

Chapter 1

Introduction

The black vine weevil, *Otiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae), is a serious economic pest of a wide range of horticultural crops including small fruits and ornamental crops in the United States. This pest feeds on over 100 plant species including evergreen, deciduous and herbaceous plants (Smith, 1932; Masaki et al., 1984).

The ecological traits of this species include the flightlessness of adults, thelytokous parthenogenesis, and the subterranean habitat during the larval and pupal stages. The adult does not have a pair of membranous hind wings, which are used for flight in other coleopteran species. The low mobility of flightless adults may contribute to the fact that outbreaks of this species are usually localized in individual nurseries and the spread of this pest mainly depends on transportation of infested plants (Nielsen & Dunlap, 1981).

All *O. sulcatus* adults are parthenogenetic females and no males have been found (Feytaud, 1918; Smith, 1932). In complete thelytokous parthenogenesis, the unfertilized eggs laid by unmated females develop into females. With this parthenogenetic mode of reproduction, *O. sulcatus* has doubled the reproductive output of amphimictic species, and a single female transported accidentally into an isolated area is capable of establishing a new population (Engelmann, 1970). Furthermore, implementing sex pheromone traps, which is a one of most effective monitoring tools in some mating species, is not useful for this species.

As in other root-feeding insects, the control of damage-causing *O. sulcatus* larvae is hampered by the difficulties of detection when the treatment is required and difficulties of access to a substantial portion of subterranean larvae (Hunter, 2001).

Management options for *O. sulcatus* populations include foliar spray of insecticides that target the adults and soil treatment with insecticides or entomopathogenic nematodes that target the subterranean larvae (Moorhouse et al., 1992a). Although the high standards for environmental horticultural crops that are frequently attacked by *O. sulcatus* are imposed by consumer demands and legal restrictions on exporting infested plants, Integrated Pest Management Program (IPM) programs for *O. sulcatus* have not yet been successfully implemented due to lack of accurate information on *O. sulcatus* biology. Numerous previous reports suggest that environmental factors such as temperature, photoperiod, food quality, pathogens and insecticides all have significant impact on *O. sulcatus* biology. However, none of these factors has been investigated in sufficient detail to be applied to control efforts against *O. sulcatus*. Inconsistency in the reports on *O. sulcatus* phenology and reproductive biology may compound mistaken predictions based on previous studies, majority of which do not have uniform control of environmental factors. Therefore, the goal of the present research was to determine the effects of major environmental factors on *O. sulcatus* development and reproduction in order to advance the understanding of *O. sulcatus* ecology and thus assist the development of *O. sulcatus* IPM programs.

Black vine weevil literature review

History and significance of the pest

The black vine weevil, *Otiorhynchus sulcatus* (Fabricius), is a serious insect pest of horticultural crops throughout Europe, the United States, Australia, Chile, and Japan (Fig. 1.1A). This species was described by Fabricius in 1792 and the genus *Otiorhynchus* was named by Germar in 1824 (Smith, 1932). The first report of damage to cultivated plants by *O. sulcatus* was made in Germany in 1834 (Smith, 1932). Of European origin, it has spread to the United States, Canada, Australia, Japan, and Chile (Moorhouse et al., 1992a). In North America, *O. sulcatus* was first noted in Massachusetts in 1835 (Alford, 1995) and economic damage was first reported in Missouri in 1871 (Riley, 1871). Since then, *O. sulcatus* has been spread across much of the northern United States and southern Canada (Warner & Negley, 1976), mainly through the shipment of potted ornamental plants. In the United States, the distribution of this pest ranges from Maine to the Carolinas in the East and California to Washington in the West (Fig. 1.1B).

Larval feeding on the roots causes serious damage to the host plant and results in reduced vigor and frequently plant death, whereas leaf notching caused by adults is not lethal damage (Fig. 1.2). Damage to recently transplanted cuttings or young plants has greater impact than damage to established plants, because their root systems cannot withstand larval feeding without adverse effect on growth (Neiswander, 1953; Foster, 1982). The larvae and adults of *O. sulcatus* are capable of feeding on more than 100 plant species including evergreen, deciduous and herbaceous plants (Smith, 1932; Masaki *et al.* 1984). Serious economic injury has been reported on *Cyclamen*, *Taxus*, *Fragaria*, and *Rhododendron*, mainly due to larval feeding on roots (Moorhouse et al., 1992a). A variety of containerized perennials in production fields,

greenhouses and nurseries are commonly infested by *O. sulcatus* and its feeding damage on roots frequently results in plant mortality (La Lone & Clarke, 1981; Cowles, 2001). For instance, yew production fields in Connecticut were nearly all infested with *O. sulcatus* and approximately 50% of the plants were unmarketable due to root damage, which results in an annual loss in excess of \$1,000,000 per year (Cowles, 2002). Leaf notching, as a result of *O. sulcatus* adult feeding, may cause consumer rejection as well as legal restrictions on transporting and selling the infested plants. High-value ornamental plants that are commonly susceptible to *O. sulcatus* are among the fastest growing business sectors of agriculture in the United States. Nationwide, floriculture and nursery crops reached \$ 13.8 billion in sales in 2001 (USDA, 2003).

Life cycle and temperature-dependent development

Outdoor populations of *O. sulcatus* have one generation per year but there is commonly considerable overlap among stages (Fig. 1.3 & Fig. 1.4). Most individuals hibernate as mature larvae in soil without an obligatory diapause (Smith 1932; La Lone & Clarke, 1981), but some adults might overwinter successfully under favorable conditions (Garth & Shanks, 1978; Nielsen & Dunlap, 1981; Evenhuis, 1982). Most adults do not survive winter in the field because most hibernation sites are exposed or too near the soil surface to serve as a buffer to lethal temperatures (Moorhouse et al. 1992a). In early spring, overwintering larvae resume development and feeding with rising temperatures. Mature larvae pupate in earthen cells and adults emerge in the field between April and mid-June with some geographical variation (Schread, 1972; Garth and Shanks, 1978). The developmental time and survival of *O. sulcatus* pupae is temperature dependent and pupal development takes 10 days at 24 °C and 50 days at 15 °C (Stenseth, 1979). Pupal development requires 182.9 degree-days over the lower

developmental threshold of 8.4 °C (Masaki & Ohto, 1995). The newly eclosed adult fractures the earthen cell in the soil and digs its way to near the surface where the adults feed nocturnally in the plant canopy, but return to the soil surface during daytime (Smith, 1932). Parthenogenetic *O. sulcatus* females lay eggs after a pre-ovipositional feeding that lasts 2-3 weeks in the field, depending on food plant (Shanks, 1980; Maier, 1981) and temperature (Stenseth, 1979). Adults drop eggs onto the soil from the feeding site (Neiswander, 1953; Breakey, 1959) or at the base of stems (Klingler, 1959). Total egg production per female is extremely variable among published reports but typically ranges from 500-1200 eggs (Cram 1965; Penman and Scott, 1976; Moorhouse et al. 1992b). Adult oviposition in outdoor conditions ceases at the end of August or early September (Cram, 1965; Garth & Shanks, 1978), although the oviposition period might extend up to two years under laboratory conditions (Moorhouse et al. 1992b).

Newly laid eggs are uniformly pearly white and relatively soft. In 1-3 days, depending on temperature, the eggs change to a uniform brown color and the shell becomes rigid (Smith, 1932). This melanisation process is an essential part of embryogenesis and all the eggs that fail to melanize are non-viable (Montgomery & Nielsen, 1979; Maier, 1981). Egg development depends on temperature and humidity. Egg hatching was successful at temperatures between 12-29 °C but no eggs survived at RH lower than 57%, at 20.5 °C (Montgomery & Nielsen, 1979). Hatching requires 186.4 degree-days above the lower developmental threshold of 6.3 °C (Masaki & Ohto, 1995). Neonate larvae crawl through the soil and begin feeding on fine roots. Later instars feed on the cortex of the larger roots and crown of plants causing serious damage (La Lone & Clarke, 1981). The rate of larval development is highly dependent on temperature (Schread, 1972) and lower the threshold temperature for development was estimated to be between 2 and 6 °C (Stenseth, 1979).

Pest management

populations have been managed by killing the damage-causing larvae or by reducing egg-laying adults. The economic damage caused by larval feeding is severe and thus control of this stage is critical. For larval control, soil treatment with organochlorine insecticides such as aldrin, dieldrin, and heptachlor provided very good control with prophylactic application (Breakey, 1959) until they were banned by the U. S. Environmental Protection Agency during 1970's. As replacements for aldrin, good control was achieved by applying a soil drench of carbofuran (Saunders, 1970), diazinon (Schread, 1972), acephate (Antonelli & Campbell, 1981), or chlorpyrifos (Blackshaw, 1984; Mannion et al., 2000). Soil drench with chlorpyrifos, an organophosphate insecticide, was commonly used for larval control in 1990's. However, chlorpyrifos has several problems such as phytotoxicity to the roots of treated plants and high toxicity to human and wildlife (Mannion et al., 2000; Cowles, 2003). As replacement for the toxic chlorpyrifos, bifenthrin proved very effective against both the larvae of scarabs and root weevils (Nielsen & Cowles, 1998; Cowles, 2001). Imidacloprid, a neonicotinoid insecticide, has provided a long residual activity against scarab larvae but it is most effective against early instars (Power et al., 1993; Smitley & Davis, 1993). A major drawback of controlling the subterranean larvae with insecticides, as in other root-feeding insects, is the difficulty of detecting them early enough and the low level of access to larval population. Thus, foliar application of insecticide has been the most commonly used management practice for *O. sulcatus* control due to relatively simple techniques. The efficacy of foliar applications depends on targeting the pre-ovipositional adults and thus careful monitoring of adult activity is a prerequisite for optimum spray timing (Labuschagne, 1999). Previous studies showed the efficacy of some foliar insecticides against

O. sulcatus adults during the 1970-1980's. Nielsen & Montgomery (1977) found that fenvalerate remained effective on foliage for 8 weeks after treatment and bendiocarb provided 7-day residual effectiveness. Nielsen & Dunlap (1988) also reported that bifenthrin remained effective for 35 days but acephate was ineffective 1 day after treatment. Permethrin also remained active more than a month (Nielsen and Montgomery, 1977; Nielsen, 1983). Treatment with pyrethroids such as fenvalerate, permethrin, and fluvalinate provided rapid knockdown of adults (Nielsen, 1983; Shanks and Chamberlain, 1988). Diflubenzuron had no significant effects on mortality of adult weevils but reduced their fecundity (Zepp et al., 1979). Adult weevils were more sensitive to ingestion than contact in tests with carbofuran, chlorpyrifos, carbaryl, bendiocarb, and acephate (Nielsen, 1983). Thus, insecticides with systemic and long-residual activity would provide better control for *O. sulcatus* adults. Despite intensive insecticide spray programs, it has been observed that a proportion of *O. sulcatus* adult populations can survive application of most insecticides including acephate, chlorpyrifos, endosulfan, carbaryl, bendiocarb, and bifenthrin (Cowles, 2003). Recent implementation of the Food Quality Protection Act requires the use of environmentally safe alternatives that are less toxic or have a narrow range such as neonicotinoids. However, no information on the effectiveness of these insecticides on *O. sulcatus* adults is available.

As an environmentally safe alternative to chemical insecticides, entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae offer effective control against *O. sulcatus* larvae (Simons, 1981). Successful *O. sulcatus* control with entomopathogenic nematodes has been reported in strawberries and woody ornamentals (Backhaus, 1994) and in glasshouse crops (Georgis and Poinar, 1984). Heterorhabditid species were more effective than steinernematids in controlling *O. sulcatus* larvae and have a threshold temperature for activity of

13-14 °C (Georgis and Poinar, 1984; Schirocki and Hague, 1997). Commercial products for *O. sulcatus* control are recommended for use when the soil temperature is warmer than 15 °C because the infectivity of nematodes is significantly influenced by soil temperature (Long et al., 2000). The most significant limitation to the field use of the nematodes is that soil temperature is too low for the effective control of the nematodes in late season when the *O. sulcatus* larvae are still causing damage. Although their efficacy has been sometimes inconsistent or unsatisfactory with conventional application techniques (Georgis & Gaugler, 1991), the nematode efficacy and consistency has been improved by combining them with synergistic agents such as neonicotinoids (Koppenhofer et al., 2000; 2002) and by developing novel formulations (Shapiro & Lewis, 1999; Shapiro-Ilan et al., 2001; 2003).

Other management efforts, which can be compatible with chemical or biological control measures, include the utilization of physical barriers, inherent plant resistance and cultural control. Some success was achieved by placing a physical barrier coated with Tanglefoot[®], grease, or Teflon[®] to exclude the flightless *O. sulcatus* adults from the plants and prevent feeding on foliage (Antonelli & Campbell, 1981; Cowles, 1995; Helm, 2001), although control was reduced where the plants were densely spaced because adults could readily migrate among the individual plants. Depending on cropping system, possible cultural control measures include removal of foliage in strawberries (Garth & Shanks, 1978), flooding in cranberry bogs (Wood & Fox, 1982), or crop rotation of annual crops (Wilcox et al., 1934). Utilization of plant resistance also has potential for reducing *O. sulcatus* damage because certain species or cultivars of plants are much less susceptible or attractive to *O. sulcatus* than others and reproductive potential of *O. sulcatus* adults is significantly influenced by the plant food (Penman and Scott, 1976; Maier, 1981). Adult weevils reared on resistant strawberry clones fed less and experienced a longer

preovipositional period and lower fecundity (Shanks & Doss, 1986). Plant resistance to *O. sulcatus* adults can be due to the lack of a phagostimulant in foliage or physical characteristics such as hairy or lepidote leaves, or curled leaf edges (Doss & Shanks, 1984; Doss et al., 1987).

Parthenogenetic reproduction and *Wolbachia*

Sexual reproduction prevails in animals and it has proven the best overall strategy to perpetuate a species in the unpredictable pressure of natural selection (Engelmann, 1970). By combining varied genes from two partners, sexual reproduction yields offspring with more flexibility to adapt to changing environments. There are, however, many examples of parthenogenetic organisms that are as persistent as their sexual counterparts through evolutionary time (Mark Welch & Meselson, 2000). The ecological advantages of parthenogenetic reproduction are primarily a twofold increase in reproductive output and a single female can start a new population (Engelmann, 1970). There are also major disadvantages. The limited genetic variation throughout generations may render them poor competitors in an unpredictable environment, as well as sensitive to parasites and diseases (Dybdahl & Lively, 1998). Over a longer period of time, lack of recombination may lead to an accumulation of deleterious mutations (Felsenstein, 1974; Lokki, 1976). Among insects, weevils (Curculionidae) are known to have a large number of parthenogenetic lineages (Suomalainen, 1940; Suomalainen et al. 1987). In thelytokous weevils, maturation of eggs is known to be apomictic (or ameiotic) (Smith & Virkki, 1978; Suomalainen et al., 1987), where meiosis is suppressed, no reduction of chromosomes occurs, and daughters are genetically identical to their mothers (Engelmann, 1970).

As in other thelytokous weevils, all *O. sulcatus* weevils are parthenogenetic females and unfertilized eggs develop into new daughters (Smith, 1932). Although it was suggested that the

males of ancestral parthenogenetic Yugoslavian species of the genus *Otiorhynchus* died out during the ice age (Kovacevic, 1981), the basic questions about parthenogenesis in *O. sulcatus* remain unanswered, in particular, the origin of parthenogenetic lineages.

Recently in some insects, parthenogenesis has been ascribed to *Wolbachia*, a maternally inherited intracellular alpha proteobacterium. *Wolbachia* infection has been shown to induce complete thelytokous parthenogenesis mostly in haplodiploid parasitic wasps (Stouthamer et al., 1990; Zchori-Fein et al., 1992; Cook and Butcher, 1999), but was also recently found in predatory thrips (Arakaki et al., 2001) and phytophagous mites (Weeks and Breeuwer, 2001). Furthermore, the symbiosis of *Wolbachia* in insect hosts plays a role in cytoplasmic incompatibility (CI) (Hsiao & Hsiao, 1985; Breeuwer & Werren, 1990; O'Neill & Karr, 1990), feminization of genetic males (Rousset et al., 1992), or male killing during developmental stages (Hurst et al., 1997; Fialho & Stevens, 2000; Hurst et al., 2000; Jiggins et al., 2000; Lawson et al., 2001). In a taxon-specific survey, Werren et al. (1995b) reported that *Wolbachia* was detected in 16.9% of Neotropical insects using the polymerase chain reaction (PCR) based diagnostic techniques. Jeyaprakash & Hoy (2000) reported that 76% of arthropod species tested were *Wolbachia*-positive by using their improved long PCR. *Wolbachia* infection has been found in numerous coleopteran species (Table 1.1) but there is no report on *Otiorhynchus* species or any other parthenogenetic weevils despite its possible implication on the host reproduction. Besides detection in a species, information on the prevalence of *Wolbachia* in different geographical strains would provide better understanding of host-symbiont interactions in more detail. However, only a few reports on the prevalence of *Wolbachia* have been published in Coleoptera (Kondo et al., 1999; Clark et al., 2001; Vega et al., 2002).

Objectives

Based on literature review and preliminary experiments, three dominant environmental factors were examined in this research: temperature as a physical factor, endosymbiont *Wolbachia* as a biological factor, and novel neonicotinoids as a chemical factor in management.

Four objectives in this research were to:

1. Determine the effects of temperature on the immature development and survival of *O. sulcatus* and develop a temperature-dependent predictive model of stage emergence.
2. Determine the effects of temperature on the reproductive success of *O. sulcatus* and develop a temperature-dependent model of each reproductive life history trait of *O. sulcatus*.
3. Investigate the prevalence of infection by the bacterial endosymbiont *Wolbachia* in *O. sulcatus* populations in the United States and the impact on *O. sulcatus* reproduction.
4. Determine the effectiveness and sub-lethal impacts of the neonicotinoid insecticides, imidacloprid and thiamethoxam, on *O. sulcatus*.

Table 1.1. Coleopteran species with *Wolbachia* and phenotypes associated with infection

Species infected	Phenotype	References
Bruchidae		
<i>Callosobruchus chinensis</i>	–	Kondo et al., 1999
Buprestidae		
<i>Brachys tessellatus</i>	Male-killing	Lawson et al., 2001
Byturidae		
<i>Byturus tomentosus</i>	–	Malloch et al., 2000
Chrysomelidae		
<i>Acromis sparsa</i>	–	Werren et al., 1995b
<i>Chelymorpha alternans</i>	–	Werren et al., 1995b
<i>Chersinellina heteropunctata</i>	–	Werren et al., 1995b
<i>Diabrotica v. virgifera</i>	CI	O'Neill et al., 1992
Cleridae		
<i>Priocera sp.</i>	–	Werren et al., 1995b
Coccinellidae		
<i>Adalia bipunctata</i>	Male-killing	Hurst et al., 1999
<i>Coleomegilla maculata fuscilabris</i>	–	Jeyaprakash & Hoy, 2000
<i>Coleomegilla maculata lengi</i>	–	Jeyaprakash & Hoy, 2000
Curculionidae		
<i>Anthonomus eugenii</i>	–	Jeyaprakash & Hoy, 2000
<i>Aramigus tessellatus</i>	–	Werren et al., 1995b
<i>Bangasternus orientalis</i>	–	Werren et al., 1995a
<i>Conotrachelus nenuphar</i>	–	McClanan et al., 2004
<i>Cossonus sp.</i>	–	Werren et al., 1995b
<i>Diaprepes abbreviatus</i>	–	Jeyaprakash & Hoy, 2000
<i>Hypera postica</i>	CI	Hsiao & Hsiao, 1985
<i>Pachnaeus litus</i>	–	Jeyaprakash & Hoy, 2000
<i>Sitophilus oryzae</i>	–	Werren et al., 1995a
Dermestidae		
<i>Attagenus unicolor</i>	–	O'Neill et al., 1992
Lampyridae		
<i>Photinus collustrans</i>	–	Jeyaprakash & Hoy, 2000
<i>Photinus tonytoxis</i>	–	Jeyaprakash & Hoy, 2000
Scolytidae		
<i>Hypothenemus hampei</i>	–	Vega et al., 2002
Tenebrionidae		
<i>Tribolium confusum</i>	CI	Fialho & Stevens, 1996
<i>Tribolium madens</i>	Male-killing	Fialho & Stevens, 2000

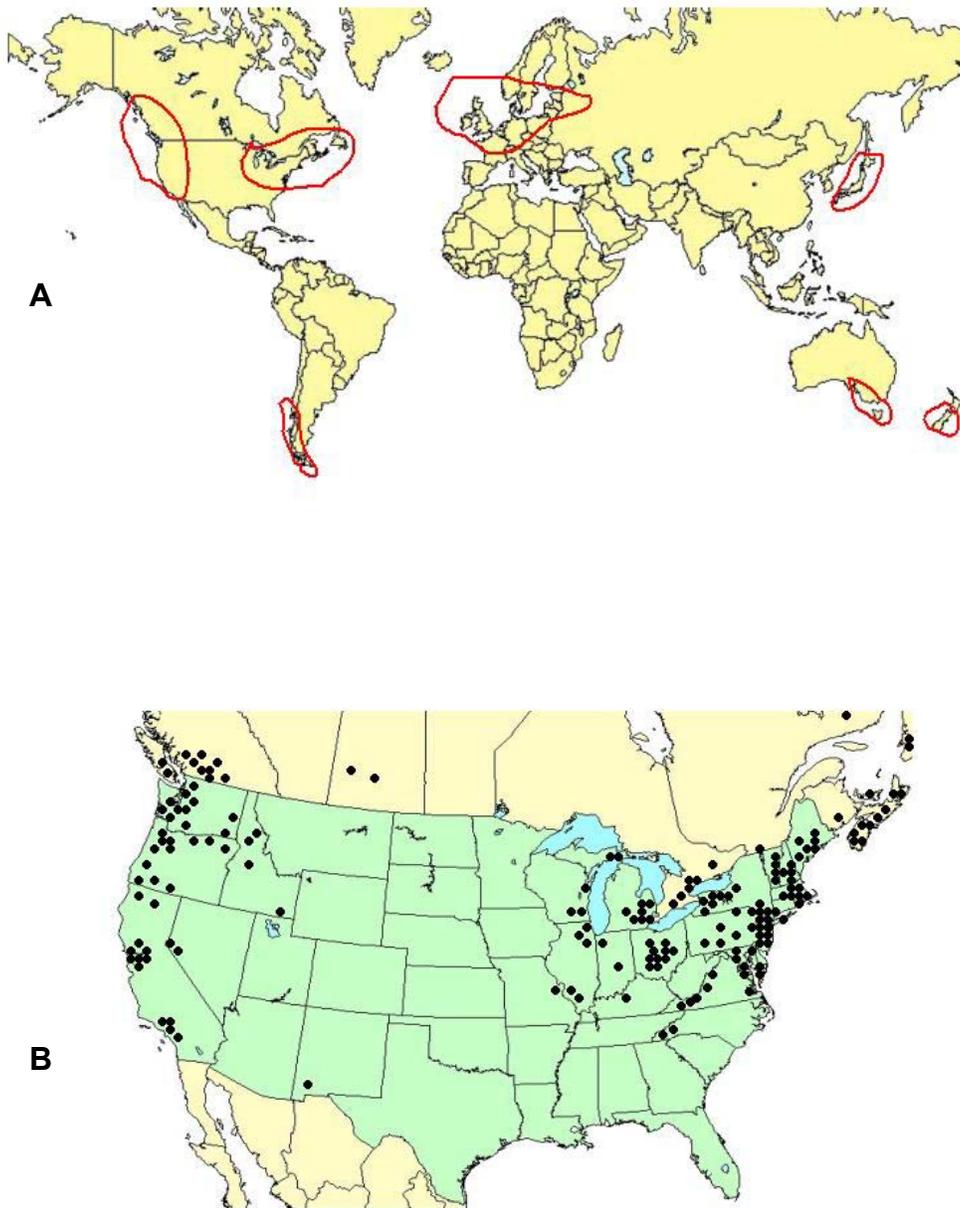


Fig. 1.1. Geographical distribution of *O. sulcatus*: (A) Approximate global distribution (from Moorhouse et al., 1992a), (B) Distribution in North America (from Johnson & Lyon, 1991).



Fig. 1.2. Plant damaged caused by *O. sulcatus* feeding in container-grown *Astilbe*: (A) leaf notch (arrow) by adult feeding on leaf margins, (B) control (left) and root damage (right) by larval feeding. Photo by Youngsoo Son.

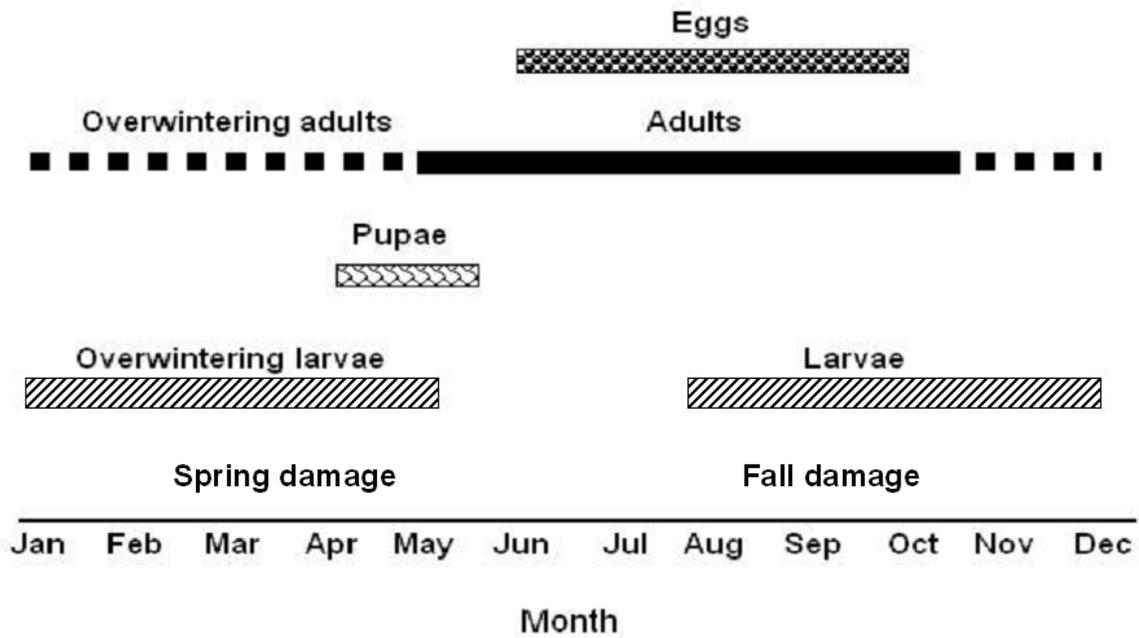


Fig. 1.3. Approximate life cycle of *Otiorhynchus sulcatus* and period of serious root damage in the field according to Moorhouse et al. (1992a).

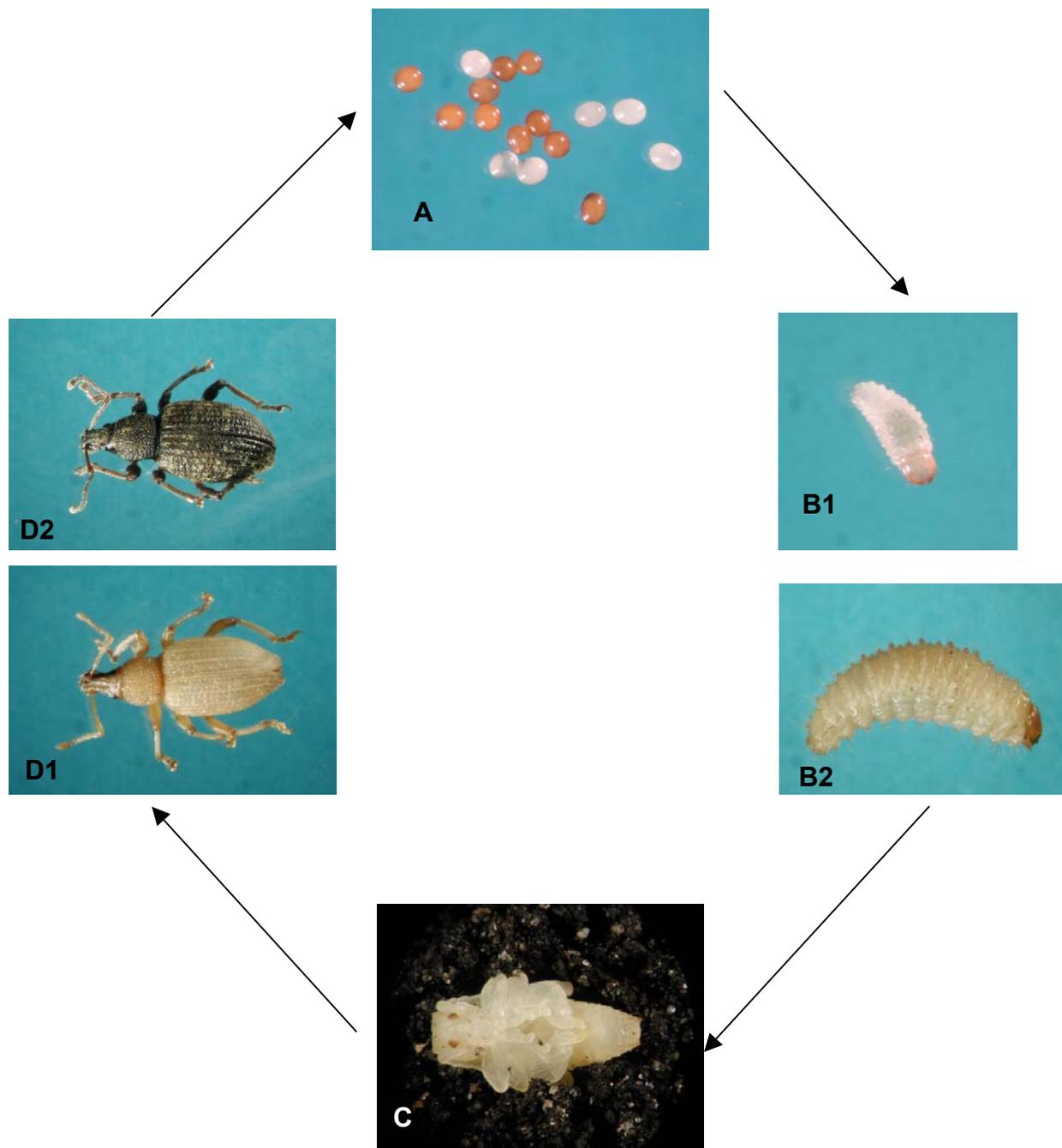


Fig.1.4. Developmental stages of *O. sulcatus*: (A) Eggs (≈ 0.8 mm), (B1) Neonate larva (≈ 1 mm), (B2) Fully grown larva (≈ 8 mm), (C) Pupa (≈ 10 mm), (D1) Teneral adult, (D2) Adult (≈ 10 mm). Notice that viable eggs turn opaque brown but non-viable eggs remain white. Photo by Youngsoo Son.

References

- Alford DV (1995) Pests of Ornamental Trees, Shrubs, and Flowers. John Wiley and Sons, New York, NY.
- Antonelli AL & Campbell RL (1981) Root weevil control on rhododendrons. Washington State University Cooperative Extension Bulletin 0970.
- Arakaki N, Miyoshi T & Noda H (2001) *Wolbachia*-mediated parthenogenesis in the predatory thrips *Franklinothrips vespiformis* (Thysanoptera: Insecta). Proceedings of the Royal Society of London, Series B: Biological Sciences 268: 1011-1016.
- Blackhaus GF (1994) Biological control of *Otiorynchus sulcatus* F. by use of entomopathogenic nematodes of the genus *Heterorhabditis*. Acta Horticulturae 364: 131-142.
- Blackshaw RP (1984) An evaluation of three insecticides as compost treatments for the control of vine weevil larvae in hardy-annual nursery stock. Journal of Horticultural Science 59: 559-562.
- Breakey EP (1959) Control of root weevils in strawberry plantings. Journal of Economic Entomology 52: 1117-1119.
- Breeuwer JAJ & Werren JH (1990) Microorganisms associated with chromosome destruction and reproductive isolation between two insect species. Nature 346: 558-560.
- Clark TL, Meinke LJ, Skoda SR & Foster JE (2001) Occurrence of *Wolbachia* in selected Diabroticite (Coleoptera: Chrysomelidae) beetles. Annals of Entomological Society of America 94: 877-885.
- Cook JM & Butcher RDJ (1999) The transmission and effects of *Wolbachia* bacteria in parasitoids. Researches on Population Ecology 41: 15-28.

- Cowles RS (1995) Black vine weevil biology and management. *Journal American Rhododendron Society* 49: 94-97.
- Cowles RS (2001) Protecting container-grown crops from black vine weevil larvae with bifenthrin. *Journal of Environmental Horticulture* 19: 184-189.
- Cowles RS (2002) Yews in Connecticut. www.entomology.umn.edu/cues/blackvw/blackvn.html.
- Cowles RS (2003) Practical black vine weevil management. *Journal of American Rhododendron Society* 57: 219.
- Cram WT (1965) Fecundity of the root weevils *Brachyrhinus sulcatus* and *Sciopithes obscurus* on strawberry in the laboratory and outdoors. *Canadian Journal of Plant Science* 45:169-176.
- Doss RP & Shanks CH Jr (1984) The influence of leaf pubescence on the resistance of selected clones of beach strawberry (*Fragaria chiloensis* (L.) Duchesne) to adult black vine weevil, *Otiorynchus sulcatus* (Coleoptera: Curculionidae). *Environmental Entomology* 16: 764-768.
- Doss RP, Shanks CH Jr, Chamberlain JD & Garth JKL (1987) Role of leaf hairs in the resistance of a clone of beach strawberry, *Fragaria chiloensis*, to feeding by adult black vine weevils, *Otiorynchus sulcatus* (Coleoptera: Curculionidae). *Environmental Entomology* 16: 764-768.
- Dybdahl MF & Lively CM (1998) Host-parasite coevolution: evidence for rare advantage and time-lagged selection in a natural population. *Evolution* 52: 1057-1066.
- Engelmann F (1970) *The Physiology of Insect Reproduction*. Pergamon Press, Oxford.
- Evenhuis HH (1978) Bionomics and control of the black vine weevil, *Otiorynchus sulcatus*. *Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent* 43: 607-611.
- Evenhuis HH (1982) Control of the black vine weevil, *Otiorynchus sulcatus* (Coleoptera: Curculionidae). *Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent* 47: 675-678.

- Felsenstein J (1974) The evolutionary advantage of recombination. *Genetics* 78: 737-756.
- Feytaud J (1918) Étude sur l'otiorhynque sillonné (*Otiorhynchus sulcatus* Fabr.). *Annales du Service des Epiphyties* 5: 145-192.
- Fialho RF & Stevens L (1996) *Wolbachia* infections in the flour beetle *Tribolium confusum*: evidence for a common incompatibility type across strains. *Journal of Invertebrate Pathology* 67: 195-197.
- Fialho RF & Stevens L (2000) Male killing *Wolbachia* in a flour beetle. *Proceedings of the Royal Society of London: Series B, Biological Sciences* 267: 1469-1474.
- Foster GN (1982) Vine weevil. The west of Scotland Agricultural College Technical Note No. 163.
- Garth S & Shanks CH Jr (1978) Some factors affecting infestation of strawberry fields by the black vine weevil in Western Washington. *Journal of Economic Entomology* 71: 443-448.
- Georgis R & Gaugler R (1991) Predictability in biological control using entomopathogenic nematodes. *Journal of Economic Entomology* 84: 713-720
- Georgis R & Poinar GO Jr (1984) Greenhouse control of the black vine weevil *Otiorhynchus sulcatus* (Coleoptera: Curculionidae) by heterorhabditid and steinernematid nematodes. *Environmental Entomology* 13: 1138-1140.
- Helm H (2001) Root weevils: troublesome rhododendron pests. *Journal American Rhododendron Society* 55: 195-198.
- Hsiao C & Hsiao TH (1985) *Rickettsia* as the cause of cytoplasmic incompatibility in the alfalfa weevil, *Hypera postica*. *Journal of Invertebrate Pathology* 45: 244-246.
- Hunter MD (2001) Out of sight, out of mind: the impacts of root-feeding insects in natural and managed systems. *Agricultural and Forest Entomology* 3: 3-9.

- Hurst GDD & Johnson AP (2000) Male-killing *Wolbachia* in *Drosophila*: a temperature-sensitive trait with a threshold bacterial density. *Genetics* 156: 699-709.
- Hurst GDD, Graf von der Schulenburg JH, Majerus TMO, Bertrand D, Zakharov IA, Baungaard J, Volkl W, Stouthamer R & Majerus MEN (1999) Invasion of one insect species, *Adalia bipunctata*, by two different male killing bacteria. *Proceedings of the Royal Society of London: Series B, Biological Sciences* 266: 735-740.
- Hurst GDD, Hurst LD & Majerus MEN (1997) Cytoplasmic sex ratio distorter. In O'Neill SL, Hoffman JH & Werren JH (ed) *Influential Passengers: Inherited Microorganisms and Arthropod Reproduction*. Oxford University Press, New York, pp 125-154.
- Jeyaprakash A & Hoy M (2000) Long PCR improves *Wolbachia* DNA amplification *wsp* sequences found in 76% of sixty-three arthropod species. *Insect Molecular Biology* 9: 393-405.
- Jiggins FM, Hurst GDD, Dolman CE & Majerus (2000) High-prevalence male-killing *Wolbachia* in the butterfly *Acraea encedana*. *Journal of Evolutionary Biology* 13: 495-501.
- Johnson WT & Lyon HH (1991) *Insects that Feed on Trees and Shrubs*. (2nd edn). Cornell University Press, Ithaca, NY.
- Klingler J (1959) Observations on the bionomics of *O. sulcatus* during an outbreak in recent years on vines in German Switzerland. *Landwirtschaftliche Jahrbucher Schweizerischen* 74: 409-438.
- Kondo N, Shimada M & Fukatsu T (1999) High prevalence of *Wolbachia* in the azuki bean beetle *Callosobruchus chinensis* (Coleoptera, Bruchidae). *Zoological Science* 16: 955-962.
- Koppenhofer AM, Cowles RS, Cowles EA, Fuzy EM & Baumgartner L (2002) Comparison of neonicotinoid insecticides as synergists for entomopathogenic nematodes. *Biological*

Control 24: 90-97.

Koppenhofer AM, Grewal PS & Kaya HK (2000) Synergism of imidacloprid and entomopathogenic nematodes. *Entomologia Experimentalis et Applicata* 94: 283-293.

Kovacevic Z (1981) Occurrence of parthenogenesis in species of the genus *Otiorhynchus* in Yugoslavia. *Zastita bilja* 32: 213-224.

Labuschagne L (1999) Black vine weevil—the millennium bug? *Antenna* 23: 213-220.

La Lone RS & Clarke RG (1981) Larval development of *Otiorhynchus sulcatus* (Coleoptera: Curculionidae) and effects of larval density on larval mortality and injury to rhododendron. *Environmental Entomology* 10: 190-191.

Lawson ET, Mousseau TA, Klaper R, Hunter MD & Werren JH (2001) *Rickettsia* associated with male-killing in a buprestid beetle. *Heredity* 86: 497-505.

Lokki J (1976) Genetic polymorphism and evolution in parthenogenetic animals. VIII. Heterozygosity in relation to polyploidy. *Hereditas* 83: 65-72.

Long SJ, Richardson PN & Fenlon JS (2000) Influence of temperature on the infectivity of entomopathogenic nematodes (*Steinernema* and *Heterorhabditis* spp.) to larvae and pupae of the vine weevil *Otiorhynchus sulcatus* (Coleoptera: Curculionidae). *Nematology* 2: 309-317.

Maier CT (1981) Reproductive success of the black vine weevil, *Otiorhynchus sulcatus* (F.), fed different foliar diets and evaluation of techniques for predicting fecundity. *Environmental Entomology* 10: 928-932.

Malloch G, Fenton B & Butcher DJ (2000) Molecular evidence for multiple infections of a new subgroup of *Wolbachia* in the European raspberry beetle *Byturus tomentosus*. *Molecular Ecology* 9: 77-90.

- Mannion CM, McLane W, Klein MG, Nielsen DG & Herms DA (2000) Insecticide dips for control of Japanese beetle and other soil infesting white grubs in B&B nursery stock. *Journal of Environmental Horticulture* 18: 89-93.
- Mark Welch D & Meselson M (2000) Evidence for the evolution of bdelloid rotifers without sexual reproduction or genetic exchange. *Science* 288: 1211-1215.
- Masaki M & Ohto K (1995) Effects of temperature on development of the black vine weevil, *Otiorhynchus sulcatus* (F.) (Coleoptera: Curculionidae). *Research Bulletin of the Plant Protection Service, Japan* 31: 37-45.
- Masaki M, Ohmura K & Ichinohe F (1984) Host range studies of the black vine weevil, *Otiorhynchus sulcatus* Fabricius (Coleoptera: Curculionidae). *Applied Entomology and Zoology* 19: 95-106.
- McClanan ME, Luckhart S & Pfeiffer DG (2004) *Wolbachia* strains associated with univoltine and multivoltine plum curculios (Coleoptera: Curculionidae). *Journal of Entomological Science* 39: 132-135.
- Montgomery ME & Nielsen DG (1979) Embryonic development of *Otiorhynchus sulcatus*: effect of temperature and humidity. *Entomologia Experimentalis et Applicata* 26: 24-32.
- Moorhouse ER, Charnley AK & Gillespie AT (1992a) A review of the biology and control of the vine weevil, *Otiorhynchus sulcatus* (Coleoptera: Curculionidae). *Annals of Applied Biology* 121: 431-454.
- Moorhouse ER, Fenlon JS, Gillespie AT & Charnley AK (1992b) Observations on the development, oviposition and fecundity of vine weevil adults, *Otiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae). *Entomologist's Gazette* 43: 207-218.
- Neiswander RB (1953) Control of the black vine weevil. *Journal of Economic Entomology* 46:

234-237.

Nielsen DG (1983) Comparative toxicities of insecticides to adult black vine weevils under laboratory conditions. *Journal of the Georgia Entomology Society* 18: 50-53.

Nielsen DG & Cowles RS (1998) Preventing white grub infestation in container-grown nursery stock. *Journal of Environmental Horticulture* 16: 202-207.

Nielsen DG & Dunlap MJ (1981) Black vine weevil reproductive potential on selected plants. *Annals of the Entomological Society of America* 74: 60-65.

Nielsen DG & Dunlap MJ (1988) Control of the black vine weevil, 1987. *Insecticide and Acaricide Tests* 14: 329-330.

Nielsen DG & Montgomery ME (1977) Toxicity and persistence of foliar insecticide sprays against black vine weevil adults. *Journal of Economic Entomology* 70: 510-512.

O'Neill SL & Karr TL (1990) Bidirectional incompatibility between conspecific populations of *Drosophila simulans*. *Nature* 348: 178-180.

O'Neill SL, Giordano R, Colbert AME, Karr TL & Robertson HM (1992) 16S rRNA phylogenetic analysis of the bacterial endosymbionts associated with cytoplasmic incompatibility in insects. *Proceedings of the National Academy of Sciences of the United States of America* 89: 2699-2702.

Penman DR & Scott RR (1976) Adult emergence and egg production of the black vine weevil in Canterbury. *New Zealand Journal of Experimental Agriculture* 4:385-389.

Power KT, Shetlar DJ, Niemczyk HD & Belcher MG (1993) Control of the Japanese beetle larvae on a golf course fairway in Tuscarawas County, OH. *Insecticide & Acaricide Tests* 18: 324-325.

Riley CV (1871) Snout beetles (Coleoptera: Curculionidae). In: *Noxious, beneficial and other*

- insects of the state of Missouri, Report 3: 5-11.
- Rousset F, Bouchon D, Pintureau B, Juchault P & Solignac M (1992) *Wolbachia* endosymbionts responsible for various alterations of sexuality in arthropods. Proceedings of the Royal Society of London, Series B: Biological Sciences 250: 91-98.
- Saunders JL (1970) Carbofuran drench for black vine weevil control on container-grown spruce. Journal of Economic Entomology 63: 1698-1699.
- Schirocki AG & Hague NGM (1997) The effect of selective culture of *Steinernema feltiae* at low temperature on establishment, pathogenicity, reproduction and size of infective juveniles. Nematologia 43: 481-489.
- Schread JC (1972) The black vine weevil. Connecticut Agricultural Experimental Station Circular, No. 211.
- Seiler J (1947) Die Zytologie eines parthenogenetischen Russelkäfers, *Otiorhynchus sulcatus* F. Chromosoma 3: 88-109.
- Shanks CH Jr (1980) Strawberry and yew as hosts of adult black vine weevil and effects on oviposition and development of progeny. Environmental Entomology 9:530-532.
- Shanks CH Jr & Chamberlain JD (1988) Effects of *Taxus* foliage and extract on the toxicity of some pyrethroids insecticides to adult black vine weevil (Coleoptera: Curculionidae). Journal of Economic Entomology 81: 98-101.
- Shanks CH JR & Doss RP (1986) Black vine weevil (Coleoptera: Curculionidae) feeding and oviposition on leaves of weevil-resistant and –susceptible strawberry clones presented in various quantities. Environmental Entomology 15: 1074-1077.
- Shapiro DI & Lewis EE (1999) Comparison of entomopathogenic nematode infectivity from infected hosts versus aqueous suspension. Environmental Entomology 28: 907-911.

- Shapiro-Ilan DI, Lewis EE, Behle RW & McGuire MR (2001) Formulation of entomopathogenic nematode infected cadavers. *Journal of Invertebrate Pathology* 78: 17-23.
- Shapiro-Ilan DI, Lewis EE, Son Y & Tedders WL (2003) Superior efficacy observed in entomopathogenic nematodes applied in infected-host cadavers compared with application in aqueous suspension. *Journal of Invertebrate Pathology* 83: 270-272.
- Simons WR (1981) Biological control of *Otiornychus sulcatus* with *Heterorhabditid* nematodes in the glasshouse. *Netherlands Journal of Plant Pathology* 87: 149-158.
- Smith FF (1932) Biology and control of the black vine weevil, USDA Technical Bulletin. No. 325.
- Smith SG & Virkki N (1978) *Animal cytogenetics 3 Insecta 5 Coleoptera*. Gebrüder Borntraeger, Berlin.
- Smitley DR & Davis TW (1993) European chafer larvae control. *Insecticide & Acaricide Tests* 18: 343-344.
- Stenseth C (1979) Effects of temperature on development of *Otiornychus sulcatus* (Coleoptera: Curculionidae). *Annals of Applied Biology* 91: 179-185.
- Stouthamer R, Luck RF & Hamilton WD (1990) Antibiotics cause parthenogenetic *Trichogramma* to revert to sex. *Proceedings of the National Academy of Sciences of the United States of America*. 87: 2424-2427.
- Suomalainen E (1940) Polyploidy in parthenogenetic Curculionidae. *Hereditas* 26: 51-64.
- Suomalainen E (1954) Zur Zytologie der parthenogenetischen Curculioniden der Schweiz. *Chromosoma* 6: 627-655.
- Suomalainen E, Saura A & Lokki J (1987) *Cytology and evolution in parthenogenesis*. CRC Press, Boca Raton, FL.

- USDA (2003) Floriculture and nursery crops situation and outlook yearbook. Economic Research Service, USDA, Beltsville, MD.
- Vega FE, Benavides P, Stuart JA & O'Neill SL (2002) *Wolbachia* infection in the coffee berry borer (Coleoptera: Scolytidae). *Annals of the Entomological Society of America* 95: 374-378.
- Warner RE & Negley FB (1976) The genus *Otiiorhynchus* in America north of Mexico (Coleoptera: Curculionidae). *Proceedings of the Biological Society of Washington* 78: 240-262.
- Weeks AR & Breeuwer JA (2001) *Wolbachia*-induced parthenogenesis in a genus of phytophagous mites. *Proceedings of the Royal Society of London: Series B, Biological Sciences* 268: 2245-2251.
- Werren JH, Zhang W & Guo LR (1995a) Evolution and phylogeny of *Wolbachia*-reproductive parasites of arthropods. *Proceedings of the Royal Society of London: Series B, Biological Sciences* 261: 55-63.
- Werren JH, Windsor D & Guo LR (1995b) Distribution of *Wolbachia* among neotropical arthropods. *Proceedings of the Royal Society of London: Series B, Biological Sciences* 262: 197-204.
- Wilcox J, Mote DC & Childs L (1934) The root weevils injurious to strawberries in Oregon. Oregon Agricultural Experimental Station Bulletin No. 330.
- Wood GW & Fox CJS (1982) Growing cranberries. Agriculture Canada Publication 1282/E: 27
- Zchori-Fein E, Roush RT & Hunter MS (1992) Male production induced by antibiotic treatment in *Encarsia formosa*, an asexual species. *Experientia* 48: 102-105.

Zepp DB, Dierks AZ & Sanders DJ (1979) Effects of diflubenzuron on black vine weevil oviposition, egg viability and adult longevity (Coleoptera: Curculionidae). *Journal of the Kansas Entomological Society* 52: 662-666.