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DISPERSAL ADAPTATIONS OF IMMATURE STAGES OF THREE SPECIES OF LEAFHOPPER (HEMIPTERA: AUCHENORRYNCHA: CICADELLIDAE)

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ABSTRACT

Xylem-feeding leafhoppers have evolved several behavioral and physiological adaptations to utilize xylem fluid of variable composition, including polyphagy and high assimilation efficiency. They also display high vagility coupled with excellent visual acuity. We investigated the spectral frequency responses of the nymphal stages of three leafhopper species: *Homalodisca coagulata*, *H. insolita*, and *Oncometopia nigricans*. Under laboratory conditions, the nymphs of *H. coagulata* and *O. nigricans* discriminated spectra and were highly attracted to hues of yellow, with safety yellow being the most attractive. The nymphs of *H. insolita* were also attracted to yellow hues, but were more attracted to cream yellow. In the laboratory, maximum jumping distances of third instar *H. coagulata*, *H. insolita*, and *O. nigricans* were 68.0, 49.7, and 39.2 cm respectively, when provided a target. The fifth instars of *H. coagulata*, *H. insolita*, and *O. nigricans* had maximum jumping distances of 78.8, 29.2, and 45.5 cm, respectively. Additionally, all nymphal stages of *H. coagulata* dispersed up to 10 meters after three days under field conditions when released into an outdoor grass-covered arena. The neonates of *H. coagulata*, *H. insolita*, and *O. nigricans* survived on average, 83.5, 70.5, and 83.0 h without plant feeding, respectively.

Key Words: leafhoppers, *Homalodisca coagulata*, *H. insolita*, *Oncometopia nigricans*, color perception, nymphal dispersal.

RESUMEN

Los saltahojas que se alimentan del xilema han producido por evolución varias adapciones fisiológicas y de comportamiento para utilizar el liquido de xilema de diferentes composiciones, incluyendo polifagia y una alta eficiencia de asimilación. Ellos demuestran también, en una alta dispersión adjunta a una agudeza visual excelente. Nosotros investigamos las respuestas de la frecuencia espectra de los estados ninfales de tres especies de saltahojas: *Homalodisca coagulata*, *H. insolita*, y *Oncometopia nigricans*. Baja condiciones del laboratorio, las ninfas de *H. coagulata y O. nigricans* discriminaron los espectros y fueron altamente atraidas a los tonos de amarillo, con el amarillo brillante siendo lo mas atractivo. Las ninfas de *H. insolita* también fueron atraidas a los tonos de amarillo, pero fueron mas atraidas al amarillo crema. En el laboratorio, la distancia maxima de salto de los tercer estadios ninfales de *H. coagulata*, *H. insolita*, y *O. nigricans* fueron 68.0, 49.7, y 39.2 cm respectivamente, cuando se proveyó una meta. Los quinto estadios de *H. coagulata*, *H. insolita*, y *O. nigricans* saltaron una distancia maxima de 78.8, 29.2, y 45.5 cm, respectivamente. Además de todas las etapas ninfales de *H. coagulata* se dispersaron hasta 10 metros después de tres dias bajo condiciones de campo cuando fueron liberadas en un área exterior de arena cubierta con pastos. Los recien nacidos de *H. coagulata*, *H. insolita*, y *O. nigricans* sobrevivieron un promedio de 83.5, 70.5, y 83.0 horas sin alimentarse de la planta, respectivamente.

Xylophagous leafhoppers seek host plants nutritionally important for development as well as for reproduction. The ability to disperse, locate, and utilize host plants is essential for leafhoppers because the composition of xylem fluid is dilute and highly variable, not only between host plant species, but also within a single plant over time (Horsfield 1977; Andersen & Brodbeck 1989a). Xylem fluid has the most dilute concentrations of dietary nitrogen and carbon of any plant tissue (Andersen et al. 1989). It is composed of >95% water with the predominate organic compounds consisting of amino and organic acids and small amounts of sugars (Andersen et al. 1989; Clark et al. 1986). Many factors are responsible for the dynamic changes associated with xylem composition including temperature, fertilization, water stress, and plant phenology (Andersen et al. 1995; Andersen & Brodbeck 1989b; Brodbeck et al. 1999).

Adult leafhoppers of the Proconiini are strong flyers. The reported host ranges for many members of this group are quite broad (Turner & Pollard 1959; Adlerz 1980; Brodbeck et al. 1993). Presently, studies relating to dispersal and abundance of leafhoppers are limited to the adult stage. The relative seasonal abundance of adult glassy-winged sharpshooters, *Homalodisca coagulata* (Say), has been well documented on a variety of host plants in its native range in the southeastern US as well as in its introduced range in parts of California (Ball 1979; Mizell & French 1986; Blua et al. 2001).

The attractancy of various colors to insects of several orders including Hemiptera, Thysanoptera, and Diptera has been well documented (Prokopy et al. 1975; Prokopy & Owens 1983; Kirk 1984). Yellow colors have been shown to be especially attractive to the greatest variety of insects (Hoback et al. 1999). However, some species of aphids and thrips are attracted to hues of blue spectra depending on their physiology and relating to their dispersal and host plant selection (Walker 1974; Chang et al. 2000). The use of colored traps to successfully monitor insect pest populations has been recognized as an important tool for many pest management programs (Vaishampayan et al. 1975; Prokopy et al. 1979; Webb et al. 1994).

The glassy-winged sharpshooter is a highly polyphagous leafhopper with a native distribution throughout the southeastern US and northern Mexico (Turner & Pollard 1959). This insect was accidentally introduced into southern California (Gill 1995). *Homalodisca insolita* (Walker) was first found in northern Florida and southern Georgia in 1950 (Pollard et al. 1959). It prefers to feed upon grasses. Its native range includes parts of Texas, Arizona, and Mexico. The black-winged leafhopper, *Oncometopia nigricans* (Walker), is another xylem-feeding leafhopper that is commonly found throughout the southeastern US. Its host plant range is similar to that reported for *H. coagulata* (Turner & Pollard 1959). All three species are competent vectors of strains of *Xylella fastidiosa* (Wells et al. 1987), a Gram negative, xylem limited bacterium that is the causative agent for several important plant diseases including phony peach, oleander leaf scorch, and Pierce's disease of grapevine.

The introduction of *H. coagulata* into California is of great concern for producers of a variety of commodities including grapes, peaches, and almonds as well as ornamental nursery plants such as oleander. Although several strains of *Xylella fastidiosa* have been reported from many plant species native to California, the indigenous vectors such as the green sharpshooter, *Draeculacephala minerva* Ball, and the red-headed sharpshooter, *Carneocephala fulgida* Nottingham, have a relatively narrow host range when compared to *H. coagulata* (Purcell & Frazier 1985). Additionally, *H. coagulata* is routinely intercepted in other regions of California, including the Napa Valley, as a result of the transportation of infested ornamentals from southern California. (Bugspot [webpage] 2003).

Our objectives were to examine characteristics important for nymphal dispersal and survivorship by determining the visual wavelength discrimination by nymphs of *H. coagulata*, *H. insolita*, and *O. nigricans* as well as the absolute jumping distances of the third and fifth instars for each species. Also, the ability of the nymphal stages of *H. coagulata* to disperse under field conditions is described. Finally, the survivorship of starved neonates of the three species was investigated to determine the potential for nymphs to be transported without plants.

MATERIALS AND METHODS

Insects and Plants

Immature leafhoppers used in all studies were taken from cultures maintained in 1-m^3 screened cages. Each cage was provisioned with a mixture of host plants depending on leafhopper species as well as life history stage. Cages for nymphs of *H. coagulata* contained glabrous soybean, (*Glycine max* (L.) 'D90-9216'), cowpea, (*Vigna unguiculata* (L.) 'California #5'), and basil, (*Ocimum basilicum* L. 'Lemon'). Cages containing adult *H. coagulata* had glabrous soybean, cowpea, and saltbush, (*Baccharis halimifolia* L.). Neonates of *H. coagulata* were removed from the adult cages daily and placed into cages for nymphs. Cages of *H. insolita* contained Texas millet, (*Panicum texicum* Buckl.), and Johnson grass, (*Sorghum halepense* (L.). *Oncometopia nigricans* culture cages were provisioned with cotton, (*Gossypium hirsutum* L. 'Deltapine 88'), *Coleus* sp., okra, (*Hybiscus esculentus* L. 'Clemson spineless'), and wild periwinkle vine, (*Vinca major* L.). All plants used in the colony cages were potted in a 3:1:1 pine bark: sphagnum moss: sand mixture before placement into colony cages. Greenhouse temperatures ranged between 25-32°C with indoor lighting to maintain a 16:8 light/dark photoperiod. Plants were replaced in each cage when they began to show signs of decline which included wilting, discoloration, or reduction in growth. The soil medium for all plants was watered to saturation twice daily.

Visual Response to Color

Wavelength detection and discrimination of the nymphal stages of *Homalodisca coagulata*, *H. insolita*, and *Oncometopia nigricans* were tested within a structure constructed from 0.3 mm plastic sheeting that was 30 cm in height and tubular in shape with a 50 cm radius. The interior of the structure, or arena, was spray painted flat black (Chase Products, Maywood, IL). Clear plastic push pins were inserted along the inner wall 5 cm from the base of the arena at 8 cm intervals. Plastic panels (5 cm^2) were painted safety yellow (Pittsburg Paints, Pittsburgh, PA), cream yellow (Lucite Paints, Pittsburgh, PA), neon blue (General Paint and Manufacturing Company, Cary, IL), and neutral gray (Rustoleum Corporation, Vernon Hills, IL). Colored panels were held in the arena with 1.9-cm binder clips and hung on the clear plastic push pins along the inside of the arena. Panels painted flat black were also placed in the arena to serve as controls. All panels were coated with Tangle-trap insect coating (The Tanglefoot Company, Grand Rapids, MI).

Leafhoppers collected from colony cages were released in the center of the arena where they could exhibit preference among the colored panels by orienting and leaping on to them. Tests were performed at random times between the hours of 11:00 am and 6:00 pm in a darkened room at 24°C. The arena was illuminated with an overhead fluorescent light source with an intensity of 915 lux measured on the floor in the center with a light meter (Extech Instruments, Waltham, MA). The arena was randomly rotated 45 degrees after each nymphal release and colored panels were randomly repositioned. Mixed nymphal life stages of each of all three species were released together in groups of 15-20 depending on availability. Colored panels were examined for trapped nymphs 1h after release in the arena. After observing the preferred color choices of the nymphs of *H. insolita*, the spectral reflectance of the cream and safety yellow panels as well as leaves and stalks of *S. halepense* was measured with a fiber optic spectrometer (USB-2000, Ocean Optics, Dunedin, FL). Leaves and stalks of *S. halepense* that were used for the reflectance measurements were chosen from healthy plants maintained as described previously.

Outdoor Dispersal Study

An arena was constructed outdoors and consisted of two concentric rings of cardboard tubes. The two rings were situated on a field of Bahiagrass, *Paspalum notatum* Flugge, at the North Florida Research and Education Center (NFREC) in Quincy, Florida. This field was chosen because *P. notatum* is not an acceptable host plant for *H. coagulata*. The field was mowed weekly to an approximate height of 6 cm. Weeds were removed daily from areas inside the arena. The two rings were concentric and were 10 and 20 m in diam. All tests with the 10-m ring were completed before testing with the 20-m ring. The cardboard tubes (30.5 in height and 7.6 cm in diam) were painted safety yellow and coated with Tangle-trap. They were placed upright on the ground at one-meter intervals along each of the rings. Small stakes were used to keep the tubes standing. Twenty individuals of each nymphal stage of *H. coagulata* were released in the center of either the 10- or 20-m ring for each test. Three days after each release, the cardboard tubes were checked for captured leafhoppers. Nymphal releases were replicated 3 times for the 10-m ring followed by three separate nymphal releases in the 20-m ring.

Jumping Distance of Nymphs

The jumping distance of 30 third and 30 fifth instars of the three leafhopper species was determined by introducing the nymphs onto a ‘platform’ placed in a water-filled 10-cm plastic Petri dish. The ‘platform’ was a 250-ml polyethylene cup 8 cm tall and 7 cm in diameter. The lid on the cup had a small slit to facilitate the introduction of aspirated nymphs. After the appropriate number of nymphs was collected, the cup was placed in the center of the water-filled dish and the lid carefully removed allowing the insects to crawl to the rim of the cup. The dish was centered onto a 2-m^2 corrugated plastic sheet (coreplast) that was coated with a thin layer of Tangle-trap. A single cardboard tube**,** the same dimensions as described previously, was painted safety yellow and was placed at the edge of each of the four corners of the coreplast sheet to provide a target for the nymphs. Ten nymphs of each stage were released between the hours of 4:00 and 6:00 PM in a darkened room with overhead fluorescent illumination and maintained at a temperature of 25°C. After 24 h nymphs were counted and the distance they jumped recorded. Each release was replicated three times.

Neonate Survival Study

Five egg masses of *H. coagulata*, *H. insolita*, and *O. nigricans* were collected on intact entire leaves of *V. unguiculata*, *H. esculentus,* and *G. hirsutum*, respectively, and placed into 10-cm diam plastic Petri dishes. The dishes were filled with approximately 10 ml of (1.2%) water agar (Fisher Chemicals cat. no. BP1423-500). A 5-cm circle was cut out of each dish lid and covered with nylon mesh. Dishes with egg masses were held at 25°C until eclosion. Thirty minutes after eclosion, the leaves were removed and the neonates were observed until death. Preliminary observations of dozens of cohorts of neonates for the three species were useful in determining approximate times of hatching and death. Death was determined when nymphs were not responsive to touch with a small sable hair paintbrush. Time measurements were rounded to the hour.

Statistical Analysis

Data from the visual acuity study were analyzed as one-way analysis of variance by general linear models procedures (GENMOD) (SAS 1990). Data from releases of individuals of each species were analyzed separately by instar. The proportion of each number of individuals of each instar ($n = 25$ to 73) that was trapped on the colored panels produced test statistics based on a pair-wise comparison with data from the safety yellow panels as the dependent variable. The proportion of the individuals captured by each of the colored panels was then compared by chi-square. Descriptive statistics (means and standard errors) were applied to data from the outdoor dispersal and neonate survival studies.

RESULTS

Visual Response to Color

The safety yellow-colored sticky panels captured a greater number of the nymphs of *H. coagulata*, regardless of instar, than the other colored panels of the arena. The proportions of nymphs captured on safety yellow was higher when compared to the proportion captured by the second most attractive color, cream yellow, and were 67.1% ($\chi^2 = 22.59$; $df = 99$; $P < 0.0001$), 81.4% ($\chi^2 = 12.29$; $df = 86$; $P < 0.0005$), 69.2% ($\chi^2 = 12.00$; $df = 87$; $P = 0.0005$), 71.4% ($\chi^2 = 2.2$; $df = 72$; $P < 0.0001$), and 81.5% ($\chi^2 = 6.2$; $df = 87$; $P < 0.0001$), for first through fifth instars, respectively (Fig. 1).

Significantly greater numbers of the nymphs of *O. nigricans* were attracted to the panels colored with safety yellow when compared to cream yellow (Fig. 1). The proportion of first through fifth instars trapped on the safety yellow panels was 71.4% ($\chi^2 = 11.81$; $df = 99$; $P < 0.005$), 78.8% ($\chi^2 = 10.22$; $df = 86$; $P < 0.01$), 88.9% ($\chi^2 = 11.40$; $df = 87$; $P < 0.005$), 86.7% ($\chi^2 = 10.22$; $df = 72$; $P < 0.001$), and 96.0% ($\chi^2 = 4115.7$; $df = 87$; $P < 0.0001$), respectively (Fig. 1).

A greater proportion of all nymphal stages of *H. insolita* were attracted to the cream yellow panels than any other color (Fig. 1). The cream yellow panels trapped 40.7, 54.8, 59.5, 51.7, and 63.3% of the first through fifth instars, respectively. However, only the third ($\chi^2 = 8.86$; $df = 87$; $P < 0.005$), and fifth ($\chi^2 = 5.10$; $df = 87$; $P < 0.05$) instar catches were statistically significant when compared to safety yellow.

The instances when the number of nymphs not captured was greater than that of captured nymphs on neon blue, neutral gray, or flat black panels were due to mortality associated with collection and handling or escape (Fig. 1).

Outdoor Dispersal Study

The average number of nymphs trapped on the cardboard tubes in the 10- and 20-m arenas was 6.0, 10.0, 10.4, 5.0, 7.0 and 3.0, 4.0, 3.3, 2.7, and 6.0 for first through fifth instars, respectively (Table 1). The weather during all tests was fair with an average day and evening temperature of 31.0° and 16.6°C, respectively.

Nymphs were observed feeding on seedlings of cut-leafed evening primrose (*Oenothera laciniata* Hill) that escaped detection during the weed check of the arena. These weeds have a fast rate of growth as well as a prostrate growth pattern making their detection difficult. This most likely reduced the number of nymphs captured on the cardboard tubes because they would remain feeding on these plants for several days and not disperse.

Jumping Distance of Nymphs

Nymphs that jumped off of the platform were trapped where they landed on the Tangle-trap-coated coreplast sheet. The longest recorded jump of third instars of *H. coagulata*, *H. insolita*, and *O. nigricans* was 68.0, 46.2, and 39.2 cm, respectively (Fig. 2). The fifth instars of *H. coagulata*, *H. insolita*, and *O. nigricans* had the longest jumps of 78.8, 29.7, and 45.5 cm, respectively (Fig 3). Many nymphs were observed walking down the side of the platform where they would encounter the water and proceed back to the top before jumping towards the yellow cardboard tubes.

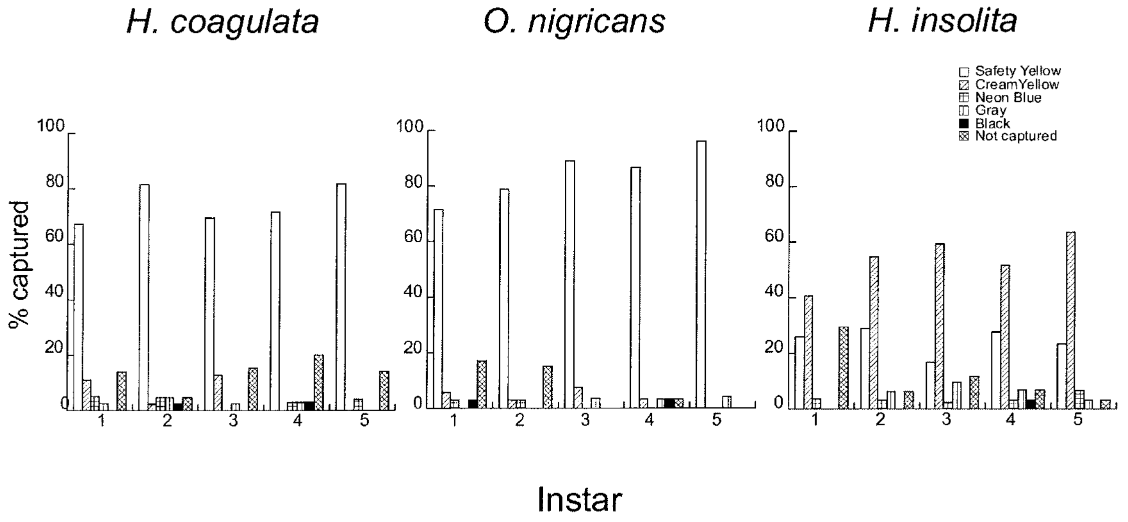

Fig. 1. Attractiveness of various colored panels to nymphal stages of *H. coagulata*, *O. nigricans,* and *H. insolita*.

TABLE 1. NUMBER OF *H. COAGULATA* NYMPHS CAPTURED BY YELLOW STICKY TRAPS IN OUTDOOR ARENAS 10 AND 20 METERS IN DIAMETER.

	Instar[1]				
Arena diameter	1	2	3	4	5
10 meters	6 ± 0.3	10 ± 0.3	10 ± 0.6	5 ± 0.0	7 ± 2.0
20 meters	3 ± 1.0	4 ± 1.0	3.3 ± 1.9	2.7 ± 0.7	6 ± 1.5

[1] Mean and SE, for each instar *n* = 20.

Neonate Survival Study

First instars of *H. coagulata*, *H. insolita*, and *O. nigricans* lived an average of 83.5, 70.5, and 83.0 h, respectively, when placed in the Petri dishes containing agar at 25°C (Table 2). Neonates eclosed from an individual egg mass within 20 min of each other, regardless of the number of eggs in each mass. Additionally, all nymphs from a single egg mass died within a 30-minute period, regardless of species. Nymphs that were held in the agar dishes probed the agar. They were quite mobile and moved around the entire inner surface of the agar dishes.

DISCUSSION

Insects are attracted to different spectra for a variety of reasons including resource finding and dispersal (Prokopy & Owens 1978). Yellow traps are especially attractive to many herbivorous insects including leafhoppers, because this spectrum represents what has been described as 'super normal' green (Staddon 1975). Spectra that represent potential optimal host plants would be expected to be and indeed are, attractive to the nymphs of *H. coagulata*, *H. insolita*, and *O. nigricans*. The adults of all three species are also attracted to yellow traps (Pollard et al. 1959; Ball 1979). Cream yellow was more attractive than safety yellow to the nymphs of *H. insolita* under the conditions of this study. The grassy host plants preferred by *H. insolita* grow in thick clumps with reduced light reaching the base of the stalks. In the field and in culture, nymphs are found only at the base of clumps of *S. halepense*. The spectral reflectance of stalks of *S. halepense* more closely resembles cream yellow than safety yellow (Fig. 4). Conversely, the spectral reflectance of the leaf blades of *S. halepense* is closer to safety yellow. Previous reports (Ball 1979) indicating the attractancy of yellow to the adults of *H. insolita* are not unexpected considering the similarity in the reflectance of leaf blades of *S. halepense* to safety yellow.

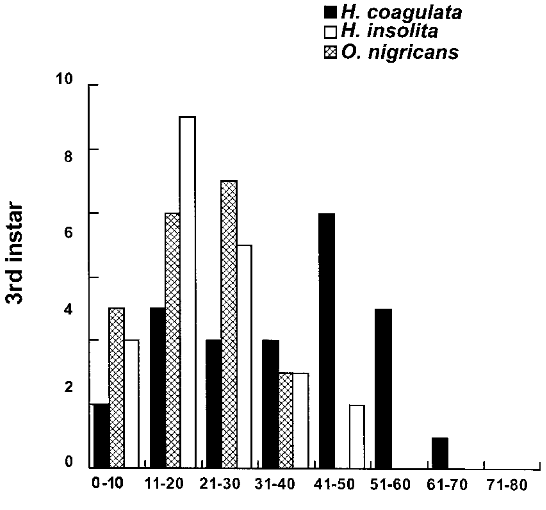

Fig. 2. Lengths of jumps in cm by third instar *H. coagulata* (*n* = 29), *H. insolita* (*n* = 27), and *O. nigricans* (*n* = 27).

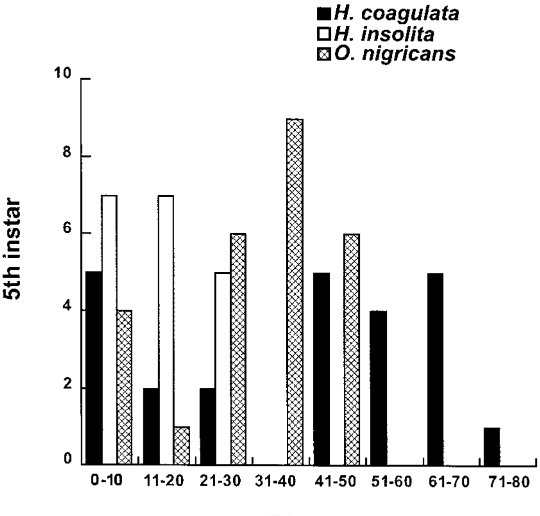

Fig. 3. Lengths of jumps in cm by fifth instar *H. coagulata* (*n* = 24), *H. insolita* (*n* = 19), and *O. nigricans* (*n* = 26).

TABLE 2. MEAN NUMBER OF HOURS NEONATES REMAINING ALIVE AFTER PLACEMENT INTO AGAR-FILLED PETRI DISHES.

	Species[1]		
	H. coagulata	*H. insolita*	*O. nigricans*
Mean survivorship in hours (± SE)	83.5 ± 0.3	70.5 ± 0.4	83.0 ± 0.4
Mean eggs per mass (± SE)	12.0 ± 1.6	19.0 ± 1.1	14.0 ± 1.0
Total *n* of neonates	72	93	74

[1] Data collected from 5 egg masses held at 25°C, >90% RH.

The dispersal ability of adult leafhoppers has been well documented (Taylor 1985). The majority of studies describing the dispersal of leafhoppers have focused primarily on movement patterns of the adults (Medler 1957; Cook 1967; Nestel & Klein 1995; Blackmer et al. 2004). The dispersal ability of leafhopper nymphs has received little attention. The nymphs of leafhoppers are capable of jumping long distances relative to their body size. This tremendous leaping ability is not only important for avoiding potential predators but for dispersing and finding host plants essential for development. We have shown that the nymphal instars of *H. coagulata* are capable of dispersing by walking and or jumping up to 10 meters in three days when placed in a field of Bahia grass. Under laboratory conditions we observed first, third, and fifth instars of *H. coagulata* moving 10 meters in one h on a flat surface.

In the field and in culture, females of *H. coagulata* and *O. nigricans* will readily oviposit on herbaceous and grassy host plants that are not suitable for successful nymphal development. The nutrient requirements of immature *H. coagulata* are different and much more restricted than those of the adults (Brodbeck et al. 1995). The adults prefer to feed on xylem fluid containing proportionally higher concentrations of amides; however, nymphs develop poorly on these diets (Brodbeck et al. 1995). Therefore, visual discrimination of wavelengths by the nymphal stages of leafhoppers is extremely important for their ability to find better quality host plants essential for successful development. Differential survivorship between instars of *H. coagulata* on a variety of hosts suggest the benefits of utilizing different host plants during development due to the changing nutritional requirements for immature stages

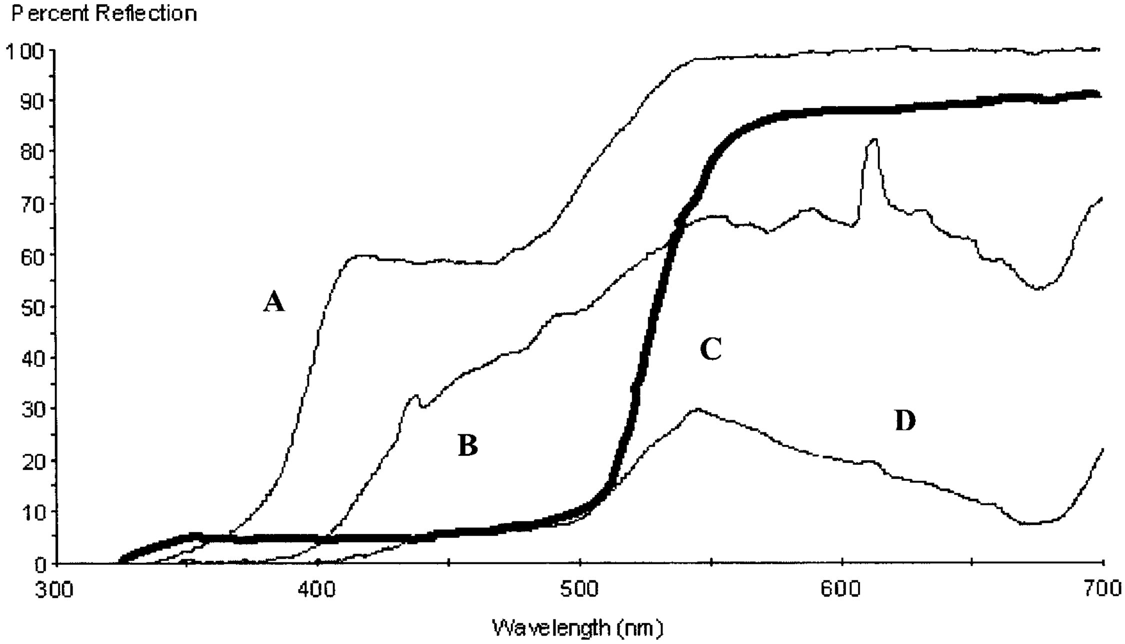

Fig. 4. Spectral reflectance of cream yellow, safety yellow, and *S. halepense* stalk and leaf blade. A, cream yellow; B, *S. halepense* stalk; C, safety yellow; D, *S. halepense* leaf blade.

and adults (Brodbeck et al. 1995; Brodbeck et al. 2004). Although egg masses of *H. coagulata* and *O. nigricans* can occasionally be found on *S. halepense* and *P. texicum*, Turner and Pollard (1959) reported the eggs masses of *H. insolita* were found almost exclusively on these two grasses as well as crabgrass, *Digitaria sanguinalis* (L.). Our field observations agree with previous reports. Additionally, in northern Florida, we also have found southern sandbur (*Cenchrus echinatus* L.) as another plant utilized by *H. insolita* as an oviposition host.

Under normal environmental conditions, newly eclosed neonates of all three species cluster together on the surface of the leaf near the egg mass for 2 to 3 h until their cuticle hardens. Nymphs were also observed to feed and become visibly larger in size during this time. After the initial period of clustering, nymphs would then disperse to the smaller stems of the host plant.

Excellent visual discrimination of wavelengths coupled with the ability to disperse and utilize a variety of host plants allow the nymphal stages of *H. coagulata* to successfully complete development within a dynamic nutritional environment of changing xylem fluid compositions. As the nutritional quality of host plants changes due to phenology and environmental conditions, instars of *H. coagulata* have the ability to disperse and seek better hosts. Future strategies related to the management of *H. coagulata* in California should consider the dispersal capabilities of the nymphal stages. In many sections of southern California, grape vineyards are located adjacent or near to citrus groves. *H. coagulata* has been shown to oviposit heavily on several varieties of citrus including lemon and orange (Al-Wahaibi & Morse 2000). Dispersal studies involving movement patterns of nymphs from citrus to adjacent or nearby vineyards have not been explored, but there is an obvious potential for such a phenomenon.

The survivorship of the neonates for up to three days without food represents an additional consideration for the accidental shipment of *H. coagulata*. Trucks, trains, or shipping containers that were used to transport plants infested with egg masses could potentially contain viable neonates. Under ideal conditions, neonate nymphs could survive transport for several days without feeding. Whether they would then be capable of feeding and becoming established remains to be investigated.

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REFERENCES CITED

ADLERZ, W. C. 1980. Ecological observations on two leafhoppers that transmit the Pierce's disease bacterium. Proc. Fla. State Hort. Soc. 93: 115-120.

ANDERSEN, P. C., AND B. V. BRODBECK. 1989a. Diurnal and temporal changes in the chemical profile of xylem exudates from *Vitis rotundifolia*. Physiol. Plant. 63-70.

ANDERSEN, P. C., AND B. V. BRODBECK. 1989b. Temperature and temperature preconditioning on flux and chemical composition of xylem exudates from muscadine grapes. J. Amer. Soc. Hort. Sci. 114: 440-444.

ANDERSEN, P. C., B. V. BRODBECK, AND R. F. MIZELL III. 1989. Metabolism of amino acids, organic acids and sugars extracted from the xylem fluid of four host plants by *Homalodisca coagulata*. Ent. exp. Appl. 50: 149-159.

ANDERSEN, P. C, B. V. BRODBECK, AND R. F. MIZELL III. 1995. Diurnal variations in tension, osmolarity, and the composition of nitrogen and carbon assimilates in xylem fluid of *Prunus persica*, *Vitis* hybrid, and *Pyrus communis*. J. Amer. Soc. Hort. Sci. 120: 600-604.

AL-WAHAIBI, A. K., AND J. G. MORSE. 2000. Oviposition of *Homalodisca spp*. (Hemiptera: Cicadellidae) and associated egg parasitism on citrus: cultivar effects, pp. 101-104 *In* M. S. Hoddle [ed.], Proceedings of the 2nd California Conference on Biological Control. University of California, Riverside.

BALL, J. C. 1979. Seasonal patterns of activity of adult leafhopper vectors of phony peach disease in north Florida. Environ. Entomol. 8: 686-689.

BLACKMER, J. L., J. R. HAGLER, G. S. SIMMONS, AND L. A. CANAS. 2004. Comparative dispersal of *Homalodisca coagulata* and *Homalodisca liturata* (Homoptera: Cicadellidae). Environ. Entomol. 33: 88-99.

BLUA, M. J., R. A. REDAK, D. J. MORGAN, AND H. S. COSTA. 2001. Seasonal flight activity of two *Homalodisca* species (Homoptera: Cicadellidae) that spread *Xylella fastidiosa* in Southern California. J. Econ. Entomol. 94: 1506-1510.

BRODBECK, B. V., R. F. MIZELL III, AND P. C. ANDERSEN. 1993. Physiological and behavioral adaptations of three species of leafhoppers in response to the dilute nutrient content of xylem fluid. J. Insect Physiol. 1: 73-91.

BRODBECK, B. V., P. C. ANDERSEN, AND R. F. MIZELL III. 1995. Differential utilization of nutrients during development by the xylophagous leafhopper, *Homalodisca coagulata*. Ent. exp. Appl. 75: 279-289.

BRODBECK, B. V., P. C. ANDERSEN, AND R. F. MIZELL III. 1999. Effects of total dietary nitrogen and nitrogen form on the development of xylophagous leafhoppers. Arch. Insect Biochem. Physiol. 42: 37-50.

BRODBECK, B. V., P. C. ANDERSEN, AND R. F. MIZELL III, AND S. ODEN. 2004. Comparative nutrition and developmental biology of xylem-feeding leafhoppers reared on four genotypes of *Glycine max*. Environ. Entomol. 33: 165-173.

BUGSPOT.ORG. 2003. http://www.bugspot.org/default.htm.

CHANG, C. C., P. J. PINTER JR, T. J. HENNEBERRY, K. UMEDA, E. T. NATWICK, Y. WEI, V. R. REDDY, AND M. SHREPATIS. 2000. Use of CC traps with different trap base colors for silver leaf whiteflies (Homoptera: Aleyrodidae), thrips (Thysanoptera: Thripidae), and leafhoppers (Homoptera: Cicadellidae). J. Econ. Ent. 93: 1329-1337.

Clark, C. J., P. T. Holland, and G. S. Smith. 1986. Chemical composition of bleeding sap from kiwi fruit vines. Ann. Bot. 58: 353-362.

Cook, W. C. 1967. Life History, Host Plants, and Migration of the Beet Leafhopper in the Western United States. USDA Tech. Bull. 1365. 1-122.

Gill, R. J. 1995. Glassy-winged sharpshooter, *Homalodisca coagulata*. Calif. Plant Pest Dis. Rep. 14: 64-65.

Hoback, W. W., T. M. Svatos, S. M. Sponer, and L. G. Higley. 1999. Trap color and placement affects estimates of insect family-level abundance and diversity in a Nebraska salt marsh. Ent. exp. Appl. 91: 393-403.

Horsfield, D. 1977. Relationships between feeding of *Philaenus spumarius* (L.) and the amino acid concentration in the xylem sap. Ecol. Entomol. 2: 259-266.

Kirk, W. D. J. 1984. Ecologically selective coloured traps. Ecol. Entomol. 9: 35-41.

Medler, J. T. 1957. Migration of the potato leafhopper-a report of a cooperative study. J. Econ. Entomol. 50: 493-497.

Mizell, R. F., and W. J. French. 1986. Leafhopper vectors of phony peach disease: Feeding site preference and survival on infected and uninfected peach, and seasonal response to selected host plants. J. Entomol. Sci. 22: 11-22.

Nestel, D., and M. Klein. 1995. Geostatistical analysis of leafhopper (Homoptera: Cicadellidae) colonization and spread in deciduous orchards. Environ. Entomol. 24: 1032-1039.

Pollard, H. N., W. F. Turner, and G. H. Kaloostian. 1959. Invasion of the southeast by a western leafhopper, *Homalodisca insolita*. J. Econ. Entomol. 52: 359-360.

Prokopy, R. J., A. P. Economopoulos, and M. W. McFadden. 1975. Attraction of wild and laboratory-cultured *Dacus oleae* flies to small rectangles of different hue, shades and tints. Ent. exp. Appl. 18: 141-152.

Prokopy, R. J., and E. D. Owens. 1978. Visual generalists with visual specialist phytophagous insects: host selection behavior and application to management. Ent. exp. Appl. 24: 609-620.

Prokopy, R. J., and E. D. Owens. 1983. Visual detection of plants by herbivorous insects. Annu. Rev. Entomol. 28: 337-364.

Prokopy, R. J., R. G. Adams, and K. I. Hauschild. 1979. Visual responses of tarnished plant bug adults on apple. Environ. Entomol. 8: 202-205.

Purcell, A. H., and N. W. Frazier. 1985. Habitats and dispersal of the leafhopper vectors of Pierce's disease in the San Joaquin Valley. Hilgardia 53(4): 1-32.

SAS Institute, Inc. 1990. SAS/STAT user's guide. SAS Institute, Inc., Cary, NC.

Staddon, J. E. R. 1975. A note on the evolutionary significance of "supernormal" stimuli. Amer. Nat. 109: 541-545.

Taylor, R. A. J. 1985. Migratory behavior in the Auchenorrhyncha, pp. 259-288 *In* L. R. Nault and J. G. Rodriguez [eds.], The Leafhoppers and Planthoppers. Wiley and Sons, New York, NY.

Turner, W. F., and H. N. Pollard. 1959. Life Histories and Behaviors of Five Insect Vectors of Phony Peach Disease. USDA Tech. Bull. 1188. 28 pp.

Vaishampayan, S. M., M. Kogan, G. P. Waldbauer, and J. T. Woolley. 1975. Spectral specific responses in the visual behavior of the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). Ent. exp. Appl. 18: 344-356.

Walker, W. F. 1974. Responses of selected Thysanoptera to colored surfaces. Environ. Entomol. 3: 295-304.

Webb, S. E., M. L. Kok-Yokomi, and D. J. Voegtlin. 1994. Effect of trap color on species composition of alate aphids (Homoptera: Aphididae) caught over watermelon plants. Florida Entomol. 77: 146-154.

Wells, J. M., B. C. Raju, H. Y. Hung, W. G. Weisburg, L. M. Paul, and D. J. Brenner. 1987. *Xylella fastidiosa* gen. nov., sp. nov: gram-negative, xylem-limited, fastidious plant bacteria related to *Xanthomonas* spp. Int. J. Syst. Bacterial. 37: 136-143.