Journal of Integrated Pest Management
PROFILES

General Biology and Current Management Approaches of Soft Scale Pests (Hemiptera: Coccidae)

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J. Integ. Pest Mngmt. (*2015*) 6(1): 17; DOI: 10.1093/jipm/pmv016

ABSTRACT. We summarize the economic importance, biology, and management of soft scales, focusing on pests of agricultural, horticultural, and silvicultural crops in outdoor production systems and urban landscapes. We also provide summaries on voltinism, crawler emergence timing, and predictive models for crawler emergence to assist in developing soft scale management programs. Phloem-feeding soft scale pests cause direct (e.g., injuries to plant tissues and removal of nutrients) and indirect damage (e.g., reduction in photosynthesis and aesthetic value by honeydew and sooty mold). Variations in life cycle, reproduction, fecundity, and behavior exist among congenerics due to host, environmental, climatic, and geographical variations. Sampling of soft scale pests involves sighting the insects or their damage, and assessing their abundance. Crawlers of most univoltine species emerge in the spring and the summer. Degree-day models and plant phenological indicators help determine the initiation of sampling and treatment against crawlers (the life stage most vulnerable to contact insecticides). The efficacy of cultural management tactics, such as fertilization, pruning, and irrigation, in reducing soft scale abundance is poorly documented. A large number of parasitoids and predators attack soft scale populations in the field; therefore, natural enemy conservation by using selective insecticides is important. Systemic insecticides provide greater flexibility in application method and timing, and have longer residual longevity than contact insecticides. Application timing of contact insecticides that coincides with crawler emergence is most effective in reducing soft scale abundance.

Key Words: biological control, chemical control, crawler emergence, cultural control, voltinism

Among the scale insects (Hemiptera: Coccoidea), members of Coccidae (the soft scales), Diaspididae (the armored scales), and Pseudococcidae (the mealybugs) are the most common and serious pests in the world (Ben-Dov et al. 2015). Most of the 1,148 soft scale species currently recognized (Ben-Dov et al. 2015) are innocuous herbivores, and a few even produce valuable products. For example, wax from *Ericerus* and *Ceroplastes* spp. is used to make candles, and as polish for furniture, ornaments, traditional medicine, and human food component in India and China (Qin 1997). The most extensively studied soft scale species are agricultural, horticultural, and silvicultural crop pests (Kosztarab 1996, Ben-Dov and Hodgson 1997). Thirty of the 50 economically important soft scale species listed by Gill and Kosztarab (1997) caused damage on ornamental plants and fruit trees in the United States. Globally, 146 soft scale species are either pests (66 species) or potential threats (80 species) to agriculture in the United States (Miller and Miller 2003). Several exotic soft scale species were introduced to North America and Europe through trade of ornamental plants and fruits (Miller and Miller 2003, Stocks 2013, Pellizzari and Porcelli 2014).

There is an enormous amount of literature on the biology, ecology, and management of soft scale pests. Ben-Dov and Hodgson's (1997) "*Soft Scale Insects. Their Biology, Natural Enemies and Control*" remains the most comprehensive collection of information on soft scales. In this paper, we summarize current knowledge most relevant to soft scale management. We also provide summaries of voltinism, crawler emergence timing, and predictive models for crawler emergence, which will prove useful in developing appropriately timed insecticide application programs.

Economic Importance

Kosztarab (1997a) estimated that worldwide management costs and losses to soft scale infestations alone reached >US$1 billion annually. The economic importance of soft scale pests is a function of their damage, wide host range, propensity to be introduced to new areas, and wide geographical distribution.

Factors Influencing the Pest Status of Soft Scales

Temperature and humidity are the main abiotic factors limiting the range and abundance of soft scales (Kosztarab 1996). Similar to other insects, developmental rate of soft scales increases with ambient temperature until an optimal temperature is reached, after which the developmental rate declines. The generation times of *Saissetia coffeae* (Walker) were 83, 68, and 49 d at 18, 24, and 30°C, respectively (Abd-Rabou et al. 2009). Li and Su (2002) reported that *S. coffeae* failed to complete development at 30°C. More than 80% of settled *Saissetia oleae* (Olivier) first instars died at temperature >30°C and relative humidity <30% (De Freitas 1972, Pucci et al. 1982). In general, conditions of relatively high temperature and humidity are beneficial to soft scale population growth (Kosztarab 1996). Warmer ambient temperatures due to heat accumulation on paved surfaces in urban areas (i.e. heat islands) increased populations of *Parthenolecanium quercifex* (Fitch) on oak trees in Raleigh, North Carolina (Meineke et al. 2013).

Host plant susceptibility affects infestation level and damge (Vranjic 1997). Susceptbility varies among plant species, varieties, and cultivars (see Host Plant Resistance). Host succeptibility varies in time and space, so outbreaks may occur in one year or one region but not in others (Vranjic 1997). *Ceroplastes sinensis* Del Guercio is a serious pest of citrus in coastal Australia (Beattie and Kaldor 1990, Beattie et al. 1991), but it is only a sporadic pest in Spain, Italy, and Greece (Gill 1988, Stathas et al. 2003a).

Nutrients in the soil and the plant also affect the severity of scale insect infestation (Kunkel 1997). Coffee (*Coffea arabica* L.) plants provided with more nitrogen, potassium, and organic compost amendments supported more *Coccus viridis* (Green) than poorly fertilized plants (Fernandes et al. 2012, Gonthier et al. 2013). Similarly, abundance of *Toumeyella parvicornis* (Cockerell) increased after pines

(*Pinus banksiana* Lamb.) were fertilized with urea (Smirnoff and Valero 1975). The increased nitrogen and free amino acid concentrations in fertilized plants provided additional resources for *C. viridis* growth and reproduction, leading to greater abundance (Fernandes et al. 2012, Gonthier et al. 2013). An increase in nitrogen concentration also leads to decreased phytochemical concentrations (Herms and Mattson 1992). Chlorogenic acid and caffeine stimulated *C. viridis* crawler movement, consequently reducing their feeding and increasing the risks of predation, on poorly fertilized plants (Fernandes et al. 2012). Fenandes et al. (2012) also suggested that coffee plants fertilized with potassium tolerated more *C. viridis* because elevated potassium supplies allowed the plants to increase growth and compensate for resources lost to the soft scales.

In urban environments, soft scale populations thrive on trees under physiological stress (such as water or nutrient deficiency; Kosztarab 1988). Environmental stress and pollution also affect soft scale abundance on urban trees (Kosztarab 1988, Xie et al. 1995). *Eulecanium giganteum* (Shinji) density was positively correlated with air pollutant concentrations (include suspended particles, dust, CO, S, NO_x and SO_2 produced as a result of automobile traffic) in Taiyuan, China (Xie et al. 1995). Xie et al. (1995) sugested that scale insect density could be used to monitor air pollution on city streets.

Host Range

Some soft scale species are polyphagous or monophagous, but most are oligophagous (Kosztarab 1996, Miller and Miller 2003). For example, *Eriopeltis* and *Luzulaspis* spp. feed on herbaceous plants; *Parthenolecanium* spp. prefer woody plants; *Physokermes* spp. feed exclusively on conifers; and *Toumeyella* spp. feed mainly on gymnosperms from the families Cupresaceae, Pineaceae, and Taxaceae (Kosztarab 1996).

The majority of introduced species are polyphagous (Miller et al. 2005). Polyphagous species are more likely to become major pests when introduced to new areas because the existing plant species may allow the soft scales to develop and reproduce, thus facilitate the introduced soft scale's establishment (Mitter and Futuyma 1983, Kosztarab 1996). Polyphagous species often develop host-induced biotypes (i.e., variability in their shape, color, and size depending on the host plant; Kosztarab 1996). Biotype and variable morphology have led to misidentification of pest species such as *Parthenolecanium corni* (Bouché) (Ebeling 1938).

Damage

Soft scales are phloem-sucking insects. After settling at a feeding site, the scale insects pierce the host plant tissue with modified stylets until reaching the phloem vessels, from where they suck plant sap. Phloem sap is rich in carbohydrates but poor in soluble nitrogen compounds, so phloem feeders have to ingest large quantities of sap to meet their nutritional requirements (Malumphy 1997). The excess carbohydrate-rich solution, known as honeydew, is excreted through a complex anal apparatus and mechanism unique to soft scales (Williams and Williams 1980). Honeydew is an ideal substrate for saprophytic sooty mold. A sooty mold colony on the leaf surface reduces photosynthetic rate (through shading photosynthetic cells and interfering with gas exchange through stomata; Kosztarab and Kozár 1988, Mibey 1997, Stauffer and Rose 1997), traps heat from the sunlight (thus potentially scorching the leaf; Gill 1997), and (along with honeydew) reduces the aesthetic and market values of fruits and ornamental plants (Williams and Kosztarab 1972, Katsoyannos 1996, Gill and Kosztarab 1997).

Soft scales damage host directly when their stylets penetrate and injure the vascular and photosynthetic tissues (Gill and Kosztarab 1997, Vranjic 1997). Saliva of some species contains proteinases and cellulases capable of breaking down cells, damaging vascular and photosynthetic tissues in the vicinity of the stylet (Carter 1973). Necrosis produced by individual scale insects is normally localized. Aggregated injury by severe infestations, however, may lead to dieback of twigs and branches (Vranjic 1997).

Feeding by soft scale removes nutrients and carbohydrates from plants, which retards plant growth and recovery (Washburn et al. 1985, Speight 1991). Furthermore, infested host plants are weakened and become more susceptible to attack by other insects and pathogens (Hanson and Miller 1984).

Life Cycle and Biology

It is difficult to generalize the life cycle and biology of soft scales because variations exist even among congenerics (Kosztarab 1996). Thus, we provide here a brief, but not universal, description of soft scale life cycle. Female life cycle consists of egg (Fig. 1), two or three nymphal instars (depending on species), and adult. In biparental species, males have a derived form of incomplete metamorphosis, which consists of two feeding nymphal instars followed by the nonfeeding "prepupal" (third-instar), "pupal" (fourth-instar), and adult (Marotta 1997).

First instars or "crawlers" disperse actively by crawling away from their mothers (Mendel et al. 1984; Fig. 2), or passively by wind or phoresis (Greathead 1997). Washburn and Frankie (1981) demonstrated that *Pulvinariella mesembryanthemi* (Vallot) crawlers disperse more readily by wind than through phoresis. Wind can carry crawlers 55 m to >4 km (Quayle 1916, Rabkin and Le Jeune 1954, Hoelscher 1967, Reed et al. 1970, Washburn and Frankie 1981, Mendel et al. 1984, Washburn and Washburn 1984, Yardeni 1987).

First instars generally remain at the feeding site after settling (Fig. 3). They lack a waxy cover or "test," and consequently are more susceptible to extreme environmental stresses and insecticides (Kosztarab 1996, Marotta 1997). Sexes are indistinguishable among the first instars (Williams 1997).

Second instars are similar in external appearance to, but larger than, the first instars. Sexual dimorphism becomes apparent in older second instars, with the males becoming elongated oval and covered with waxy, translucent platelike tests or "puparia" (Kosztarab 1996). Males develop through the "prepupal" and the "pupal" intars (both instars characterized by developing wing buds) under the protective tests (Miller and Williams 1990). Adult males have two pairs of wings, but the hind wings are either absent or reduced to halters (or "hamulohalteres"; Giliomee 1997). Adult males emerge from the tests and disperse by flight. The sexual behavior of male soft scales is poorly understood but likely similar to those of armored scales and mealybugs. Adult male armored scales and mealybugs locate females through pheromones (Moreno et al. 1972, Millar et al. 2012, Waterworth and Millar 2012). Being weak fliers, male armored scales only mate with nearby females (Rice and Moreno 1970, Moreno et al. 1972).

Fig. 1. Eggs within the brood chamber (left) of the oak lecanium scale, *Parthenolecanium quercifex* (Fitch).

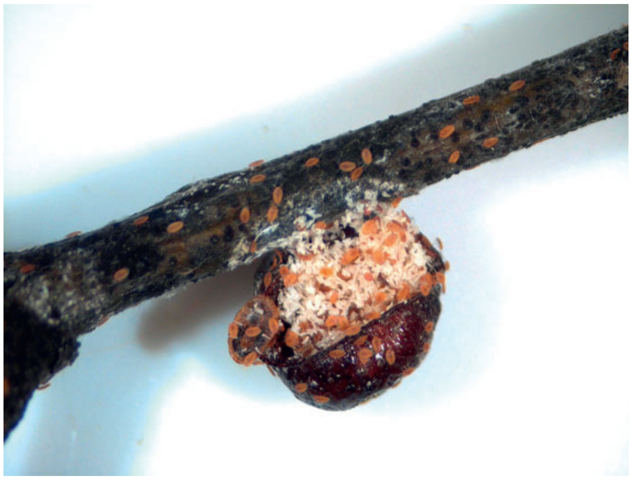

Fig. 2. Crawlers of the oak lecanium scale emerging and dispersing from adult female.

Fig. 3. First-instar oak lecanium scales settled on their feeding sites, in proximity to a leaf vein of willow oak.

Fig. 4. Second instars of the oak lecanium scale, after moving from the leaves to the branches to overwinter.

Female second instars are broadly oval (Fig. 4). Most species develop through third instar, but some species do not [e.g., *E. pela* (Qin 1997)]. A female third instar (Fig. 5) looks similar to an adult, and lasts only 2–4 d. As a result, the third instar is not always identified in life cycle studies (Marotta 1997).

Fig. 5. By spring, the second instars of oak lecanium turn to third instars. A second instar that was in the process of shedding the silvery exuvia could be seen in the middle of the twig.

Fig. 6. Adult female oak lecanium scales on a willow oak twig. Their bodies swell and turn reddish color as they mature.

Adult females are wingless and neotenic (i.e., resemble the nymphal stage; Fig. 6). An adult female undergoes a series of changes prior to oviposition, such as increase in size, color change, dorsoventral swelling, and formation of either a cavity under the venter (known as the "brood chamber" and occurs in Ceroplastinae, and Coccinae tribe Coccini, Paralecaniini and Saissetiini, Eulecaniinae, and Myzolecaniinae), or a white, waxy ovisac beneath or behind the body (in Filippiinae, Eriopletinae, and the Coccinae tribe Pulvinariini; Marotta 1997).

Most univoltine species overwinter as second instars; others overwinter as adults (Kosztarab 1996). Some species, such as *C. sinensis*, can overwinter as either third instar or adult (Stathas et al. 2003a). In species where nymphs feed on the foliage, second instars migrate to, and overwinter on, twigs and branches. This migration often coincides with or precedes specific changes in host phenology (Marotta and Tranfaglia 1997), most notably leaf senescence (Michelbacher and Ortega 1958).

Soft scales reproduce either sexually or parthenogenetically (Saakyan-Baranova et al. 1971, Kosztarab 1996). Some species [e.g., *P. corni* and *Pulvinaria vitis* (L.)] can reproduce sexually and parthenogenetically (Schmutterer 1952, Canard 1958, Phillips 1963, Pellizzari 1997); the mechanism that regulates the variable mode of reproduction in these soft scale species is poorly understood.

Fecundity varies greatly among species. Per capita fecundity was less than 24 eggs for *Eucalymnatus tessellatus* (Signoret) (Vesey-Fitzgerald 1940), up to 6,355 eggs for *Ceroplastes destructor* Newstead (Wakgari and Giliomee 2000), and 382–395 crawlers for *Phalacrococcus howertoni* Hodges and Hodgson (Amarasekare and Mannion 2011). Fecundity also varies among individuals. Per capita fecundity of *Coccus hesperidum* L. ranged from 70 to 1,000 eggs (Tereznikowa 1981) and that of *S. oleae* ranged from 566 to 5,533 offspring (Beingolea 1969). Fecundity was positively correlated to body volume in *P. corni* (Birjandi 1981), and to weight in *Rhodococcus turanicus* (Archangelskaja) (Fan et al. 2013). Host plant, climatic conditions, and altitude may be responsible for variations in sex ratios, parthenogenesis, and fecundity in *C. hesperidum* (Thomsen 1929; Nur 1979, 1980), *E. pela* (Danzig 1980, 1986, 1997), *P. corni* (Thiem 1933a, 1933b; Canard 1958, Saakyan-Baranova et al. 1971), *P. vitis* (Newstead 1903; Schmutterer 1952; Danzig 1959, 1980, 1986; Malumphy 1992), and *S. coffeae* (Thomsen 1929; Nur 1979, 1980).

Among the 70 soft scale species reviewed (almost exclusively agricultural, horticultural, and silvicultural pests), 53% are strictly univoltine, 7% are strictly bivoltine, and 4% are strictly multivoltine (Table 1). Some multivoltine species have as many as five generations annually (e.g., *C. hesperidum* in southern California; Gill 1988). No subfamily, tribe, or genus has a higher tendency to include multivoltine species than the others.

Many soft scale species exhibit great variations in voltinism depending on host, geographical and climatic conditions (Table 1; Marotta and Tranfaglia 1997). A cosmopolitan soft scale species may develop more generations in a warmer country, or a warmer climatic zone within a country. For example, *Ceroplastes rubens* (Maskell) has one generation in Japan and China (Itioka and Inoue 1991, Xia et al. 2005) and two generations in Australia (Loch and Zalucki 1997). *Ceroplastes destructor* is univoltine in central and southern New South Wales but bivoltine in northern New South Wales, Australia (Qin and Gullan 1994). *Saissetia oleae* is univoltine in the inland regions of Greece where hot and dry summers and cold winters prevail (Argyriou 1963), but bivoltine in the coastal regions of Iberian Peninsula and Israel where high summer humidity and mild winters are common (Peleg 1965, De Freitas 1972).

Voltinism also differs among host plant species or cultivars. *Ceroplastes floridensis* is univoltine on *Rhododendron* spp. from Florida to Maryland (Kehr 1972), bivoltine on holly (*Ilex* spp.) in Georgia (Hodges et al. 2001), and multivoltine on citrus and holly in Florida (Johnson and Lyon 1991). *Coccus hesperidum* is univoltine or bivoltine on the "Valencia late" orange variety but multivoltine on the "Hamlin" variety (Panis 1977a). A higher nutritional quality of certain host, or an increased insect enzymatic activity on certain host (Ishaaya and Swirski 1976), may allow soft scales to develop faster and complete additional generations within a year. Host plant phenology, genetic, and induced resistance to infestation also may be responsible for the observed variations (Marotta and Tranfaglia 1997).

Some nominally univoltine species are able to develop multiple generations per year under optimal and (often) controlled conditions in laboratory or greenhouse. For example, although *C. hesperidum* can develop from one to six generations per year outdoors, a seventh generation can develop in greenhouses (Saakyan-Baranova 1964). *Parasaissetia nigra* (Nietner) is usually univoltine with a partial second generation outdoors, but can produce up to six generations in greenhouses (Ben-Dov 1978). Table 1 does not include voltinism information obtained from greenhouse or laboratory studies.

Integrated Pest Management (IPM)

Soft scales are among the most prevalent and difficult arthropod pests to control in the southern United States (Fulcher et al. 2012). There is a need to optimize soft scale monitoring and management by IPM practitioners (Fulcher et al. 2012).

Monitoring

Soft scale infestations are detected by looking for populations and damage symptoms. Sampling plans typically determine insect density on a prescribed number of leaves or branches, but procedures vary among crop systems (e.g., citrus in Trumble et al. 1995, Grafton-Cardwell et al. 1999, Martínez-Ferrer et al. 2015; olive in Tena et al. 2007; and tea in Naeimamini et al. 2014). Scouts should be trained and equipped (with handlens, sticky traps, etc.) to detect cryptic signs and symptoms. Honeydew, sooty mold, and honeydew-seeking ants are general signs of phloem-feeding insect infestations; they can be used to pinpoint the areas where plants may be inspected for the presence of soft scales. Monitoring or mating disruption of soft scales with pheromone baits is not available.

Degree-day models and plant phenological indicators predict crawler emergence and inform scouts and IPM practitioners on when to initiate sampling and treatment (Mussey and Potter 1997, Herms 2004). Only a small number of IPM practitioners implement these predictive models because of the high diversity of pests (and plants) that require management (each may require a unique model, but see Kulhanek 2009), the time needed to learn, calculate and implement the models (LeBude et al. 2012), and the difficulty in interpreting the observed plant phenophase. Few predictive models for soft scales have been published (Table 2), further impeding their adoption.

Crawler presence can be confirmed by looking for the crawlers on the leaves and branches, or by deploying a modified sticky trap. The sticky trap is made of a double-sided tape (or a single-side tape with the adhesive surface facing outward) wrapped around a twig or branch where gravid soft scales are present. The trap is inspected regularly for captured crawlers.

Despite its importance in determining insecticide application timing, crawler emergence period is reported for only 49 soft scale species (Table 3). In the United States, *P. corni* crawlers emerge earlier in the southern states (Hodges and Braman 2004, Klingeman et al. 2002) than those in the northern states (Asquith 1949, Krischik and Davidson 2003, Herms 2004, Hoover et al. 2011). Crawlers of most univoltine species emerge in the spring through the summer, i.e. April through June in the United States and October through February in the Southern Hemisphere (Table 3).

Economic Threshold

On ornamental plants grown in nurseries or landscapes, pest management tactics are often applied whenever scale insect populations or damage becomes noticeable (Bethke 2010). Economic thresholds vary among perennial fruits and nut crops. The economic thresholds of *C. floridensis* in citrus orchards of Egypt are 24.4, 26.6–28.4, and 25.1–27.0 individuals per twig in June, October, and December, respectively (Salem and Zaki 1985, Helmy et al. 1986).

Cultural Control

The goal of cultural control is to make the environment less favorable to pest development and reproduction. Proper fertilization, pruning, and irrigation maintain plant vigor, promote plant tolerance to pest damage, and reduce sap-sucking insect population growth (CAST 2003, Dreistadt 2008, Kabashima and Dreistadt 2014). However, few studies have demonstrated the efficacy and underlying mechanism of these cultural management practices. Pruning is effective in removing infested plant tissues and reducing populations of *S. oleae* and *Coccus pseudomagnoliarum* (Kuwana) (Kabashima and Dreistadt 2014). Pruned olive trees harbored 200% fewer nymphs and 50% fewer adult *S. oleae* compared to unpruned trees (Ouguas and Chemseddine 2011). Excessive irrigation increased the developmental rate of *C. destructor* (Milne 1993).

Host Plant Resistance

It is generally recommended that pest-resistant plant species or cultivars should replace those that are susceptible to pests and damage (Kabashima and Dreistadt 2014). However, few studies investigated resistance or tolerance of various host plant species or cultivars to soft scales in the field. Potter and Redmond (2013) reported that American

Table 1. Voltinism of soft scale pests on host species and locations identified in the cited references

Subfamily	Tribe	Genus	Species	Host cited in the references	Location(s)	Generations per year[a]	Reference(s)
Cardiococcinae	Cardiococcini					N/A	
Ceroplastinae	Ceroplastini	*Ceroplastes*	*albolineatus*	*Pittocaulon praecox*	Mexico	2	(Narada and Lechuga 1971)
			ceriferus	*Various*	Italy; Maryland, Virginia, USA	1	(Kosztarab 1996, Mori et al. 2001)
				Citrus spp.	Japan	1	(Ohgushi 1969)
				Burford holly (*Ilex cornuta* 'Burfordi')	Georgia, USA	1-2	(Hodges and Braman 2004)
			cirripediformis	Fruit trees	Chile	1	(Bayer CropScience Chile 2014)
				Citrus spp.	Georgia	1	(Tulashvili 1930)
				Various	California, USA	1	(Ben-Dov 1993, Kosztarab 1997b)
				Various	Texas, USA	2	(Johnson and Lyon 1991)
				Guava	Egypt	2	(Bakr et al. 2010)
				Passion fruit (*Passiflora edulis*)	Central coast, Peru	3	(Marin-Loayza and Cisneros-Vera 1996)
			destructor	*Citrus* spp.	New Zealand	1	(Olson et al. 1993, Lo et al. 1996)
				Citrus spp., guava (*Psidium guajava*), *Syzygium malaccensis*	South Africa	1	(Wakgari and Giliomee 2000)
				Various	Central and southern New South Wales, Australia	1	(Qin and Gullan 1994)
				Citrus spp.	Queensland, Northern New South Wales, Australia	2	(Smith 1970, Qin and Gullan 1994)
			floridensis	Apple, persimon	Yunnan, China	1	(Yun 1994)
				Rhododendron spp.	Florida to Maryland, USA	1	(Kehr 1972)
				Holly (*Ilex* spp.)	Georgia, USA	2	(Hodges et al. 2001)
				Citrus spp.	Greece	2	(Argyriou and Kourmadas 1980)
				Citrus spp., grapefruit, mango	Israel	2(3 partial)	(Yardeni and Rosen 1995, Pellizzari 1997)
				Citrus spp., *Cinnamomum japonicum*	Fujian, China	2	(Kaiju 2011)
				Citrus spp.	Queensland, Australia	2	(Smith et al. 1997)
				Citrus, guava, banana	Egypt	2-3	(Salem and Hamdy 1985, Helmy et al.1986, Abd-Elhalim Moharum 2011)
				Various	Florida, USA	3	(Johnson and Lyon 1991)
				Orange, Passion fruit (*Passiflora edulis*)	Peru	3	(Marin-Loayza and Cisneros-Vera 1996)
Ceroplastinae	Ceroplastini	*Ceroplastes*	*japonicus*	Poplar, bay laurel, maple, persimmon	China; Italy	1	(Pellizzari and Camporese 1994, Davis et al. 2005, Yongxiang 2008)
				Various	Croatia	1	(Masten-Milek et al. 2007)
				Citrus spp.	Japan	1	(Ohgushi 1969)
			pseudoceriferus	Persimmon	China; Korea	1	(Park et al. 1990, Wang et al.2006)
				Lychee, mango	Southern Taiwan, Republic of China	3	(Wen and Lee 1986)
			rubens	Various	Shanghai and Kunming, China	1	(Tao et al. 2003, Xia et al. 2005)
				Citrus spp.	Japan	1	(Yasumatsu 1958)
				Citrus spp., *Schefflera actinophylla*	Australia	2	(Loch and Zalucki 1997)
			rusci	Fig tree	Mediterranean coast, France	1	(Benassy and Franco 1974)
				Fig tree (*Ficus carica*)	Algeria; Greece; Turkey	2	(Argyriou and Santorini 1980, Ozsemerci and Aksit 2003, Biche et al. 2012)
				Quince	Egypt	2	(Ragab 1995)
				Citrus spp., fig tree	Italy; Spain	2	(Inserra 1970, Longo and Russo 1986, De la Cruz Blanco et al. 2010, Pellizzari et al. 2010)
				Soursop (*Annona muricata*), fig	Southern Vietnam	4	(Vu et al. 2006)
			sinensis	*Ilex* spp.	Virginia, USA	1	(Williams and Kosztarab 1972, Kosztarab 1996)
				Citrus spp., pear	Greece; Italy	1	(Frediani 1960, Stathas et al. 2003a)
				Citrus spp.	Coastal districts, Australia	1	(Snowball 1970)
				Citrus spp.	New Zealand	1	(Cottier and Wellington 1939)

(continued)

Table 1. Continued

Subfamily	Tribe	Genus	Species	Host cited in the references	Location(s)	Generations per year[a]	Reference(s)
				Citrus reticulata Blanco, *Citrus sinensis* Osbeck	Northern Spain	1	(Martínez-Ferrer et al. 2015)
Cissococcinae	Cissococcini	*Vinsonia*				N/A	
Coccinae	Coccini	*Coccus*	*hesperidum*	Citrus	Eastern Sicily, Italy	1	(Longo and Benfatto 1982)
				Citrus	Southern France	1–3	(Panis 1977a)
				Citrus	Western Sicily, Italy	2–3	(Monastero 1962)
				Citrus spp.	South Africa	3	(Annecke 1966)
				Various	New Zealand; southern California, USA	3–5	(Bernal et al. 1998, Charles et al. 2005)
Coccinae	Coccini	*Coccus*	*hesperidum*	Various	Israel	6	(Avidov and Harpaz 1969)
			pseudomagnoliarum	*Citrus* spp.	Greece	1	(Argyriou and Ioanides 1975)
					Israel	1	(Ben-Dov 1980)
					Southern Italy	1	(Barbagallo 1974)
					Turkey	1	(Oncuer and Tuncyureck 1975)
					Australia	1	(Smith et al. 1997)
				Citrus spp., hackberry	California, USA	1	(Flanders 1942)
			viridis	*Citrus* spp.	Queensland, Australia	3–4	(Smith et al. 1997)
		Eucalymnatus	tessellatus	Palms (Arecaceae), crepe-jasmine, mango	South Florida, USA	1, 2	(Hamon and Williams 1984)
		Kilifia	*acuminata*	Mango	Egypt	2, 3	(Hassan et al. 2012, Angel and Radwan 2013)
		Mesolecanium	*nigrofasciatum*	*Acer, Platanus, Prunus*	Pennsylvania, Maryland, Eastern USA	1	(Simanton 1916, Kosztarab 1996, Meyer et al. 2001)
				Blueberry, peach, plum, maple, sycamore, mistletoe			
	Paralecaniini	*Pseudocribrolecanium*	*andersoni*	Citrus	South Africa	3–4	(Brink and Bruwer 1989)
	Pulvinariini	*Milviscutulus*	*mangiferae*	Mango	Coastal plain, Israel	3	(Avidov and Zaitzov 1960)
		Neopulvinaria	*innumerabilis*	Various hardwoods	Colorado, USA	1	(Cranshaw et al. 1994)
				Red oak	Georgia, USA	1	(Hodges and Braman 2004)
				Maple (*Acer* spp.), honeylocust (*Gleditsia triacantho*), linden (*Tillia* spp.)	Minnesota, USA	1	(Krischik and Davidson 2003)
		Protopulvinaria	*pyriformis*	Various fruit trees	Chile	2	(Bayer CropScience Chile 2014)
				Citrus spp.	Spain	2	(Lloréns 1990)
				Avocado	Israel	2	(Blumberg and Blumberg 1991)
				Hedera helix	Israel	3	(Blumberg and Blumberg 1991)
		Pulvinaria	*acericola*	Red maple	Georgia, USA	1	(Hodges and Braman 2004)
				Maple, dogwood, holly, andromeda, gum	Virginia, USA	1	(Day 2008)
			amygdali	Peach, plum, quince	New York, USA	1	(Harman 1927)
Coccinae	Pulvinariini	*Pulvinaria*	*citricola*	Various	Japan; Florida, Maryland, Virginia, USA	1	(Williams and Kosztarab 1972, Gill 1988)
			delottoi	Iceplant (Aizoaceae)	Southern Africa; Northern California, USA	1	(Tassan and Hagen 1995, Gill 1988)
			floccifera	Burfofd holly, bradford pear	Georgia, USA	1	(Hodges and Braman 2004)
				Camellia, holly, taxus, rhododendron, hydrangea, maple, English ivy	Virginia, USA	1	(Williams and Kosztarab 1972, Day 2008)
				Guava, citrus, fig	Egypt	1	(Abd-Rabou et al. 2012)
				Taxus baccata, Pittosporum toriba, Ilex aquifolia, *Citrus* spp., *Camellia sinensis*	Iran	1	(Hallaji-Sani et al. 2012)
				Citrus	Japan	1	(Takahashi 1955)
				Various	Spain	1	(Soria et al. 1996)
				Citrus	Tokyo, Japan	2	(Takahashi 1955)

(continued)

Table 1. Continued

Subfamily	Tribe	Genus	Species	Host cited in the references	Location(s)	Generations per year[a]	Reference(s)
				Conifers	Turkey	2	(Ülgentürk et al. 2004)
			hydrangeae	Hydrangea, cherry, others	Australia; Europe; Japan; California, East Coast, USA	1	(Williams and Kosztarab 1972, Gill 1988)
			polygonata	Mango	India	1	(Chatterji and Datta 1974)
				Various	China	2–3	(Peng et al. 1990)
				Citrus	Taiwan	3	(Takahashi 1939)
			psidii	Guava	Egypt	2, 3	(Baker et al. 2012)
			rhois	poison oak (*Rhus diversiloba*), peach, plum, apple and currant (*Ribes*), prune	California, USA	1	(Essig 1958)
			vitis	Peach	Canada	1	(Phillips 1963)
				Poplar, alder, beech, willow, hawthorne	New Zealand	1	(Charles et al. 2005)
				Various	Eastern USA	1	(Essig 1915)
		Pulvinariella	*mesembryanthemi*	Iceplant (Aizoaceae)	Northern California, USA	2	(Tassan and Hagen 1995)
					Southern California, USA	3–4	(Tassan and Hagen 1995)
Coccinae	Saissetiini	*Parasaissetia*	*nigra*	*Ficus, Hedera*	California, Florida, USA	1 (2 partial)	(Smith 1944)
		Parthenolecanium	*corni apuliae*	Grapevine (*Vitis vinifera*)	Italy	2	(Nuzzaci 1969a)
			corni corni	*Coryllus*	Greece	1	(Santas 1985)
				Hazelnut	Turkey	1	(Ecevit et al. 1987)
					France	1	(Canard 1958)
				Various	New Zealand	1	(Charles et al. 2005)
				Plum	Krasnodar, Russia	1	(Borchsenius 1957)
				Various	Virginia, USA	1	(Day 2008)
				Deciduous fruits, nuts (*Prunus* spp.) and ornamental trees and shrubs (Toyon, *Ceanothus* spp.)	California, USA	1	(Kawecki 1958, Madsen and Barnes 1959)
				Grape	Chile	2	(Bayer CropScience Chile 2014)
				Black poplar (*Populus nigra*)	Hungary	2	(Kosztarab 1959)
				Peach	Pennsylvania, USA	2	(Asquith 1949)
				Peach	Krasnodar, Russia	2	(Borchsenius 1957)
				Black locust (*Robinia pseudoacacia*)	Krasnodar, Russia	3	(Borchsenius 1957)
			fletcheri	Conifers (*Biota, Cupressus, Juniperus, Tsuga, Thuja*)	Hungary	1	(Kosztarab 1997b)
				Conifers, arborvitae, yew, pachysandra, Eastern red cedar	Virginia, USA	1	(Kosztarab 1997b)
				Arborvitae, yew, juniper, cypress, hemlock	Pennsylvania, Illinois, USA	1	(Stimmel 1978, Hoover 2006)
			orientale	Peach	Henan, Shandong, China	1	(AQSIQ 2007)
				Locust and grape	Henan, Shandong, China	2	(AQSIQ 2007)
			perlatum	*Citrus* spp.	Argentina	1	(Teran and Guyot 1969)
			persicae	Various fruit trees	Chile	1	(Bayer CropScience Chile 2014)
				Various	Israel	1	(Ben-Dov 1993)
				Various ornamental plants	USA	1	(Kosztarab 1996)
				Grapevine (*Vitis vinifera)*	Australia; Southern Greece	1	(Stathas et al. 2003b, Buchanan 2008)
				Various	New Zealand	1–2	(Charles et al. 2005)
				Various	Former Soviet Union	2	(Borchsenius 1957)
				Various	Central Asia	2	(Ben-Dov 1993)
			pomeranicum	Yew	Europe	1	(Del-Bene 1991)
			pruinosum	Walnut	California, USA	1	(Michelbacher and Swift 1954)
				Grapevine (*Vitis vinifera*)	Australia	1	(Buchanan 2008)
			quercifex	Oaks (*Quercus* spp.), hickory, birch, persimmon, American sycamore	Virginia, USA	1	(Williams and Kosztarab 1972)
				Coast live oak, valley oak	California, USA	1	(Swiecki and Bernhardt 2006)

(continued)

Table 1. Continued

Subfamily	Tribe	Genus	Species	Host cited in the references	Location(s)	Generations per year[a]	Reference(s)
			rufulum	*Quercus frainetto, Q. cerris, Q. ithaburensis ssp. macrolepis*	Greece	1	(Gounari et al. 2012)
				Quercus robur	Northeastern Italy	1	(Rainatto and Pellizzari 2009)
		Saissetia	*coffeae*	Various fruit trees	Chile	1	(Bayer CropScience Chile 2014)
				Olive tree	Chile	2	(González and Lamborot 1989)
				N/A	California, USA	1-2	(Hamon and Williams 1984)
				Various	New Zealand	2+	(Charles et al. 2005)
				Various	Florida, USA	2+	(Gill 1988)
				Olive tree	Israel	3, 4	(Rosen et al. 1971)
			oleae	Citrus	Corsica, French Riviera, France; Greece; Israel; Calabria, Sicily, Italy; Portugal; Almanzora, Spain; Tunisia; Aegean Sea coast, Turkey	1	(Argyriou 1963, Peleg 1965, Panis 1977b, De Freitas 1972, Jarraya 1974, Tuncyurek and Oncuer 1974, Blumberg et al. 1975, Longo and Russo 1986)
				Olive tree	Greece; Italy; Spain	1	(Bibolini 1958, Argyriou 1963, Briales and Campos 1986; Noguera et al. 2003)
				Various fruit trees	Chile	1	(Bayer CropScience Chile 2014)
				Various	Inland California, USA	1	(Dreistadt 2004)
				Various	Coastal California, USA	2	(Dreistadt 2004)
				Olive tree	Coastal Greece; Israel; Italy; Portugal; Spain	2	(Argyriou 1963, Nuzzaci 1969b, Rosen et al. 1971, Viggiani et al. 1973)
				Citrus	Coastal Greece; Israel; Spain	2	(Argyriou 1963, Blumberg et al. 1975, Llorens-Climent 1984)
				Citrus	Florida, USA; coast of Morocco; Portugal	3	(Panis 1977b)
				Citrus	Subtropical areas, Australia	4	(Waterhouse and Sands 2001)
				Citrulus sp.	Peru	5–6	(Beingolea 1969)
Cyphococcinae	Cyphococcini					N/A	
Eulecaniinae	Eulecaniini	*Didesmococcus*	*unifasciatus*	Stone fruits	Central Asia	1	(Babayan 1973)
		Ericerus	*pela*		China	1	(Zhao et al. 1998)
					Japan	1	(Kuwana 1923)
					Russia	1	(Danzig 1980)
				Various	Tropical zones	2	(Qin 1997)
		Eulecanium	*caryae*	Beech, willow, birch, hickory, peach	Quebec, Canada; Virginia, Michigan, USA	1	(Wallner 1969, Williams and Kosztarab 1972, Kosztarab 1996)
			cerasorum	Stone fruit, walnut, pear	California, Maryland, USA	1	(Madsen and Barnes 1959, Kosztarab 1996)
			ciliatum	*Acer campestre, A. pseudoplatanus, Crataegus monogyna, C. oxyacantha*	Turkey	1	(Ülgentürk and Çanakçioğlu 2004)
			excressens	Ornamental plants and brodleaved trees	England; California, USA	1	(Gill 1988, Alford 2007)
			kunoense	Various	California, USA	1	(McKenzie 1951, Husseiny and Madsen 1962)
			tiliae	*Quercus frainetto, Q. cerris, Q. ithaburensis ssp. Macrolepis*	Greece	1	(Gounari et al. 2012)
				Various	Bulgaria, Georgia, Russia; California, USA	1	(Hadzibejli 1967, Tzalev 1968, Kosztarab and Kozár 1988)
			sericeum	Abies, Picea	Georgia	1	(Hadzibejli 1967)
				Conifers (*Abies, Picea*)	Germany	1	(Kosztarab 1997b)
		Nemolecanium	*graniformis*	Greek fir (*Abies cephalonica*)	Greece	1	(Stathas 2001)
		Palaeolecanium	*bituberculatum*	*Corylus, Juglans regia*, Rosaceae	Europe	1	(Schmutterer 1952)
				Apple	Turkey	1	(Özgökçe et al. 2001)
		Physokermes	*hemicryphus*	Spruce	Germany	1	(Schmutterer 1956)
				Abies cephalonica, A. borisii regis	Greece	1	(Gounari et al. 2012)

(continued)

Table 1. Continued

Subfamily	Tribe	Genus	Species	Host cited in the references	Location(s)	Generations per year[a]	Reference(s)
				Picea	Central Europe	1	(Kosztarab and Kozár 1988)
					Pennsylvania, USA	1	(Stimmel 1996)
			inopiatus	Greek fir (*Abies cephalonica*)	Greece	1	(Stathas and Kozár 2010)
			insignicola	Monterey and Bishop pines (*Pinus rdiata and P. muricata)*	California, USA	1	(Gill 1988)
			piceae		Colorado, USA	1	(Cranshaw et al. 1994)
					Serbia	1	(Graora et al. 2012)
			shanxiensis	N.A.	China	1	(Wu and Yu 2000)
		Rhodococcus	*turanicus*	Stone fruits	Armenia	1	(Babayan 1986)
				Apricot	Xinjiang, China	1	(Fan et al. 2013)
		Sphaerolecanium	*prunastri*	Purpleleaf plum, *Pyracantha* spp.	Pennsylvania, USA	1	(Hoover et al. 2011)
Eulecaniinae	Eulecaniini	*Sphaerolecanium*	*prunastri*	Stone fruits	Greece; Israel; high altitude regions, Italy	1	(Silvestri 1939, Ben-Dov 1968, Argyriou and Paloukis 1976)
				Stone fruits	Southern plains, Italy	2	(Silvestri 1939)
Eriopeltinae	Eriopeltini	*Eriopeltis*	*festucae*	Grass	California, USA	2	(Patch 1905)
Filippiinae	Filippiini	*Lichtensia*	*viburni*	Olive, *Pistacia lentiscus*, *Hedera hélix*	Mediterranean basin	2	(Pellizzari 1997)
Myzolecaniinae	Myzolecaniini	*Neolecanium*	*cornuparvum*	Magnolia	Virginia, New York, USA	1	(Herrick 1931, Kosztarab 1996)
		Pseudophilippia	*quaintancii*	*Pinus taeda* (Loblolly pine)	Eastern USA	2	(Clarke et al. 1989a)
		Toumeyella	*liriodendri*	Yellow poplar, magnolia, linden, *Michelia, Gardenia, Gordonia, Cephalanthus, Tilia*	Alabama, California,Illinois, Indiana, Kentucky, Mississippi, Ohio, Pennsylvania, Tennessee, Virginia, West Virginia, USA	1	(Burns and Donley 1970, Gill 1988, Hoover 2006, Day 2008)
			parvicornis	Jack pine (*Pinus banksiana*), Scots pine (*P. sylvestris*), red pine (*P. resinosa*)	Canada	1	(Rabkin and Le Jeune 1954)
				Pinus contorta, P. sylvestris	Colorado, Nebraska, USA	1	(Cooper and Cranshaw 2004, Clarke 2013)
				Pinus caribaea var. *Bahamensis*	Northeastern USA	1	(Malumphy et al. 2012)
				Pinus spp.	Maryland, North Carolina, Virginia, USA	2	(Miller 1985, Clarke 2013)
				Pinus spp.	Georgia; Southern USA	3-4	(Williams and Kosztarab 1972, Hamon and Williams 1984, Clarke 2013)
			pini	*Pinus taeda* L. (Loblolly pine)	Gerorgia, USA	3	(Clarke et al. 1989b)
				Pinus sylvestris, Pinus mugo, Pinus edulis, Pinus nigra	Colorado, USA	1	(Cranshaw et al. 1994, Cooper and Cranshaw 2004)
			pinicola	Pines	California, USA	1	(Kattoulas and Koehler 1965)
			virginiana	*Pinus* spp.	Virginia, USA	2	(Williams and Kosztarab 1972, Kosztarab 1997b)
Pseudopulvinariinae						N/A	

[a] N/A, not specified.

Higher level taxonomy is based on Hodgson (1994) and Ben-Dov et al. (2015).

Table 2. Degree-day and plant phenological indicator models for soft scale pests

Soft scale species	Celcius degree-day, DDC (Fahrenheit degree-day, DDF)	Base temperature	Host plant[a]	Location	Reference(s)
Degree-day models					
Ceroplastes ceriferus	843–930 DDC	12.78°C (55°F)	Burford holly (*Ilex cornuta* 'Burfordii')	Athens, GA	(Hodges and Braman 2004)
Eulecanium cerasorum	1028 DDC (1851 DDF)	1.7°C (35°F)	Sweetgum (*Liquidambar styraciflua*)	Lexington, KY	(Mussey and Potter 1997)
	748 DDF	10°C (50°F)	N/A	Wooster, OH	(Herms 2004)
	818 DDC	4.4°C (40°F)	Hackberry (*Celtis occidentalis*); Norway maple (*Acer platanoides*)	Lexington, KY	(Hubbard and Potter 2005)
Neolecanium cornuparvum	1938 DDF	10°C (50°F)	N/A	Wooster, OH	(Herms 2004)
Neopulvinaria innumerabilis	898–1321 DDC	10.56°C (51°F)	Red oak (*Quercus falcata*)	Athens, GA	(Hodges and Braman 2004)
	930 DDF	10°C (50°F)	N/A	Midland, MI	(Herms 2004)
Parthenolecanium corni	1100–1582 DDC	10.56°C (51°F)	Pin oak (*Quercus palustris*); willow oak (*Quercus phellos*); red maple (*Acer rubrum*)	Athens, GA	(Hodges and Braman 2004)
	1198–1263 DDC	12.78°C (55°F)	Pin oak; willow oak; red maple	Athens, GA	(Hodges and Braman 2004)
	1073 DDF	10°C (50°F)	N/A	Midland, MI	(Herms 2004)
	767 DDF	10°C (50°F)	N/A	Wooster, OH	(Herms 2004)
Parthenolecanium fletcheri	884 DDF	10°C (50°F)	N/A	Midland, MI	(Herms 2004)
Pulvinaria acericola	1044 DDC (1879 DDF)	4.4°C (40°F)	Red maple	Lexington, KY	(Mussey and Potter 1997)
	892–1229 DDC	10.56°C (51°F)	Red maple	Athens, GA	(Hodges and Braman 2004)
Pulvinaria floccifera	1422–1941 DDC	10.56°C (51°F)	Burford holly	Athens, GA	(Hodges and Braman 2004)
	851 DDF	10°C (50°F)	N/A	Wooster, OH	(Herms 2004)
Physokermes piceae	1154 DDF	10°C (50°F)	N/A	Midland, MI	(Herms 2004)
	894 DDF	10°C (50°F)	N/A	Wooster, OH	(Herms 2004)
Toumeyella liriodendri	532–616 DDC	10.56°C (51°F)	Tulip poplar (*Liriopendron tulipifera*)	Athens, GA	(Hodges and Braman 2004)
Toumeyella pini	783 DDF	10°C (50°F)	N/A	Wooster, OH	(Herms 2004)
Plant phenological indicator models					
Soft scale species	Plant species		Phenophase	Location	References
Eulecanium cerasorum	Northern catalpa (*Catalpa speciosa*)		First bloom	Lexington, KY	(Mussey and Potter 1997)
	Washington hawthorne (*Crataegus phaenopyrum*)		50% bloom	Lexington, KY	(Mussey and Potter 1997)
	Washington hawthorne		Full bloom	Wooster, OH	(Herms 2004)
Pulvinaria innumerabilis	Tulip poplar		Beginning to bloom; 50% bloom	Athens, GA	(Hodges and Braman 2004)
	Northern catalpa		Full bloom	Midland, MI	(Herms 2004)
	Oakleaf hydrangea		First bloom	Wooster, OH	(Herms 2004)
Parthenolecanium corni	Oak leaf hydrangea (*Hydrangea quercifolia*)		Full bloom	Athens, GA	(Hodges and Braman 2004)
	American elder (*Sambucus canadensis*)		Full bloom	Midland, MI	(Herms 2004)
	Washington hawthorne		Full bloom	Wooster, OH	(Herms 2004)
Parthenolecanium fletcheri	American elder		First bloom	Midland, MI	(Herms 2004)
Pulvinaria acericola	Littleleaf linden (*Tilia cordata*)		95% bloom	Lexington, KY	(Mussey and Potter 1997)
	Tulip poplar		Beginnig to bloom	Athens, GA	(Hodges and Braman 2004)
	Oak leaf hydrangea		Beginning to bloom	Athens, GA	(Hodges and Braman 2004)
Physokermes piceae	Golden-rain tree (*Koelreuteria paniculata*)		First bloom	Midland, MI; Wooster, OH	(Herms 2004)
	Littleleaf linden 'Greenspire'		First Bloom	Wooster, OH	(Herms 2004)
	American elder		Full bloom	Wooster, OH	(Herms 2004)
	Bumald spirea (*Spirea* x *bumalda*)		Full bloom	Wooster, OH	(Herms 2004)
Toumeyella liriodendri	Honeysuckle (*Lonicera* sp.)		Beginning to bloom	Athens, GA	(Hodges and Braman 2004)
	Flowering dogwood (*Cornus florida*)		Beginning to bloom, or 50% bloom	Athens, GA	(Hodges and Braman 2004)
	Snowball viburnum (*Viburnum macrocephalum*)		50% bloom	Athens, GA	(Hodges and Braman 2004)
Toumeyella pini	Washington hawthorne		Full bloom	Wooster, OH	(Herms 2004)

The models predict crawler emergence or egg hatch. Starting date of the degree-day models was 1 January. Degree-day approximation method used by Herms (2004) was not specified, whereas that used by the other studies was single-sine or sine-wave method.
[a] N/A, not specified.

elm (*Ulmus americana* L.) cultivars supported a larger population of *P. corni* and *Neopulvinaria innumerabilis* (Rathvon) than Asian elm (*U. parvifolia* Jacq. and *U. propinqua* Koidz.) cultivars. Kozár (1972) found that 10 peach (*Prunus persica* (L.) Stokes) varieties were highly susceptible to infestation by *P. corni*, whereas nine were either lightly infested or not infested. Host plant resistance to scale insects is likely conferred by an interaction between plant genetic, physiology, and biochemistry (McClure 1985).

Biological Control

Many hymenopteran parasitoids of soft scale are members of Aphelinidae, Encyrtidae, Eulophidae, and Pteromalidae (Hayat 1997, Prinsloo 1997, Viggiani 1997, Kapranas and Tena 2015). Major predators of soft scales include beetles [Coccinellidae, Anthribidae (*Anthribus* spp.), and Nitidulidae (*Cybocephalus* spp.); Ponsonby and Copland 1997, Hodek and Honek 2009] and neuropterans (Chrysopidae, Hemerobiidae, Coniopterygidae, and Raphidiidae;

Table 3. Crawler emergence time of soft scale pests

Species	Time of the year	Location	Host cited in the references[a]	References
Ceroplastes albolineatus	Mar. (1st generation) Sept. (2nd generation)	Mexico D.F., Mexico	*Pittocaulon praecox*	(Narada and Lechuga 1971)
Ceroplastes ceriferus	Late-April	Texas, USA	Various	(Johnson and Lyon 1991)
	Late-May to mid-June	Athens, Georgia, USA	Burford holly (*Ilex cornuta* 'Burfordii')	(Hodges and Braman 2004)
	June to mid-July	Pennsylvania, USA	Various	(Hoover et al. 2011)
	June	Maryland, Tennessee, USA	Various	(Smith et al. 1971, Klingeman et al. 2002) (New Jersey Department of Agriculture [NJDA] 2006)
	Mid-June	New Jersey, USA	N/A	(Lai 1993)
	Early Sept. to mid-Oct.	Northern Guizhou, China	Tea	
Ceroplastes cirripediformis	Early-Feb. (1st generation) Early-June (2nd generation) Early-Oct. (3rd generation)	Peru	Passion fruit (*Passiflora edulis*)	(Marín-Loayza and Cisneros-Vera 1996)
	Late Feb. to early-Mar.	Chile	Various fruit trees	(Bayer CropScience Chile 2014)
	Early-April	Palmira, Valle del Cauca, Colombia	*Passiflora edulis flavicarpa*	(Kondo Rodríguez 2009)
	Late April	Texas, USA	Various	(Johnson and Lyon 1991)
Ceroplastes destructor	Early-Dec.	Kerikeri, New Zealand	Seminole tangelo (*Citrus paradisi* x *C. reticula*)	(Olson et al. 1993)
	Nov.	New South Whales, Australia	Citrus (*Citrus* spp.)	(Snowball 1969)
	Mid-Oct. (1st generation) Early-April (2nd generation)	Queensland, Australia	Citrus	(Smith 1970)
	Mid-Nov.	Cape Province, South Africa	*Citrus reticulata*, *Syzygium malaccensis*	(Wakgari and Giliomee 2000)
Ceroplastes floridensis	Early-June	Daegu, South Korea	Persimmon	(Han and Lee 1964)
	Early-Jan. (1st generation) Early-May (2nd generation) Early-Oct. (3rd generation)	Peru	Orange, passion fruit (*Passiflora edulis*)	(Marín-Loayza and Cisneros-Vera 1996)
	Early Feb. (1st generation) Mid-Aug.(2nd generation)	Egypt	Banana	(Abd-Elhalim Moharum 2011)
	May (1st generation) Aug. (2nd generation)	Israel	Mango	(Swirski and Greenberg 1972)
	April–May (1st generation) July–Aug. (2nd generation) Oct.–Nov. (3rd generation)	Florida, USA	Avocado, citrus, crape myrtle, deodar cedar, elm, holly, Indian hawthorn, loblolly pine, oak	(Johnson and Lyon 1991)
	May–June (1st generation) Nov. (2nd generation)	Tifton, Georgia, USA	*Ilex* spp.	(Hodges et al. 2001)
	Late April–May (1st generation) Late July–Aug. (2nd generation)	Texas, USA	N/A	(Drees et al. 2005)
	April (1st generation) Aug. (2nd generation)	Fujian Province, China	*Cinnamomum japonicum*	(Kaiju 2011)
Ceroplastes japonicus	Mid-May	Croatia	Various	(Masten-Milek et al. 2007)
	Early-June	Korea	N/A	(Davis et al. 2005)
	June	Italy	Bay laurel and maple	(Pellizzari and Camporese 1994)
Ceroplastes pseudoceriferus	Mid-June	Korea	Persimmon	(Park et al. 1990)
	Late-Jun. (1st generation) Late-Sept. (2nd generation) Late-Mar. (3rd generation)	Southern Taiwan, Republic of China	Lychee, mango	(Wen and Lee 1986)
Ceroplastes rubens	June, July	Japan	Citrus, persimmon	(Itioka and Inoue 1991)
	Mid-Sept. (1st generation) Feb. (2nd generation)	Queensland, Australia	Various	(QDAFF 2014)
Ceroplastes rusci	Early-May (1st generation) Aug. (2nd generation)	Italy	Fig tree	(Inserra 1970)
	Late May to Early-June (1st generation) Late Aug. to early Sept. (2nd generation)	Extremadura, Spain	Fig tree	(De la Cruz Blanco et al. 2010)
Ceroplastes sinensis	Feb.	Northland, New Zealand	Citrus	(Lo et al. 1996)
	Late-June	Virginia, USA	*Ilex* spp.	(Kosztarab 1996)
	Early-July	Central Greece	*Citrus sinensis*	(Stathas et al. 2003a)
	Nov.	New South Wales, Australia	Citrus	(Snowball 1970)
	June-July	Northern Spain	*Citrus reticulata, C. sinensis*	(Martínez-Ferrer et al. 2015)
Coccus hesperidum	Dec. and Jan.	Chile	Various fruit trees	(Bayer CropSCience Chile 2014)
Coccus pseudomagnoliarum	April	Davis, California, USA	Chinese hackberry (*Celtis sincmis*)	(Dreidstadt 2004)

(continued)

Table 3. Continued

Species	Time of the year	Location	Host cited in the references[a]	References
	June	Greece	Citrus	(Argyriou and Ioannides 1975)
	June	Italy	Citrus	(Barbagallo 1974)
	June	Spain	Citrus	(Tena and Garcia-Mari 2008)
	June	California, USA	Citrus	(Bernal et al. 2001)
Coccus viridis	Sept.	South Florida	Various	(Fredrick 1943)
Didesmococcus unifasciatus	Early June	Central Asia	Stone fruits	(Babayan 1973)
Eulecanium caryae	Mid-May to mid-June	Ohio, USA	N/A	(Shetlar 2002)
	Late-June	Michigan, USA	Beech, willow, birch	(Wallner 1969)
Eulecanium cerasorum	May	Tennessee, USA	Apple, buckeye, dogwood, elm, locust, maple, pear	(Klingeman et al. 2002)
	Late-May	Kentucky, USA	Sweetgum (*Liquidambar styraciflua*), hackberry (*Celtis occidentalis*), sugar maple (*Acer saccharum*), Norway maple (*Acer platanoides*), honeylocust	(Mussey and Potter 1997, Hubbard and Potter 2005)
	Late-May to early-June	California, USA	Pear	(Madsen and Barnes 1959)
	June to early-July	Pennsylvania, USA	Crabapple, dogwood, elm, maple, honeylocust, Japanese zelcova, pear, sweetgum, *Wisteria* spp.	(Hoover et al. 2011)
		New Jersey and Midwestern USA	Various	(Krischik and Davidson 2003, Herms 2004, NJDA 2006)
Eulecanium kunoense	Early to mid-May (females) March (males)	Walnut Creek, California, USA	Various	(Madsen 1962)
Eulecanium tiliae	Late-May to Mid-June	Armenia, Eurasia	Apple, pear, plum; broad-leaved trees and shrubs	(Babayan 1976)
Lichtensia viburni	Early to mid-June (1st generation) Mid-Aug. (2nd generation)	Mediterranean basin	Olive, *Pistacia lentiscus, Hedera helix*	(Pellizzari 1997)
Mesolecanium nigrofasciatum	Mid-May to mid-June	Ohio, USA	Various	(Shetlar 2002)
	Late May to early June	North Carolina, USA	Blueberry	(Meyer et al. 2001)
	June	Pennsylvania, USA	Peach, sycamore	(Simanton 1916, Hoover et al. 2011)
	June	New Jersey, USA	N/A	(NJDA 2006)
Neolecanium cornuparvum	May, Aug.	New Jersey, USA	N/A	(NJDA 2006)
	July, Sept.	New York, USA	*Magnolia* spp.	(Herrick 1931)
	Late-July to early-Aug.	Ohio, USA	*Magnolia* spp.	(Herms 2004)
	Late-Aug.	Pennsylvania, USA	*Magnolia* spp.	(Hoover et al. 2011)
	Late-Aug. and Sept.	Michigan, USA	*Magnolia* spp.	(Wallner 1969)
	Early-Sept.	Virginia, USA	*Magnolia* spp.	(Kosztarab 1996)
Neopulvinaria innumerabilis	May	Tennessee, USA	Alder, ash, beech, boxwood, dogwood, elm, lilac, linden, locust, maple, oak	(Klingeman et al. 2002)
	Mid to late-May	Athens, Georgia, USA	Red oak	(Hodges and Braman 2004)
	Early-June	Virginia, USA	Various	(Day 2008)
	Mid-June	Colorado, New Jersey, USA	Various hardwoods	(Cranshaw et al. 1994, NJDA 2006)
	Mid-June to mid-July	Pennsylvania, USA	Maple, pear	(Hoover et al. 2011)
	Mid-June to early-July	Midwestern USA	Maple, honey locust, linden (*Tilia* spp.)	(Krischik and Davidson 2003)
Parasaissetia nigra	Dec. and Jan. May (partial 2nd)	California, USA	Various	(Smith 1944)
Parthenolecaium corni	May	Tennessee, USA	Fruit trees and ornamental plants	(Klingeman et al. 2002)
	Late-May to mid-June(1st generation) Early autumn (2nd generation)	Athens, Georgia, USA	Pin oak *(Quercus palustris*), red maple (*Acer rubrum*), *willow oak (Q. phellos*)	(Hodges and Braman 2004)
	Late May to early-July	California, USA	Broom (tribe Genisteae)	(Birjandi 1981)
	Early-June	Virginia, USA	Various	(Day 2008)
	June and July	Midwestern USA	Various	(Krischick and Davidson 2003, Herms 2004)
	Mid-June	New Jersey, USA	N/A	(NJDA 2006)
	Mid-June to mid-July (1st generation) Mid-Aug. (2nd generation)	Pennsylvania, USA	Various	(Asquith 1949, Hoover et al. 2011)
	Mid-July	California, USA	Pear, elm	(Essig 1915, Madsen and Barnes 1959)
	Oct. to early-Nov. (1st generation) Jan. (2nd generation)	Chile	Grapes	(Bayer CropScience Chile 2014)
Parthenolecanium fletcheri	Early-June	Virginia, USA	Arborvitae, yew, pachysandra, eastern red cedar	(Day 2008)

(continued)

Table 3. Continued

Species	Time of the year	Location	Host cited in the references[a]	References
	June	Pennsylvania, USA	Arborvitae (*Thuja* spp.), yew	(Hoover 2006)
Parthenolecanium fletcheri	Mid to late-June	Midwestern USA	Various	(Krischik and Davidson 2003, Herms 2004)
	Late June	Central Europe	*Cupressus, Juniperus Platycladus, Thuja, Tsuga*	(Malumphy et al. 2011)
	July, mid-Aug.	New Jersey, USA	N/A	(NJDA 2006)
Parthenolecanium orientale	Mid-May	China	Grapevine (*Vitis vinifera*)	(Li 2004)
Parthenolecanium persicae	Early-May	Southern Greece	Grapevine	(Stathas et al. 2003b)
	Mid-May to mid-June	Ohio, USA	Various	(Shetlar 2002)
	Late-July	Henrico County, Virginia, USA	Barberry	(Kosztarab 1996)
	Mid-Nov.	Chile	Fruit trees	(Bayer CropScience Chile 2014)
Parthenolecanium pruinosum	Late-May to June	California, USA	Walnut	(Michelbacher 1955)
Parthenolecanium quercifex	Late-May	Virginia, USA	Oaks, hickory, birch	(Schultz 1984)
Parthenolecanium rufulum	Late-May	Northeastern Italy	English oak (*Quercus robur*)	(Rainato and Pellizzari 2009)
Physokermes hemicryphus	Late-July	Greece	*Abies cephalonica, A. borisii regis*	(Gounari et al. 2012)
Physokermes piceae	Mid-June	Wooster, Ohio, USA	N/A	(Herms 2004)
	Late-June	Colorado, USA	Spruce	(Cranshaw et al. 1994)
Protopulvinaria pyriformis	April (males) May (females)	Florida, USA	Avocado	(Moznette 1922)
Pulvinaria acericola	Late-May to Early-June	Virginia, USA	Maple, dogwood, holly, andromeda, gum	(Day 2008)
	June to early-July	Pennsylvania, USA	Azalea	(Hoover et al. 2011)
	June 8 to 14	Lexington, Kentucky, USA	Red maple	(Mussey and Potter 1997)
Pulvinaria amygdali	Mid-June	New York State, USA	Peach, plum, quince	(Harman 1927)
Pulvinaria floccifera	Late-May and June	Pennsylvania, USA	Holly, ivy, *Taxus* spp.	(Hoover et al. 2011)
	Early-June	Virginia, USA	Camellia, holly, *Taxus* spp., rhododendron, hydrangea, maple, English ivy	(Day 2008)
	Mid-June	New Jersey	N/A	(NJDA 2006)
	Mid to late-June	Athens, Georgia, USA	Burford holly, Bradford pear	(Hodges and Braman 2004)
	June	Tennessee, USA	*Callicarpa* spp., *Camellia* spp., holly, hydrangea, maple, yew	(Klingeman et al. 2002)
	Late-June to early-July	Connecticut, Rhode Island, USA	Various	(Westcott 1973)
	Mid-July to late-June	Guilan and Mazandaran provinces, Iran	Citrus, *Taxus baccata, Pittosporum toriba, Ilex aquifolia, Camellia sinensis*	(Hallaji-Sani et al. 2012)
Pulvinaria hydrangeae	July	Europe; Australia; New Zealand; USA	Various	(Alford 2007)
Pulvinaria polygonata	March	India	Mango, citrus	(Chatterji and Datta 1974)
Pulvinaria psidii	Early-April (1st generation) Mid-June to early-July (2nd generation) Early to mid-Sept. (3rd generation)	Egypt	Guava	(Baker et al. 2012)
Pulvinaria rhois	Mid-April	California, USA	Prune, apple, peach, plum	(Essig 1915)
Pulvinaria vitis	Late-May	Germany; former Soviet Union	Various	(Schmutterer 1952, Borchsenius 1957)
	Early to mid-June	Ontario, Canada	Peach	(Phillips 1963)
	July–Aug.	Pacific Northwest USA	Grape	(Hollingsworth 2014)
Pulvinariella mesembrianthemi	Early-May Late-May	Oakland, California, USA El Cerrito, California, USA	Ice plant (*Carpobrotus* sp.)	(Washburn and Frankie 1981)
Rhodococcus turanicus	Mid-May	Armenia	Stone fruits	(Babayan 1986)
	Sept.–Nov. (partial 2nd generation)	Eastern Spain	Citrus, olive	(Bibolini 1958, Argyriou 1963, Peleg 1965, Nuzzaci 1969b, De Freitas 1972)
	June to July (for 1 generation)	Eastern Spain	Citrus, olive	(Briales and Campos 1986, Noguera et al. 2003, Tena et al. 2007)
	Mar. to Oct. (for 2 generations)	Eastern Spain	Citrus, olive	(Panis 1977b, Llorens-Climent 1984, Noguera et al. 2003)
	Oct.–Nov.	Argentina, Chile, Peru, southern Australia	Various fruit trees	(Simmonds 1951, García 1969, González and Lamborot 1989)
Sphaerolecanium prunastri	Mid-May to mid-June	Ohio, USA	Various	(Shetlar 2002)
	June	Pennsylvania, USA	Purpleleaf plum, *Pyracantha* spp.	(Hoover et al. 2011)
Toumeyella liriodendri	Aug.	New Jersey, Pennsylvania, Tennessee, USA	Tulip tree, magnolia, linden	(Klingeman et al. 2002, NJDA 2006, Hoover et al. 2011)
	Sept.	Virginia, USA	Tulip tree, magnolia	(Day 2008)
	Late Aug. to Sept.	Midwestern USA	Tulip tree, magnolia, basswood, buttonbush, hickory, linden, redbud, walnut	(Krischik and Davidson 2003)

(continued)

Table 3. Continued

Species	Time of the year	Location	Host cited in the references[a]	References
Toumeyella parvicornis	June to early-July (in 1 generation)	Colorado and Nebraska, USA	*Pinus* spp.	(Clarke 2013)
	May to late-July (in 2 generations)	Maryland, Virginia, North Carolina, USA	*Pinus* spp.	(Clarke 2013)
Toumeyella pini	Late May to Early-June	Colorado, USA	*Pinus sylvestris, Pinus mugo, Pinus edulis, Pinus nigra*	(Cranshaw et al. 1994)
	Mid-June to mid-July	Pennsylvania, USA	*Pinus* spp.	(Hoover et al. 2011)
	June 20	Wooster, Ohio, USA	N/A	(Herms 2004)
Toumeyella pinicola	Feb.	Southern California, USA	*Pinus* spp.	(Dreistadt 2004)
	Mid-April to mid-May.	San Mateo Co., California, USA	*Pinus* spp.	(Kattoulas and Koehler 1965)
	Late April	San Francisco Bay area, California, USA	*Pinus* spp.	(Dreistadt 2004)
	Aug. (males)	San Mateo Co., California, USA	*Pinus* spp.	(Kattoulas and Koehler 1965, Gill 1988)

[a] N/A, not specified.

Miller et al. 2004, Ben-Dov et al. 2015, Oswald 2014). Other beetles, hemipterans, thrips, flies, caterpillars, mites, and spiders are ocassional or opportunistic predators of soft scales (Clausen 1978, Kosztarab 1996, Harris 1997, Ponsonby and Copland 1997, Hodges and Braman 2004, Rakimov et al. 2015).

Resident natural enemies kill many soft scales in the outdoor environment. Two encyrtid, two pteromalid, and one aphelinid parasitoid species were responsible for 10–60% mortality in *P. quercifex* population (Schultz 1984). Three aphelinid, nine encyrtid, one eulophid, and one pteromalid species contributed up to 37.5 and 4.5% mortality in nymph and adult *Eulecanium cerasorum* (Cockerell), respectively, whereas *Hyperaspis* sp. (Coccienllidae) reduced crawler abundance by 47.6% (Hubbard and Potter 2005). *Anthribus nebulosus* (Forster) (Anthribidae) reduced *Physokermes inopinatus* Danzig and Kozár population by 55% and *Physokermes piceae* (Schrank) population by 59% (Kosztarab and Kozár 1983), whereas *Anthribus niveovariegatus* Reolofs reduced *E. pela* population by 75% (Deng 1985). Where spiders were left undisturbed, *C. floridensis* population was below damaging level (Mansour and Whitecomb 1986). Parasitoids, predators, entomopathogenic fungi, leaf abscission, and rainfall resulted in 96% mortality in *C. viridis* populations (Rosado et al. 2014). Insecticide treatment against *P. corni* on fruit trees in California's Central Valley can be omitted if a large (but unspecified) number of scale insects are parasitized in the summer (Bentley and Day 2010).

Conserving existing natural enemy populations is an important strategy in managing soft scale pests. Studies are needed to assess the mechanism, adoption, and effectiveness of habitat manipulation, which include provision of alternative food sources, alternative prey or hosts, shelter and favorable microclimatic conditions (Landis et al. 2000), for soft scale management. In the only relevant study to date, Paredes et al. (2015) reported that the presence of ground cover, which increased vegetation diversity and natural enemy shelter, did not reduce *S. oleae* abundance in Spanish olive groves.

Using selective or compatible insecticides that minimally affect natural enemy survival and behavior also can conserve their populations (Ruberson et al. 1998, Raupp et al. 2001). Extensively use of broad-spectrum pyrethroids, carbamates, and organophosphates can reduce natural enemy abundance and effectiveness, and lead to scale insect pest outbreaks (McClure 1977, Raupp et al. 2001, Wakgari and Giliomee 2001, Prabhaker et al. 2007). Insect growth regulators, neonicotinoids (when applied to the soil), oil, and spirotetramat have lower impact on the survival and effectiveness of scale insect natural enemies (Sclar and Cranshaw 1996, Coll and Abd-Rabou 1998, Smith and Krischik 2000, Wakgari and Giliomee 2001, Rebek and Sadof 2003, Prabhaker et al. 2007, Frank 2012). Rebek and Sadof (2003) cautioned that the true impact of these selective, compatible, or "reduced risk" insecticides on the natural enemies of scale insects depended on the extent scale insect abundance was reduced by the insecticides, the timing of application, the mode of contact with the insecticide residue, and the sublethal effects of these insecticides on the pests and the natural enemies; these are largely unknown for soft scale pests and their natural enemies.

Ants can interfere with foraging and reproductive behaviors of natural enemies through direct attack or incidental disturbance (Bartlett 1961, Bach 1991, Buckley and Gullan 1991, Itioka and Inoue 1996a, 1996b). Ant-exclusion increased predator abundance and reduced soft scale abundance (Vanek and Potter 2010).

Natural enemies, especially parasitoids, are successful in many classical and augmentative biological control programs (Kapranas and Tena 2015). The introduction of *Anicetus beneficus* Ishii and Yasumatsu (Encyrtidae) achieved successful control of *C. rubens* in Japanese citrus orchards within 2.5 yr (Yasumatsu 1951, 1953, 1958, 1969; Smith 1986; Takagi 2003). The introduction of *Metaphycus luteolus* (Timberlake) and *Metaphycus helvolus* (Compere) reduced *C. pseudomagnoliarum* populations in southern California (Bartlett 1978), but it was unsuccesful in the San Joaquin Valley (Gressit et al. 1954, Bartlett 1978, Kennett 1988, Kennett et al. 1995) because of mismatch of the natural enemy species with local environmental conditions (Bernal et al 2001). Suppression of some soft scale populations may require a complex of native and introduced natural enemy species (Schweizer et al. 2002).

Although formulation and high production cost limited earlier adoption, recent advances have allowed greater use of entomopathogenic fungi in crop production (Evans and Hywel-Jones 1997). The efficacy of entomopathogenic fungi depends on appropriate environmental conditions (Evans and Hywel-Jones 1997). In humid tropical regions, *Verticillium lecanii* (Zimmermann) Viegas is the main mortality factor of *C. viridis* (Murphy 1997). Efficacy of entomopathogenic fungi also depends on pest species. More *C. destructor* died from *V. lecanii* and *Fusarium* spp. infections than *C. sinensis* on citrus in Northland, New Zealand (Lo and Chapman 1998).

Chemical Control

Insecticides registered for soft scale management can be broadly categorized into contact and systemic insecticides. Systemic insecticides, which include members of organophosphates, neonicotinoids, tetramic acid derivatives, and diamides, function as contact insecticides when applied as topical sprays directly on the scale insects. When applied as soil drench, soil injection, basal trunk spray, trunk injection, granular broadcast, and pellet broadcast, systemic insecticides are absorbed by plant tissues and translocated to the canopy. Their application flexibility and efficacy make systemic insecticides the preferred management tool against scale insect pests on large trees, in sensitive areas and in the urban landscape.

Systemic insecticides have longer residual efficacy than contact insecticides. Some ornamental plant growers and landscape care professionals use systemic insecticides to prevent infestation and damage by certain recurring pests, such as soft scales (Chong, personal observations). Systemic insecticides provide sufficient population suppression of certain scale insect species with only one application per year (Frank 2012; Chong, unpublished data). Typically, the application is made just before crawler emergence to ensure the highest concentration of active ingredients in the plant tissues. Although systemic insecticides have the benefits of greater flexibility and residual longevity, recent studies suggest that neonicotinoids should be used carefully because of their potential impact on pollinator health (Cowles 2014, Pisa et al. 2014, Johnson and Corn 2015) and their implication in spider mite outbreaks (Raupp et al. 2004, Szczepaniec and Raupp 2012a, 2012b; Szczepaniec et al. 2011, 2013).

Contact insecticides registered for soft scale management in the United States include carbamates, organophosphates, pyrethroids, neonicotinoids, juvenile hormone mimics, fenoxycarb, pyriproxyfen, flonicamind, buprofezin, tolfenpyrad, spirotetramat, diamides, azadirachtin, horticultural oils, and insecticidal soaps. A layer of wax, which is impenetrable to aqueous insecticide solution, covers the body of older nymphs and adults. Targeting crawlers and settled first instars, which lack or have only a thin protective wax layer, can achieve the greatest efficacy (Kosztarab 1996, Marotta 1997, Kabashima and Dreistadt 2014). Repeated applications (sometimes biweekly depending on insecticide residual longevity) may be needed because crawlers emerge over several weeks or months. IPM practitioners can use short residual or compatible insecticides (such as horticultural oil and insect growth regulators) to minimize impact on pollinators, natural enemies, and other nontarget organisms (Kosztarab and Kozár 1988, Kabashima and Dreistadt 2014).

Voltinism affects the frequency of contact insecticide application. When timed and applied properly, insecticides can reduce the population of univoltine species within one season (Chong, unpubished data). Suppressing the population of a multivoltine species may require multiple applications targeting crawlers of different generations (Bethke 2010, Chong, unpublished data).

Acknowledgments

We thank four anonymous reviewers for their constructive comments. This project was supported by United States Department of Agriculture, National Institute of Food and Agriculture (USDA-NIFA) under project number SC-1700473 and grant number 2010-34103-21144. This is Technical Contribution No. 6286 of the Clemson University Experiment Station.

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Received 12 March 2015; accepted 30 September 2015.