. The low transmission rates found in these trials does not seem to be related to the physiological status of the elm at the time of the trial because wounding and successful isolation occurred from May to late July. However, it is possible that the low number of wounds may be directly related to beetle condition as many insects died soon after placement in either fabric cages or in plastic containers. Woffenbarger and Buchanan (1939) found that *S. multistriatus* survived without food or water only 2.2 days on average, while those beetles caged with recently cut twigs survived 7.6 days. The high mortality rate of *S. schevyrewi* within days in the *in-vivo* and *in-vitro* trials suggests that *S. schevyrewi* adults do not live very long under field conditions or that the environment in the assays was not optimal for the insects. We speculate that the rapid death of the beetles may be from parasites, adverse environmental conditions or poor vigour of adult beetles emerging from the caged stem sections. Examination of the emerged *S. schevyrewi* adults revealed that most were host to mites. It is not known if these mites were detrimental to the health of the beetles. The temperatures during the *in-vivo* trials were relatively high, with average maximum daily temperatures of 22.7–24.3 in May to 29.8–32.5 C in July–August of 2006-2007. Coupled with the low humidity (15–25% RH) typical in Colorado, these conditions could reduce survival of adult *S. schevyrewi* in the field. However, the *S. schevyrewi* survived only about 48 hr in the *in-vitro* tests that were carried out in an air-conditioned laboratory in plastic containers with damp paper towels as a source of humidity. Even though the ability of *S. schevyrewi* to vector *O. novo-ulmi* and cause infections in elms had a low success rate in this study, it is consistent with the levels discussed above.

As of 2009, *S. schevyrewi* had essentially replaced *S. multistriatus* in parts of the western USA (Lee et al. 2009). For example, in Colorado *S. multistriatus* made up less that 0.1% of the elm bark beetles trapped in the last 4 years (2009-2012) (Michael Winks, APHIS, Personal communication). The replacement of one exotic by another exotic in a new environment will be an interesting story to follow. Currently, the incidence of DED in Colorado is decreasing but has not been eliminated which suggests that *S. schevyrewi* is no better or is a less effective vector of the DED pathogens compared with *S. multistriatus*. Paired inoculation studies are needed to better understand any differences in vector efficiencies. Based on our findings, current management programs that remove declining elms as elm bark beetle breeding sites, rapid removal of DED-infected elms prior to beetle emergence and the planting of DED-resistant elms should continue to be effective management tactics with *S. schevyrewi* as a new vector.

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References

Collins, C. W.; Buchanan, W. D.; Whitten, R. R.; Hoffman, C. H. 1936: Bark Beetles and other possible insect vectors of the Dutch Elm Disease *Ceratostomella ulmi* (Schwarz) Buisman. J. Econ. Entomol. **29**, 169–176.

Faccoli, M. 2001: Elm bark beetles and Dutch elm disease: tests of combined control. J. Pest. Sci. **74**, 22–29.

Faccoli, M.; Battisti, A. 1997: Observations on the transmission of *Ophiostoma ulmi* by the smaller elm bark beetles (Scolytus spp.). In: Proc. Integrating Tactics into the Management of Bark Beetles and Reforestation Pests. Ed. by Gregoire, J. C.; Liebhold, A. M.; Stephen, F. M.; Day, K. R.; Salom, S. M. USDA For. Serv. Gen. Tech. Rept. NE-236. pp. 172–176.

Holmes, F. W. 1980: Bark Beetles, *Ceratocystis ulmi*, and Dutch elm disease. In: Vectors of Plant Pathogens. Ed. by Harris, K. F.; Maramorosch, K. New York: Academic Press, pp. 133–147.

Jacobi, W. R.; Koski, R. D.; Harrington, T. C.; Witcosky, J. J. 2007: Association of *Ophiostoma novo-ulmi* with *Scolytus schevyrewi* Semenov (Scolytidae) in Colorado. Plant Dis. **91**, 245–247.

Lanier, G. N. 1981: Behavior-modifying chemicals in Dutch elm disease vector control. In: Proceedings of the Dutch Elm Disease Symposium and Workshop, October 5-9, 1981, Winnipeg, Manitoba, Canada. Ed. by Kondo, E. S.; Hiratsuka, Y.; Denyer, W. B. G. Winnipeg, Manitoba, Canada: Manitoba Department of Natural Resources, Forest Protection and Dutch Elm Disease Branch, . pp. 371–394.

Lee, J. C.; Seybold, S. J. 2010: Host acceptance and larval competition in the banded and European elm bark beetles, *Scolytus schevyrewi* and *S. multistriatus* (Coleoptera: Scoytidae): potential mechanisms for competitive displacement between invasive species. J. Insect Behav. **23**, 19–34.

Lee, J. C.; Aguayo, I.; Aslin, R.; Durham, G.; Hamud, S. M.; Moltzan, B. D.; Munson, A. S.; Negron, J. F.; Peterson, T.; Ragenovich, I. R.; Witcosky, J. J.; Seybold, S. J. 2009: Co-occurrence of the invasive banded and European elm bark beetles (Coleoptera: Scolytidae) in North America. Ann. Entomol. Soc. Am. **102**, 426–436.

Lee, J. C.; Hamud, A. S.; Negron, J. F.; Witcosky, J. J.; Seybold, S. J. 2010: Semiochemical-mediated flight strategies of two invasive elm bark beetles: a potential factor in competitive displacement. Environ. Entolomol. **39**, 642–652.

Lee, J. C.; Negron, J. F.; McElwey, S. J.; Williams, L.; Witcosky, J. J.; Popp, J. B.; Seybold, S. J. 2011: Biology of the invasive banded elm bark beetle (Coleoptera: Scolytidae) in the Western United States. Ann. Entomol. Soc. Am. **104**, 705–717.

National Agricultural Pest Information System (NAPIS) 2010: Centre for Environmental and Regulatory Information System (CERIS). West Lafayette: Purdue University.

Negron, J. F.; Witcosky, J. J.; Cain, R. J.; LaBonte, J. R.; Duerr, D. A. I. I.; McElwey, S. J.; Lee, J. C.; Seybold, S. J. 2005: The banded elm bark beetle: a new threat to elms in North America. Am. Entomologist. **51**, 84–94.

Parker, K. G.; Readio, P. A.; Tyler, L. J.; Collins, D. L. 1941: Transmission of the Dutch elm disease pathogen by *Scolytus multistriatus* and the development of infection. Phytopathology **31**, 657–663.

Parker, K. G.; Collins, D. L.; Tyler, L. J.; Connola, D. P.; Ozard, W. E.; Dietrich, H. 1947: The Dutch elm disease: Association of *Ceratostomella ulmi* with *Scolytus multistriatus*, Its advance into new areas, methods of determining its distribution and control of the disease. Cornell University Agricultural Experiment Station, Memoir 275, November 1947.

Peacock, J. W. 1981: Citywide mass trapping of *Scolytus multistriatus*. In: Proceedings of the Dutch Elm Disease Symposium and Workshop, October 5-9, 1981, Winnipeg, Manitoba, Canada. Ed. by Kondo, E. S.; Hiratsuka, Y.; Denyer, W.B.G. Winnipeg, Manitoba, Canada: Manitoba Department of Natural Resources, Forest Protection and Dutch Elm Disease Branch, pp. 406–426.

Rabaglia, R. J.; Lanier, G. N. 1984: Twig feeding by *Scolytus multistriatus* (Coleoptera:Scolytidae: within-tree distribution and use for assessment of mass trapping. Can. Entomol. **116**, 1025–1032.

Sinclair, W. A.; Campana, R. J., editors. 1978: Dutch elm disease: perspectives after 60 years. Northeast Regional Research Publication, Agriculture **8**(5), 52 pp. Ithaca: Cornell University Agricultural Experiment Station.

Stipes, R. J.; Campana, R. J., editors. 1981: The American Phytopathological Society. Compendium of Elm Diseases, 96 pp. St. Paul: Am. Phytopathol. Soc.

Vega, F. E., Blackwell, M. (editors.) 2005: Insect-Fungal Associations: Ecology and Evolution. New York: Oxford University Press.

Wang, Z.-T. 1992: *Scolytus schevyrewi* Semenov. In: Forest Insects of China, 2nd edn. Ed. by Xiao, G., Beijing: China For. Pub. House, pp 633–634.

Webber, J. F. 1990: Relative effectiveness of *Scolytus scolytus*, *S. multistria*tus, and *S. kirschi* as vectors of Dutch elm disease. Eur. J. For. Pathol. **20**, 184–192.

Webber, J. F.; Brasier, C. M. 1984: Transmission of Dutch elm disease: a study of the process involved. In: Invertebrate-microbial Interactions. Ed. by Anderson, J; Rayner, A. D. M.; Walton, D., Cambridge: Cambridge University Press, pp. 271–306.

Webber, J. F.; Gibbs, J. N. 1989: Insect dissemination of fungal plant pathogens of trees. In: Insect-Fungus Interactions. Ed. by Wilding, N.; Collins, N. M.; Hammond, P. M.; Webber, J. F. London: Academic Press, pp 161–193.

Woffenbarger, D. O.; Buchanan, W. D. 1939: Notes on elm twig crotch injuries produced by *Scolytus multistriatus* Marsham. J. Econ. Entomol. **32**, 377–381.