



A Review of the Literature on *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphididae)

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A REVIEW OF THE LITERATURE ON *TOXOPTERA CITRICIDA* (KIRKALDY) (HOMOPTERA: APHIDIDAE)

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ABSTRACT

Literature is reviewed on the brown citrus aphid (BCA), *Toxoptera citricida* Kirkaldy, a serious pest of citrus recently introduced to Florida. Information is summarized on the aphid's distribution, host range, biology, population ecology, natural enemies, entomopathogens, transmission of plant viruses, and management.

Key Words: citrus tristeza virus, coccinellidae, control, parasitoids, predators, syrphidae

RESUMEN

Es revisada la literatura sobre el pulgón pardo de los cítricos, *Toxoptera citricida* Kirkaldy, una plaga de cítricos recién introducida en la Florida. La información está resumida en cuanto a la distribución del áfido, sus plantas hospederas, biología, ecología, enemigos naturales, entomopatología, transmisión de virus, y control.

The brown citrus aphid, *Toxoptera citricida*, (BCA) was first discovered in Florida in November, 1995 in Broward and Dade Counties. BCA is a major concern to citrus growers throughout the state because of its high efficiency in transmitting citrus tristeza virus (CTV). In view of the current interest in this insect, the purpose of this manuscript is to summarize information available on its biology, ecology, and management, and its role as a vector of CTV. The volume of literature on CTV warrants a separate review and I have therefore referenced only review articles and those specifically concerned with CTV transmission by the BCA.

The BCA, a.k.a. the oriental citrus aphid, was formerly called "*Aphis citricidus*" (1935-1960) and then *Toxoptera citricidus* before the species name was changed to its present form to agree in gender with the genus name (Stoetzel 1994a). In earlier literature (prior to 1940) it was commonly referred to as "*Aphis tavaresi*". Other synonyms include "*Myzus citricidus*" and "*Paratoxoptera argentinensis*", but usage of these names is rare. Essig (1949) lists "*Aphis citricola*" Van der Goot as synonymous with *T. citricida*, but Hille Ris Lambers (1975), upon re-examination of the original material collected by Van der Goot in Chile (Van der Goot 1912), concluded that *A. citricola* is synonymous with *Aphis spiraeicola* Patch, the green citrus aphid, and this was later confirmed by Eastop and Blackman (1988). *A. citricola* has been used as a synonym for *A. spiraeicola* in some literature (e.g. Komazaki 1982, 1988), although in pre-1950 publications it often appears as a synonym for BCA. Further confusion arises in studies where the BCA has been mistaken for its close relative *T. aurantii* Kirkaldy, and such cases are difficult to identify.

Many of the large number of publications which refer to BCA make only passing reference to it, or report it as one of many species collected in a general survey of citrus insects. I have therefore reviewed in detail only those articles which I felt provided original data, useful observations, or novel insights. The information has been organized under subject headings to provide readers with quick access to particular areas of interest.

DESCRIPTION & DISTRIBUTION

Toxoptera citricida was first described by Kirkaldy (1907) who placed it in the genus *Myzus*. Good descriptions can also be found in Essig (1949), Stroyan (1961), Bänziger (1977), Denmark (1978), Stoetzel (1994b), and Halbert and Brown (1996). The latter provides a detailed description complete with drawings and a key for distinguishing other aphids common in Florida citrus. The cytotaxonomy of the Genus *Toxoptera*, including BCA, has been described by Kurl (1980).

The BCA is thought to have originated in Southeast Asia (Kirkaldy 1907; Rocha-Peña et al. 1995) and is common throughout Asia, including China, Cyprus, India, Japan, Laos, Taiwan, Viet Nam (Essig 1949), Sumatra (Takahashi 1926; Mason 1927), Nepal (Knorr & Moin Shah 1971), Sri Lanka (Van Der Goot 1918; Peiris & Bertus 1958), Malaysia (Ting 1963; Ting & Arasu 1970), the Philippines (Gavarra & Eastop 1976) and Thailand (Bänziger 1977). Pacific islands with records include Hawaii (Kirkaldy 1907), Fiji (Lever 1940), Mauritius (D'Emmerez De Charmoy 1918; Mamet 1939), Réunion (Moreira 1967), Samoa (Laing 1927), and Tonga (Carver et al. 1994). BCA has been present in Australia for many years, possibly since the last century (Hely 1968) and can also be found in New Zealand (Cottier 1935).

Specimens of BCA collected by J. S. Tavares in Zambezi were described by Del Guercio in 1908 who named it "*Aphis tavaresi*" (Del Guercio 1917). Anderson (1914) and Theobald (1915) both reported collections of BCA from British East Africa. Other african countries with records include Cameroon, Congo, Ghana, Kenya, Morocco, South Africa, Tanzania, Uganda, Zaire, Zimbabwe (Essig 1949), Ethiopia (Del Guercio 1917; Abate 1988; Godfrey-Sam-Aggrey & Balcha 1988), Mozambique, (Saraiva 1929; Annecke 1963) Somalia (Theobald 1928; Chiaromonte 1933), and Tunisia (Halima et al. 1994). It is still absent from Israel (Bar-Joseph & Loebenstein 1973; Raccah & Singer 1987). Essig (1949) reported BCA as present in Italy, Malta and Spain, but these reports are questionable and remain unconfirmed. Although apparently present in Turkey (Yumruktepe & Uygun 1994) the BCA is still absent from much of mediterranean Europe (Mendel 1956; Jamoussi 1967).

Accidental introductions of BCA (and CTV) to South America are thought to have been made in either Brazil or Argentina during the 1920's when these regions were expanding their citrus production and importing material from Australia and South Africa (Rocha-Peña et al. 1995). Since that time it has spread to Bolivia (Squire 1972; Timmer et al. 1981), Peru (Roistacher 1988), Uruguay, Chile, and Colombia, (Rocha-Peña et al. (1995). It has even been found in jungle regions of the Peruvian Amazon (Ortiz 1981). BCA was first reported in Venezuela in 1976 (Geraud 1976), although it had been present in neighboring Guyana since at least 1968 (Bissessar 1968) and in Surinam since 1961 (van Hoof 1961). BCA first appeared in the Caribbean islands in Trinidad in 1985 (Yokomi et al. 1994). In 1991 it was found in Guadeloupe, Martinique and St. Lucia (Aubert et al. 1992) and in 1992, in Puerto Rico and the Dominican Republic (Lastra et al. 1992). It is now also present in Jamaica and Cuba (Yokomi et al. 1994). The BCA had spread into Central America as far north as Costa Rica by 1989 (Lastra et al. 1991, Voegtlin and Villalobos 1992), to Nicaragua and El Salvador in 1991 (Lastra et al. 1992, Lee et al. 1992), and to Belize in the fall of 1996 (Halbert 1996). In the fall of 1995, the BCA arrived in Florida in the Ft. Lauderdale area and, within one year, spread as far north as Melbourne on the east coast and Ft. Meyers on the west (Halbert 1997). By the summer of 1997, BCA was widely distributed throughout southern central and coastal regions of Florida, although it remained absent from much of the ridge citrus north of Highlands county.

HOST RANGE

The host range of the BCA is largely restricted to the Genus *Citrus*, although there are many reports of it colonizing other rutaceous plants. A list of the host plants from which BCA has been reported is provided in Table 1. The majority are woody shrubs, although some are perennial vines and annual herbs. Symes' (1924) report of a single infestation on cotton was from Rhodesia. Tao & Tan (1961) collected their specimens in Taiwan. Collections by Mondal et al. (1976) are from India and those of Carver (1978) are all from Australia. Van Harten & Ilharco (1975) and Remaudiere et al. (1985) reported collections from Africa. Ghosh & Raychaudhuri (1981) reported finding the BCA feeding on rosaceous fruit trees in India (apple, cherry, peach etc.—species names not provided), although I suspect this to be a possible mis-identification of *T. aurantii*. The record from white yam, *Dioscorea rotundata*, (Reckhaus 1979) is from Togo and that for *Passiflora* sp. (Bakker 1974), from Kenya. All collections reported by inspectors of the Florida Department of Agriculture and Consumer Services, Division of Plant Industry, are from Florida.

Most non-rutaceous plants are not normally suitable hosts for the BCA and it should be noted that collections from these plants do not imply they are suitable for development and reproduction of the aphid. These may be colonized occasionally by variant individuals when suitable citrus foliage is unavailable, or alates may be collected that are resting rather than feeding. Several generations of BCA were reared successfully in the laboratory on seedlings of West Indian cherry (a.k.a. acerola), *Malpighia punicifolia*, in Puerto Rico, although natural colonization of this plant could not be elicited by placing flushed seedlings adjacent to infested citrus (Michaud 1996). Halbert et al. 1986 has been erroneously cited as a host record for BCA on soybean, *Glycine max*, (Stibick 1993) but this work examined only transmission of soybean mosaic virus by BCA. Many of the anomalous occurrences (e.g. cotton) probably represent isolated events or colonizations by variant populations that are atypical of the species' normal host range, although others probably represent mis-identifications (Stoetzel 1994b).

TABLE 1. HOST RECORDS FOR THE BROWN CITRUS APHID. NOTE: ALL PLANTS IN THE GENUS CITRUS ARE HOSTS AND ARE NOT LISTED BY SPECIES.

Anacardiaceae*Mangifera* sp. (Carver 1978)*Mangifera indica* (Stibick 1993)*Rhus* sp. (Mondal et al. 1976)Bombaceae*Bombax ceiba* (Tao & Tan 1961)Burseraceae*Commiphora mollis* (Remaudière et al. 1985)Camelliaceae*Camellia japonica* (Tao & Tan 1961)Caryophyllaceae*Dianthus* sp. (Mondal et al. 1976)Dioscuraceae*Dioscorea rotundata* (Reckhaus 1979)Ebenaceae*Diospyros kaki* (Essig 1949)*Diospyros* sp. (Carver 1978)Ericaceae*Azalea* sp. (Essig 1949)*Rhododendron* sp. (Stibick 1993)Euphorbiaceae*Bridelia monoica* (Tao & Tan 1961)*Bridelia ovata* (Tao & Tan 1961)*Clutia abyssinica* (Remaudière et al. 1985)Fagaceae*Quercus* sp. (Mondal et al. 1976)Flacouatiaceae*Xylosna congestum* (Tao & Tan 1961)Juglandaceae*Engelhardtia spicata* (Mondal et al. 1976)Leguminosae*Cassia absus* (Mondal et al. 1976)*Cassia* sp. (Mondal et al. 1976)Lauraceae*Cinnamomum camphora* (Tao & Tan 1961)*Litsia polyantha* (Mondal et al. 1976)

TABLE 1. (CONTINUED) HOST RECORDS FOR THE BROWN CITRUS APHID. NOTE: ALL PLANTS IN THE GENUS CITRUS ARE HOSTS AND ARE NOT LISTED BY SPECIES.

Malpighiaceae

Malpighia puniceifolia (J. P. Michaud unpublished)

Malvaceae

Gossypium hirsutum (Symes 1924; Carver 1978)

Moraceae

Cudrania triscuspidata (Essig 1949)

Ficus carica (Essig 1949)

Ficus ingens (Remaudière et al. 1985)

Ficus retusa (Tao & Tan 1961)

Malclura cochinchinensis (Carver 1978)

Mysinaceae

Maesa chisea (Mondal et al. 1976)

Maesa sp. (Mondal et al. 1976)

Nyctaginaceae

Bougainvillea spectabilis (Remaudière et al. 1985)

Oxalidaceae

Oxalis pes-caprae Carver (1978)

Passifloraceae

Passiflora foetida (Mondal et al. 1976)

Passiflora sp. (Bakker 1974)

Rosaceae

Cottoneaster sp. (Carver 1978)

Crataegus sp. (van Harten & Ilharco 1975)

Eriobotrya sp. (Tao & Tan 1961)

Malus domestica (van Harten & Ilharco 1975)

Malus sylvestris (Mondal et al. 1976)

Pyrus communis (Essig 1949; van Harten & Ilharco 1975; Mondal et al. 1976)

Pyrus sp. Carver (1978)

Rubiaceae

Lasianthus chinensis (Tao & Tan 1961)

Rutaceae

Calodendrum capense (Carver 1978)

Choisya ternata (Carver 1978)

Citrifortunella floridana (Fla. Dept. Agr. & Cons. Serv., D.P.I., Gainesville, FL.)

Citrifortunella microcarpa (Fla. Dept. Agr. & Cons. Serv., D.P.I., Gainesville, FL.)

Citrus spp.

Clausena lanisum (Fla. Dept. Agr. & Cons. Serv., D.P.I., Gainesville, FL.)

TABLE 1. (CONTINUED) HOST RECORDS FOR THE BROWN CITRUS APHID. NOTE: ALL PLANTS IN THE GENUS CITRUS ARE HOSTS AND ARE NOT LISTED BY SPECIES.

<i>Eremocitrus glauca</i> (Carver 1978)
<i>Evodia hupehensis</i> (Meneghini 1948)
<i>Geijera parviflora</i> (Carver 1978)
<i>Flindersia xanthoxyla</i> (Carver 1978)
<i>Fortunella</i> sp. (Stibick 1993)
<i>Fortunella maragarita</i> (Carver 1978)
<i>Murraya exotica</i> (Stibick 1993)
<i>Murraya paniculata</i> (Tao & Tan 1961; Carver 1978)
<i>Poncirus trifoliata</i> (Essig 1949; Tao & Tan 1961; Carver 1978)
<i>Severinia buxifolia</i> (Carver 1978)
<i>Toddalia asiatica</i> (Essig 1949)
<i>Triphasia trifolia</i> (Fla. Dept. Agr. & Cons. Serv., D.P.I., Gainesville, FL.)
<i>Vepris undulata</i> (Carver 1978)
<i>Zanthoxylum fagara</i> (Fla. Dept. Agr. & Cons. Serv., D.P.I., Gainesville, FL.)
<i>Zanthoxylum ornatum</i> (Mondal et al. 1976)
<i>Zanthoxylum</i> sp. (Mondal et al. 1976)
<u>Ternstroemiaceae</u>
<i>Schima wallichii</i> (Mondal et al. 1976)
<u>Ulmaceae</u>
<i>Ulmus procera</i> (Carver 1978)
<i>Trema orientalis</i> (Essig 1949)
<u>Urticaceae</u>
<i>Boehmeria</i> sp. (Mondal et al. 1976)

BASIC BIOLOGY

The BCA feeds only on newly expanded shoots, leaves and flower buds of its host plants. Newly expanding terminals are suitable for BCA growth and reproduction for usually a period of only 3-4 weeks, depending on environmental conditions. Therefore, a BCA colony has a relatively narrow time window within which to mature and produce alates prior to the demise of its food resource. This is an important consideration in the development of management strategies since only those colonies exporting alates are of importance in terms of the secondary transmission of CTV. In this context it is unfortunate that no laboratory studies have yet examined the environmental conditions that induce the production of alate morphs in BCA. Crowding of nymphs seems to induce alate formation (J. P. Michaud unpublished), but declining food quality and temperature may also play a role. However, once shoot hardening progresses beyond some threshold point, BCA nymphs either fail to mature or leave the terminal in search of new flush on other branches.

Despite the fact that the BCA can apparently move long distances in a short period, it is not clear to what extent this results from natural dispersal as opposed to accidental movement by man. My own observations indicate that the majority of alates

probably do not fly far from their nascent colony. This is borne out by the fact that foci of BCA infestations are often localized in citrus groves and can be observed to expand more slowly than those of *Aphis gossypii* (Gottwald et al. 1995). Furthermore, suction and yellow-trap catches often underestimate the number of active BCA colonies in a particular vicinity (e.g. Yokomi et al. 1997). Consequently, BCA infestations tend to be endemic in citrus groves, surviving at low density on bits of asynchronous flush and root sprouts until a new flush cycle provides sufficient food for a population outbreak. Weather conditions such as thermal updrafts or tropical storms may play some role in dispersal. For example, the discovery of BCA in Jamaica in 1993 was preceded by the passage of a strong tropical depression (Lee et al. 1995, p. 209). However, long-range dispersal by alates is probably rare and movement of infested plant material by humans may be a more important mechanism. Gottwald et al. (1993) estimated very low probabilities for colonization of Florida citrus by BCA through arial dispersal from the Caribbean, specifically Cuba, but the true mechanism by which it ultimately arrived in Florida was never established.

The earliest detailed study of the biology and life history of the BCA is by Symes (1924) in Southern Rhodesia. The author reported as many as 30 generations per year, depending on availability of citrus flush. The time for development to adult was estimated to range from 8 to 21 d. The BCA is anholocyclic (without sexual generations) throughout most of its range in tropical and subtropical regions. In New Zealand, Cottier (1935) observed the anholocyclic apterae to overwinter, although their development was greatly retarded. Komazaki et al. (1979) observed a holocyclic generation of BCA under temperate conditions in Japan. However, the authors found very few overwintering eggs of BCA on trees compared to the numbers of *A. gossypii* and *A. spiraeicola* eggs. Furthermore, although hatching rates were similar across species, the survival rate of hatched BCA nymphs was very low and surviving adult fundrices produced no second generation. In the laboratory, Komazaki (1990) compared the development and reproduction of BCA fundrices hatched from eggs with that of subsequent viviparous generations and found that the former took longer to mature at all temperatures tested, and had a lower reproductive rate. Because of low overwintering populations, the BCA is the last of the citrus aphids to appear on spring flush in Japan (Komazaki 1988).

Takanashi (1989) compared the reproductive rates of alate and apterous morphs of the BCA feeding on *Citrus natsudaidai* in the laboratory. The pre-reproductive period was longer for alatae than for apterae at both 20° and 25°C, and estimates of both age-specific fecundity and net reproductive rate were higher for apterae at both temperatures. Komazaki (1982) determined that the maximum intrinsic rate of increase for the BCA occurred at a constant temperature of 27°C, even though the fecundity and net reproductive rate of individual apterous females was maximal at 21.5°C. In general, the pre-reproductive period, post-reproductive survival, and longevity were all shortened as temperature increased.

Galatoire (1983) calculated life table statistics for 3 cohorts of BCA grown in outdoor enclosures in Argentina. She reported mean life expectancies for apterous females ranging from 28 to 48 d; the shorter life expectancies correlated with higher mean daily temperatures and reduced duration of the third and fourth nymphal instars. Age-specific mortality rates varied among cohorts, presumably in response to the different ambient conditions they experienced, although >80% of individuals survived to become adults in all 3 cohorts. Daily fecundity of adult apterae averaged between 5 and 6 nymphs per female per day, and total fecundities ranged between 73 and 81 nymphs. The highest mean replacement rate (59 females/female) was observed in a cohort which experienced a moderate regime of daily temperatures, but the highest instantaneous rate of increase was observed in the cohort experiencing the highest

mean daily temperatures. This result was attributed to reduced generation time under the warmer conditions.

There is also evidence that the performance of BCA varies on different species of citrus. Komazaki (1982) observed differences between BCA reared on *Citrus unshui* and those reared on *C. aurantium*. He also discovered a temperature-host plant interaction effect on development. *C. unshui* yielded aphids with shorter pre-reproductive periods and greater longevities and fecundities than did *C. aurantium*. The threshold temperature for BCA development was also lower on *C. unshui* (8.0°C) than on *C. aurantium* (8.4°C). However, the survival rate on *C. unshui* was 0% at 29.7°C, but 60% on *C. aurantium* at 29.9°C.

Komazaki (1984) succeeded in rearing 4 generations of BCA on an artificial diet of 20% sucrose at pH7, but the growth rate, fecundity, and longevity of these aphids were reduced relative to those fed on citrus.

POPULATION DYNAMICS

Given that the BCA feeds only on tender new citrus terminals, many authors have observed population outbreaks to occur about 2 wk following heavy rainfall that induces citrus flush (Schwarz 1965a; Klas 1979). Typically, there are two BCA population peaks per year in subtropical regions, one in the spring and another in the fall. This has been observed in Argentina (Nickel & Klingauf 1985), Australia (Khan 1976; Carver 1978), Brazil (Chagas et al. 1982), Kenya (Seif & Islam 1988), Puerto Rico (J. P. Michaud unpublished), Taiwan (Tao & Tan 1961), and Japan (Nakao 1968; Shindo 1972). Komazaki (1981) reported three annual population peaks in Japan during one year's observations.

Geraud (1979) studied the life cycle and population dynamics of BCA in Venezuela, but I was unable to obtain a copy of this thesis. Nickel & Klingauf (1985) studied BCA population dynamics for a 2-yr period in Misiones, Argentina. They compared the longevity of exposed colonies with those in exclusion cages and others growing under climate-controlled conditions indoors. The maximum longevity of exposed outdoor colonies was only 12 d (mean = 7.5) compared with a range of 16-26 d in the exclusion cages and 19-33 d under temperature-controlled conditions. The improved survival of colonies in the exclusion cages was attributed, in part, to their protection from natural enemies, primarily *Cycloneda sanguinea* (Coleoptera: Coccinellidae) and, in part, to physical protection afforded by the enclosures. Periods of heavy rain and hot dry weather were both correlated low BCA population densities. Heavy rainfall appeared to impede flight activity as measured by catches in yellow bowl traps. Anderson (1914) also noted a popular belief that BCA populations are checked by heavy showers. However, Nickel & Klingauf (1985) concluded that temperature is an important determinant of BCA population trends and that temperature extremes in winter and summer had a negative impact on development and flight activity. A negative effect of high temperatures on BCA populations was also inferred by Hall (1930).

NATURAL ENEMIES

The BCA is unusual as an aphid species with few effective parasitoids throughout its range (Stary 1970). One exception may be Japan where *Lysiphlebia japonica* Ashmead (Hymenoptera: Aphidiidae) reportedly exerts some level of control (Kato 1969, 1970; Takanashi 1990, 1991). This species was imported to Florida in 1996 and released at 29 sites throughout the state, and to Puerto Rico where it was released at 2 sites. To date (Aug, '97) there no have been no recoveries of this insect from Puerto

Rico. In April 1997, a few weeks after releases were made, a number of specimens of *L. japonica* were recovered at several sites in St. Lucie County, Florida. This would indicate at least one generation of *L. japonica* was successful under field conditions in Florida. However, it is still uncertain whether permanent establishment of this species will occur and, if so, whether any significant control of BCA will result.

Symes (1924) reports collecting a single unidentified Braconid (probably an Aphidiid) parasitoid from BCA in South Africa, although Abate (1988) found no parasitoids of BCA in his survey of citrus disease vectors in Ethiopia. *Lysiphlebus testaceipes* Cresson attacks BCA in Venezuela (Stary & Cermeli 1989) and in Brazil (Gallo et al. 1978), although Murakami et al. (1984) did not recover this or any other species of parasitoid from BCA during their survey in the Cerrados region. *L. testaceipes* is frequently observed parasitizing the BCA in Puerto Rico, but fewer than 5% of mummies yield viable adults (Yokomi & Tang 1996). In Cuba, *L. testaceipes* frequently parasitizes *T. aurantii* but is only rarely found on BCA (Batista et al. 1995). Carver (1984) found that *L. testaceipes* (imported to Australia) readily oviposited in BCA but rarely completed development. Similarly, Carver & Woolcock (1985) reported incomplete parasitism of BCA by *Aphelinus asychis* Walker in Australia. *L. testaceipes* is frequently found parasitizing BCA in most citrus-growing regions of Florida, although very few mummies can be found with emergence holes (J. P. Michaud unpublished).

Nickel & Klingauf (1985) reported that, in Argentina, *Aphidius colemani* Viereck parasitized up to 50% of BCA in some colonies in the fall, although no information is presented on the survival of the parasitoid in this host. Stary & Cermeli (1989) made collections of *A. colemani* from 10 spp. of aphids in Venezuela, but did not find it attacking BCA. Valencia & Narciso Cárdenas (1973) reported collection of *Aphidius matricariae* Haliday from BCA in Peru. De Huiza & Ortiz (1981) collected 4 spp. of aphidiid wasps from aphids in Peru, including *A. colemani* and *A. matricariae*, but only *L. testaceipes* emerged from BCA. Carver (1978) noted parasitism of BCA by *A. colemani* in Australia, although she noted that such mummies were rare in the field. Messing & Rabasse (1995) observed that *A. colemani* from Réunion Island oviposited in various aphid species in which the wasp did not complete development. Newman (1924) reports *Aphelinus mali* (Aphelinidae) emerging from BCA in Western Australia. Flanders & Fisher (1959) reported collections of *Lipolexis* sp., *Trioxys* sp., and two *Aphelinus* spp. from BCA in Kwantung Province, China. Yokomi et al. (1993) reported a collection of *Lipolexis scutellaris* and *L. gracilus* from BCA in Malaysia and Tang et al. (1996) report *Aphelinus spiraeocolae* Evans and Shauff attacking BCA in China.

In most studies of the natural enemies of BCA, emphasis has been placed on predatory insects, primarily ladybeetles (Coleoptera: Coccinellidae), and hoverflies (Diptera: Syrphidae) as species causing the greatest mortality to BCA populations. Kato (1968) reported *Eristrophe balteatus* de Geer, *Paragus quadrifasciatus* Meigen, *Sphaerophoria cylindrica* Say, and *Syrphus serarius* Wiedemann as hoverfly species feeding on BCA in Japan. Symes (1924) reported *Xanthogramma aegyptium* Wiedemann as the most common syrphid preying on BCA in Rhodesia. Catling (1970) reported *Allograpta pfeiferi* Bigot and *Baccha* sp. as syrphid predators of BCA in South Africa. Abate (1988) found *Sphaerophoria rueppellii* Wiedmann attacking BCA in Ethiopia, as well as *Leucopis* spp. (Diptera: Chamaemyiidae). Lever (1946) lists *Xanthogramma* (*Ischiodon*) *scutellare* F. and *Syrphus corollae* var. *vitiensis* Bez. as the important syrphids attacking aphids, including BCA, in Fiji. Goncalves & Goncalves (1976) collected 10 species of syrphids from aphids in São Paulo and Rio de Janeiro states in Brazil. Those attacking BCA included *Allograpta exotica* (Wiedmann.), *Ocyptamus gastrotractus* (Wiedmann) (= *Baccha gastrotracta*) and *Pseudodorus clavatus* (F.) (= *Baccha clavata*). Bartoszeck (1980) also reported the latter two spp. as predators of BCA in the state of Maranhao, Brazil. Leal et al. (1976) reported *O. gas-*

troctactus to be the most abundant syrphid on BCA in Pernambuco, Brazil and concluded it was the only predator affording any control. *P. clavatus* and *Ocyptamus fuscipennis* Say are the most abundant syrphids attacking BCA in Puerto Rico, although *Allograpta exotica*, *A. radiata*, and *Ocyptamus cubanus* have also been collected (J. P. Michaud unpublished). Valencia and Nárciso Cardenas (1973) collected *P. clavatus* and *Allograpta* spp. in their survey of aphid natural enemies in Peru, but did not find them feeding on BCA. *P. clavatus* is also abundant on BCA in Cuba (Batista et al. 1995) and in Trinidad where *O. gastroctactus* is also important (White 1995). Collections from Florida suggest that *P. clavatus* is by far the most abundant and ubiquitous syrphid on BCA, but *Toxomerus geminatus* (Say) and *Leucopis* sp. (Diptera: Chamaemyiidae) have also been recorded (J. P. Michaud unpublished).

Michaud (1996) observed relatively good biological control of BCA in Puerto Rico throughout the summer months of 1996. Fewer than 5% of suitable citrus terminals were infested with BCA in most citrus groves between May and August, largely due to the activities of various species of coccinellids, the adults and larvae of which destroyed many colonies in their early stages. The following species of coccinellids have been collected from BCA in Puerto Rico: *Chilocorus cacti* (L.), *Cladis nitidula* (F.), *Coleophora inaequalis* (F.), *Coleomegilla innotata* (Mulsant), *C. sanguinea limbifer* (L.), *Diomus* sp., *Egius platycephalus* Mulsant, *Hippodamia convergens* (Guerin), *Hyperaspis* sp., *Olla v-nigrum* (Mulsant), *Procula feruuginea* (Oliver), and *Scymnus* (*Schymnus*) *floralis* (F.) (J. P. Michaud unpublished). The most abundant species were *C. inaequalis* and *C. sanguinea*. Small species such as *Diomus* sp., *Hyperaspis* sp. and *S. floralis* prey only on early instars of BCA and appear to have only minimal impact on aphid populations. *C. sanguinea* is the most common coccinellid on BCA in the Dominican Republic (Borbón et al. 1992) and Cuba (Batista et al. 1995). It is also abundant feeding on BCA in Venezuela (Morales & Burandt 1985) and Brazil (Lara et al. 1977; Bartoszeck 1980). Additional coccinellid spp. recorded from BCA in Brazil include *Cleothera* sp., *Diomus* sp., *Exoplectra* sp., and *Scymnus* sp. (Bartoszeck 1980). Chagas et al. (1982) concluded that the coccinellids *C. sanguinea*, *Nephaspis* sp., *Stethorus* sp. and *Scymnus* sp. in particular, were the most important predators of BCA in São Paulo state and provided data on their seasonal abundance in citrus. Other coccinellids collected from BCA in this study included *Cleothera* sp., *Cycloneda conjugata*, *Delphastus* sp., *Hyperaspis* sp. *Lindorus lophanthus*, *Neaporis* sp., and *Pentilia* sp. Valencia and Narciso Cárdenas (1973) reported *C. sanguinea* and *H. convergens* as predators of BCA in Peru. Coccinellid species attacking BCA in Florida include *Brachiacantha decora* (Casey), *Brachiacantha dentipes* (F.), *C. cacti*, *Chilocorus stigma* (L.), *Coccinella septempunctata* L., *C. inaequalis*, *Curinus coeruleus* (Mulsant), *C. s. sanguinea*, *Harmonia axyridis* (Pallas), *H. convergens*, *Hyperaspis ornatella* Gordon, *O. v-nigrum*, and *Scymnus* sp. (J. P. Michaud unpublished).

Kato (1969) listed *Scymnus hilaris* Motschulsky, *Coccinella septempunctata bruckii* Mulsant, *H. axyridis*, *Propylaea japonica* (Thunberg), *Chilocorus kuwanae* Silvestri and *Hyperaspis japonica* (Crotch) as coccinellid species attacking BCA in Japan. Komozaki (1981) reported that *S. hilaris* was an important predator of BCA in Japan and that its numerical response to increasing BCA populations was relatively good. Nakao (1968) reported *Stethorus japonica* Kamiya as another coccinellid species preying on BCA in Japan, although *Telsimia nigra* Weise and *C. kuwanae* were the most abundant species in that study.

Maelzer (1978) states that *Leis conformis* (Boisduval.) is an important predator of BCA in South Australia. *Cheilomenes propinqua* is listed by Catling (1970) as a coccinellid feeding on BCA in South Africa. Symes (1924) lists *Chilomenes lunata* F., *Alesia bohemani* Mulsant, *A. geisha* Gorb., *Halyzia exiguenotata* F., *Lotis* sp., and *Scymnus trepidulus* Weise as coccinellids feeding on BCA in Rhodesia, noting that the

first two species were most common. Abate (1988) lists *Exochomus* sp., *Hyperaspis senegalensis* (Mulsant), *Pharoscymnus madagassus* (Weise) and *Pharoscymnus* sp. as coccinellid predators of BCA in Ethiopia. Lever (1946) listed *C. inaequalis* and *Coccinella repanda* var. *transversalis* F. as important predators of aphids in Fiji, including BCA.

A study by Nickel & Klingauf (1985) in sub-tropical Argentina indicated that *C. sanguinea* was the most important predator in that particular region. They measured predator-prey ratios varying between 1-40 and 1-10, suggesting relatively good levels of biological control which they attributed to the semi-natural conditions surrounding their study sites. Recruitment of predators from outside citrus groves was judged to be an important factor. The relatively low numbers of predators present in winter months (May-August) was attributed to low rates of recruitment resulting from low BCA population densities.

Lacewings (Neuroptera) are also predators of aphids that may contribute to suppression of their populations. Nakao (1968) reports *Micromus novitus* Navás and *Eumicromus numerosus* Navás (Hemerobiidae) as lacewings feeding on BCA in Japan. Valencia and Narciso Cárdenas (1973) collected *Chrysopa* sp. (now *Chrysoperla* sp. chrysopidae) feeding on BCA in Peru. Chagas et al. (1982) reported the seasonal abundance of *Chrysopa* sp., *Hemerobius* sp. and *Megalomus* sp. found feeding on BCA in São Paulo state, Brazil. *Nusalala uruguaya* (Hemerobiidae) has been recorded from BCA in Brasil (Souza et al. 1989) and a *Ceraeochrysa* sp. (Chrysopidae) occurs on BCA in Puerto Rico (J. P. Michaud unpublished), although it is rare. Abate (1988) reported *Anisochrysa boninensis* (Okamoto) as a Chrysopid predator of BCA in Ethiopia. White (1995) reported *Chrysopa silvana* Naval from BCA in Trinidad, although it was not deemed a significant source of mortality. To date, *Ceraeochrysa lineaticornis* (Fitch), and *Micromus posticus* (Walker) have been collected from BCA in Florida (J. P. Michaud unpublished).

Several studies have suggested that BCA may be toxic to certain predators, or nutritionally inadequate for their successful development. Tao & Chiu (1971) reported that 5 of 13 coccinellid species fed BCA, including *C. repanda*, suffered injury or death, while the others remained unaffected. Souza et al. (1989) reported that larvae of *N. uruguaya* fed BCA did not survive to pupation and Tao & Chiu (1971) reported similar findings for two species of *Chrysopa*. However, Venzon & Carvalho (1993) found *Toxoptera* spp. (BCA?) to be a suitable diet for *Ceraeochrysa cubana* (Hagen) in Brasil and *Ceraeochrysa* sp. in Puerto Rico has been successfully reared to adult stages on BCA (J. P. Michaud unpublished). Parker & Singh (1973) found that the coccinellids *Chilocorus politus* Muls., *Coccinella arcuata* F. and *Micraspis (Alesia) discolor* (F.) all expressed a non-preference for BCA in feeding trials, although *Menochilus (Cheilomenes) sexmaculatus* (F.) did not. Morales & Burandt (1985) found that *C. sanguinea* collected in Venezuela and fed BCA in the laboratory failed to complete development. On the other hand, *C. sanguinea* and *C. inaequalis* collected in Puerto Rico developed normally and had good survival on an exclusive diet of BCA (J. P. Michaud unpublished), suggesting that there may exist regional differences between biotypes of predator species with respect to their ability to utilize BCA as food. Interestingly, no studies have found any indication of BCA toxicity to syrphids.

Ants are notorious for interfering with the beneficial activities of aphid predators and/or parasites and BCA may sometimes benefit from a mutualistic association with certain ant species. Observing ant and aphid populations in a citrus orchard in Japan, Shindo (1972) concluded that the ant *Pristomyrex pungens* Mayr interfered with the behavior of BCA predators (syrphids and coccinellids). Tao & Wu (1968) recommended the removal of ant nests in the vicinity of BCA-infested trees in conjunction with chemical treatments for control of the aphid. Bartoszeck (1980) recorded the ants *Eu-*

cryptocerus placidus (F. Sm.) and *Camponotus godmani* Forel in association with BCA in Brazil. Fire ants, *Solenopsis invicta* Buren, are often observed tending BCA in Florida and Puerto Rico (J. P. Michaud unpublished) and are known to remove parasitized aphids and mummies of *L. testaceipes* from aphid colonies (Vinson & Scarborough 1991). They have also been observed removing predatory larvae and dead aphids from BCA colonies, and carrying live aphids to fresh, uninfested terminals (J. P. Michaud unpublished). Other ant species observed tending BCA in Puerto Rico include *Brachymyrmex obscurion* Ford, *Monomorium ebeninum* Ford, *Paratrechina longicornis* (Latrielle), *Pheidole fallax* Mayr, *Solenopsis globularia* (F. Smith), and *Wasmannia auropunctata* (Roger) (J. P. Michaud unpublished). In Florida, *B. obscurion*, *Camponotus sexguttatus* (F.), and *Pseudomyrmex ejectus* (F. Smith) have been collected at BCA colonies (J. P. Michaud unpublished).

ENTOMOPATHOGENS

Rondon et al. (1981) found the entomophagous fungus *Verticillium lecanii* (Zimm.) Viégas to be the most important biological control agent during population outbreaks of the BCA in the Carabobo and Yaracuy states of Venezuela in 1979 and 1980. The predators reported as important in this study were *C. sanguinea*, *O. gastrostactus* and *Zelus* spp. The authors noted that ideal ambient conditions for sporulation and germination of the fungus (temperatures ranging from 18-24°C at a high relative humidity) were prevalent during the 2-yr period of the study. The fungus was reported to survive unsuitable conditions in dried aphid mummies, and on aphid cadavers that occur on suckering shoots growing in the interior of the tree where they are protected from direct sunlight. The most suitable nutrient media for growing the fungus in the laboratory were 523, nutrient agar, malt-agar, and PDA. These workers stated that "the elevated pathogenicity on nymphs of different instars, adults, apterous and alate, for which there was >80% mortality in the first 2 wk, prevented culmination of the insect's life cycle". However, the infection rate of 1.2% of colonies reported by White (1995) in Trinidad is probably a more typical value for the natural occurrence of this fungus on BCA. *V. lecanii* has also been recovered from BCA in Puerto Rico, where it appears to be a sporadic and localized source of aphid mortality (J. P. Michaud unpublished). De Romero and Romero (1985) evaluated mycelial growth and conidia yield of *V. lecanii* collected from BCA in Argentina on 2% potato agar. Batista et al. (1995) reported satisfactory results with applications of both *V. lecanii* (Micotal-1 & Y-57 strains) and *Paecilomyces fomesoroseus* (INISA V strains) against the BCA in Cuba, despite the fact that they observed no natural attacks by entomopathogenic fungi. Samways & Grech (1986) found that the fungus *Cladosporium oxysporum* (Berk. and Curt.) had considerable impact on BCA populations in field trials in South Africa, which they attributed to the action of an unidentified toxin, rather than direct hyphal growth. Other fungi are currently under evaluation for pathogenicity to BCA.

CTV TRANSMISSION

CTV is a closterovirus which causes multiple disease syndromes in citrus. The most important are quick decline of trees on sour orange rootstock and stem-pitting in susceptible scions irrespective of rootstock. Tristeza is possibly the most serious virus disease of citrus world-wide and yet it is poorly understood. It is not yet possible to attribute particular symptoms on a particular citrus cultivar to specific viral sequences, nor is it known which sequences influence transmissibility by its most efficient insect vector, the BCA. Meneghini (1946) in Brazil presented the first evidence of CTV transmission by the BCA. Meneghini (1948) showed semi-persistent transmis-

sion of CTV; viruliferous BCA starved for 48 h lost their ability to transmit the virus, while a 24 h starvation period did not affect the percentage of trees infected. This was later confirmed by Costa & Grant (1951). Kennedy et al. (1962) suggested that tristeza virus was probably stylet borne. Retuerma & Price (1972) claimed that both acquisition and transmission of CTV by BCA can occur within a few seconds of feeding and concluded this was proof that CTV was stylet borne, a conclusion subsequently questioned by others. Singh (1978) successfully achieved CTV transmission feeding leaf and bark extracts to BCA through a stretched parafilm membrane and suggested that CTV may not be a typical stylet-borne virus, but may also be transmitted in a circulative, non-propagative manner. Such bimodal transmission was also suggested by Lim & Hagedorn (1977) but this explanation is not generally accepted and further evidence of short probing transmission is required (Bar-Joseph et al. 1979). The fact that CTV is phloem-limited makes transmission by brief probing less likely. The current consensus is that CTV transmission best fits the semi-persistent mode (Bar-Joseph et al. 1979; Raccach & Singer 1987) in which the virus is acquired and transmitted by aphids with feeding times ranging from several minutes to several hours, but usually not by brief probing.

Historically, introduction of the BCA has invariably resulted in the accelerated spread of CTV throughout entire citrus growing regions, the best example being the virtual destruction of the citrus industry in Brazil and Venezuela during the 1970's, most of which was rooted on sour orange (Lee et al. 1995). A number of studies have shown that the BCA is a relatively efficient vector of CTV when compared with other aphids that feed on citrus. Schwartz (1965b) observed that infections of trap plants with BCA were closely correlated with the numbers of BCA collected from the plants. In the Philippines, Celino et al. (1966) showed that BCA was a more effective vector than either *T. aurantii* or *A. gossypii*. Sharma (1989) tested 20 isolates of CTV and found that 12 were most efficiently transmitted by BCA, 5 by *A. gossypii*, and 3 by *Myzus persicae*. Yokomi and Damsteegt (1991) quantified the efficiency with which the BCA transmitted CTV in comparison to *A. gossypii* and found the former species to be significantly more efficient. Balaraman & Ramakrishnan (1979) showed that BCA was more efficient than either *A. gossypii* or *T. aurantii* at transmitting the 2 strains of CTV they tested, and that higher percentage transmission occurred with the severe strain than with the mild strain. The authors found that a minimum of 15 viruliferous aphids/plant were required for 100% transmission when feeding periods were 24 h each for acquisition and transmission.

A number of studies have shown that variant strains of CTV differ in their transmissibility by aphids (Bar-Joseph & Loebenstein 1973; Raccach et al. 1978; Raccach et al. 1980). Sharma (1989) showed that severe strains of CTV he tested were transmitted by BCA with higher efficiency than the mild strains; acquisition periods were shorter and retention periods were longer. The fact that citrus varieties vary with regard to their suitability for CTV acquisition by BCA further complicates the picture (Bar-Joseph et al. 1979).

A concise review of the literature on CTV transmission by aphids, including a list of infectivity studies on BCA and *A. gossypii*, is provided by Roistacher & Bar-Joseph (1987) (reproduced in Roistacher & Bar-Joseph 1989). Bar-Joseph et al. (1983) provide a review of the epidemiology and control of CTV, as does Lee (1994). Bar-Joseph et al. (1989) and Lee & Rocha-Peña (1992) are both comprehensive reviews of the history of CTV, its host range, diagnosis, and molecular characterization.

In addition to CTV, the BCA has been implicated in vectoring other plant viruses, although some reports are questionable and lack confirmation. Potyviruses transmitted by BCA include yam mosaic virus (Thouvenel & Fauquet 1979), soybean mosaic virus (Halbert et al. 1986), sugar cane mosaic virus (reported as mosaic of abacá,

Musa textilis, by Gavarra & Eloja (1965)) and chili veinal mottle virus (Ong et al. 1979). BCA did not transmit potato virus Y or pepper veinal mottle virus, other viruses infecting chilli peppers, *Capsicum annum* (Gowda & Reddy 1989). In the same series of experiments, BCA failed to transmit cucumber mosaic cucumovirus, which, although not a potyvirus, is non-persistently transmitted by many aphid species.

Using electron microscopy, Maharaj & da Graca (1988) found virions of citrus vein enation virus, a probable luteovirus, in the hindgut lumen and accessory salivary glands of BCA and subsequently (Maharaj & da Graca 1989), showed transmission by the aphid. Persistent transmission of citrus vein enation virus has been demonstrated in both *A. gossypii* and *M. persicae* (Hermoso de Mendoza et al. 1993). Portillo & Beñatena (1986) claimed that BCA was capable of transmitting citrus psorosis virus to various *Citrus* spp. in Argentina. However, the assays were based primarily on symptoms and this conclusion has yet to be confirmed by molecular studies. Protacio (1965) reported that BCA can potentially transmit the agent of cadang-cadang disease to coconut palms, but this disease is now thought to be caused by a viroid and there is no evidence for insect transmission of viroids.

Broadbent & Fraser (1976) concluded that BCA was not responsible for vectoring the organism that causes citrus dieback in Australia. Similarly, BCA was shown not to be responsible for vectoring citrus leaf mottle disease in the Philippines (Salibe & Cortez 1967), or the greening disease of citrus that is vectored by *Trioza erythrae* (McLean & Oberholzer 1965).

MONITORING AND CONTROL

Sticky traps and pan traps have both been used for monitoring flight activity of the BCA, and are more economical than suction traps in terms of capital outlay. However, sticky traps are attractive to many insects and must be replaced frequently. Furthermore, aphids caught in such traps inevitably require special solvents to remove and are usually badly damaged, making identification difficult. Pan traps yield specimens in better condition but also need to be emptied on a regular basis and are prone to flooding during periods of heavy rain. Furthermore, it should be kept in mind that traps only monitor the flight activity of alates, provide little information on the survival or location of aphids in citrus groves, and are not a substitute for effective survey techniques, i.e. physically searching groves for established colonies.

Alate BCA are not strong fliers and few fly far from their parent colony (Gottwald et al. 1995). Gavarra & Eastop (1976) obtained better catches of BCA in yellow Moericke trays at 152 cm height than they did in trays at ground level. Consequently, optimal placement of traps is probably above ground level, but lower than the height of surrounding trees. Lara et al. (1976) used water traps to compare the attractiveness of various colors to a number of different insects in citrus. In general, they found yellow and white to be the most attractive to all species, including the BCA and its predators *C. sanguinea* and *Chrysopa* sp. However, Schwarz (1965c) found that the relative attractiveness of yellow and green to BCA changed seasonally, and varied from year to year.

The decision whether or not to apply an insecticide to a BCA infestation will be affected by many factors, primarily the type of trees infested. These can be arranged in order of tolerance (lowest to highest): (1) budwood sources, (2) nursery stock, (3) newly-planted saplings and, (4) mature, producing trees (Knapp et al. 1996). Given the Budwood Certification Program presently in effect in the state of Florida which regulates the maintenance of budwood sources free of severe strains of CTV, the first two categories demand a very low tolerance of BCA infestations. Such trees are best protected either by screened enclosures, soil applications of systemic insecticides, or a combination of both. Alternatively, geographic isolation of budwood groves in non-

citrus producing areas might provide a more permanent solution. Heavy infestations on young trees may impede their growth (Hely 1968) and the tolerance level for BCA on saplings is consequentially lower than that for mature trees. There is some indication that BCA infestations can reduce flowering and fruit set (Hall 1930; Smit 1934; Hely 1968), and occasionally lead to dropping of flower buds and young fruit on a large scale (Symes 1924), although good quantitative data is lacking. This suggests that a lower injury threshold may exist for trees in flower and early stages of fruit set. Apart from these circumstances, tolerance levels for BCA infestations on producing trees will likely vary with the local incidence of severe CTV strains capable of producing decline on sour orange-rooted trees or stem-pitting on scions of orange or grapefruit, and with their proximity to susceptible trees. Otherwise, there is little indication of direct damage to mature trees, even under heavy feeding pressure.

The earlier reports of successful chemical control of BCA usually recommended foliar sprays of lime-sulphate, nicotine sulphate, or soap and nicotine. Hall (1930) recommended spraying winter colonies to reduce populations prior to spring flush. Tao & Tan (1961) recommended chemical treatment of CTV-infected trees, which tend to bloom and flush early, in order to prevent migration of aphids to healthy trees which flush later. Young resets typically flush earlier than mature trees and could be inspected for BCA prior to the flush of mature trees and spot-treated as required to preclude outbreak populations when flush availability increases. Ideally, growers should attempt to prevent BCA infestations developing on CTV-infected trees, as opposed to CTV susceptible, uninfected trees, as there is no evidence to suggest that even the best systemic compounds can protect against CTV transmission. In practise, this will only be possible for growers with good information on the location of CTV infections in their groves. Foliar formulations of various insecticides can be used to kill aphids on contact, but they can also be expected to have greater impact on non-target and beneficial insects than systemic materials. Consequently, their use should be limited to spot applications of heavily infested areas only.

Calza et al. (1968) evaluated 9 organophosphate and carbamate compounds against BCA in São Paulo, Brazil. Tao & Wu (1968) painted tree trunks with a 30% aqueous solution of the systemic insecticide monocrotophos (Azodrin) and found it more effective against BCA than dimethoate, vamidothion, or formothion when applied in this manner. In a later study (Tao & Wu 1969) they found that 2 spring applications of monocrotophos at 12.5% a.i. gave good control of BCA and had minimal impact on natural enemies in the grove. Buitendag & Bronkhorst (1986) found monocrotophos to be without phytotoxicity to citrus trees and calculated application rates for control of BCA on trees of different sizes. These authors also calculated rates for trunk applications of Dicrotophos against BCA (Buitendag & Bronkhorst 1984) and described a method for injecting systemic insecticides directly into trees (Buitendag & Bronkhorst 1980). While systemic compounds may generally have lower impact on natural enemies, their use as granular formulations or soil drenches on producing trees is often narrowly restricted to particular seasons to minimize contamination of ground water runoff. Foliar applications should be considered a last resort, unless compounds can be selected which minimize impact on beneficial insects within the grove. For example, Portillo (1977) showed that various concentrations of pirimicarb were effective against BCA in laboratory tests, and relatively low in toxicity to *C. sanguinea*. In addition, spot treatments of heavily infested trees or blocks, as opposed to blanket treatment of entire groves, would provide refuges for natural enemy populations and speed their recolonization of treated areas.

Koli et al. (1978) tested 0.05% sprays of 6 insecticides against BCA on citrus seedlings in India and found that phosphamidon gave the best initial knockdown and the most prolonged activity. Trevizoli & Gravena (1979) compared trunk and foliar sprays

of ethiofencarb, dimethoate, malathion and pirimicarb and found that all methods and materials were effective against BCA. However, they found that trunk sprays of pirimicarb and dimethoate had less impact on predator populations (*C. sanguinea* and *Chrysopa* sp.) than did foliar sprays.

Milne & de Villiers (1977) determined application rates for delivery of dimethoate by microjet and drip irrigation that gave season-long control of BCA and other homopterans. Milne (1977) protected bagged nursery seedlings from BCA for a period of 5-6 wk with a single soil-drench application of dimethoate (40% EC, 1.0 ml/bag). Buitendag & Bronkhorst (1983) describe a method for using bands to hold Temik® granules against the trunks of trees. This method provided good control of BCA on young citrus trees, but its effectiveness declined when trunk diameter increased above 125 mm. Shevale et al. (1987) found that foliar applications of phosphamidon, dimethoate, methyl demeton, monocrotophos and quinalphos (each at 0.025% conc.) all provided >95% reduction of BCA within 24 h of treatment, although phosalone did not. Significant recolonization by BCA was evident in all treatments by day 15. Under the particular conditions of this study, phosphamidon and dimethoate were judged to be the most cost-effective.

Jothi et al. (1990) obtained control of BCA on lime in India with foliar application of botanical insecticides. They found that oils of Mahua (*Bassia latifolia*) and pongamia (*Pongamia pinnata*) at 1% and seed extracts of pongamia and neem (*Azadirachta indica*) at 2% applied early in the flush cycle gave adequate control, and resulted in BCA populations significantly lower than controls after 7 days. Field trials conducted in Puerto Rico by Yokomi et al. (1995) indicate that foliar treatments of ethion (2.5 lb ai/A) + oil (5 gal), ethion + abamectin (2.5 lb and 1.1 gal ai/A, respectively) + oil (5 gal), and pirimicarb (0.25 lb ai/A), and acephate (1.0 lb ai/A) all produced close to 100% mortality of BCA, whereas chlorpyrifos (2.5 lb ai/A) yielded 88% mortality. Knapp et al. (1996) provide current recommendations for management of BCA in Florida citrus, (budwood sources, nurseries, and producing trees), and include a list of currently approved materials.

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FORAGING AND NESTING ECOLOGY OF *ACROMYRMEX OCTOSPINOSUS* (HYMENOPTERA: FORMICIDAE) IN A COSTA RICAN TROPICAL DRY FOREST

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ABSTRACT

Leaf-cutting ants (*Acromyrmex* sp. and *Atta* sp.) in Costa Rica show many intra- and interspecific differences in ecology. Recent taxonomic studies question whether the *Acromyrmex octospinosus* populations on the Pacific and Atlantic slopes of Costa Rica are a single species. We therefore examined the foraging and nesting ecology of *A. octospinosus* in the tropical dry forest of Palo Verde National Park on the Pacific slope of Costa Rica and compared our findings with published data on the ecology of *A. octospinosus* in the tropical moist forest of La Selva Biological Station on the Atlantic slope. The Pacific *A. octospinosus* foraged primarily on the leaves of herbs and other small plants, fallen leaves, fruit, flowers, and insect frass, but does not cut the leaves of large trees. Worker size distribution within colonies was bimodal with only