Ann. appl. Biol. (1992), 121, 431–454
Printed in Great Britain

A review of the biology and control of the vine weevil, *Otiorhynchus sulcatus* (Coleoptera: Curculionidae)

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(Accepted 3 July 1992)

Summary

At the turn of the century, damage by *Otiorhynchus sulcatus* was sporadic and limited to small areas. Increasing horticultural intensification and the adoption of husbandry techniques favourable to the weevil, such as the use of polythene mulches, increased its pest status. The development of the early inorganic pesticides reduced the number of serious outbreaks of this pest and weevil control was further improved by the development of the persistent organochlorine insecticides in the 1940's. The banning of a number of the more persistent insecticides over recent years has now left the horticultural industry in a very vulnerable position.

O. sulcatus is now a pest on a range of horticultural crops throughout the temperate regions of the world. Infestations are most common in Europe (where it originated) and the USA, and nearly 150 plants species have been identified as potential hosts to *O. sulcatus*. Damage is most frequently caused by the root feeding larval stage. Populations as low as one larva plant^{-1} can kill sensitive species such as *Cyclamen*. Severe damage by the leaf feeding adults is less common, although low levels of damage or contamination by adults may be unacceptable in certain situations. There is one generation a year. Oviposition by the flightless parthenogenetic females occurs over the summer months with oviposition rates of *c.* 500 and 1200 eggs adult^{-1} for outdoor and laboratory populations, respectively. *O. sulcatus* mainly overwinters as larvae, although significant numbers of adults may survive in areas where winter temperatures are not too severe.

A number of natural enemies, such as hedgehogs, frogs and predatory beetles, help to maintain *O. sulcatus* populations at a low level in natural environments, but they are less successful in intensive horticultural systems where persistent chemicals have been heavily relied on to maintain the population below the economic threshold level. Increasing environmental concern is now forcing growers to consider new pest control strategies. Controlled release formulations of non-persistent products, such as fonofos and chlorpyrifos, have shown potential as control agents for *O. sulcatus* larvae. Biological control agents, such as insect parasitic nematodes, have been developed commercially and new microbial control agents are in the process of development. Most of the new control products are directed towards control of *O. sulcatus* larvae. Adult vine weevils are nocturnal and a much more difficult target for the new control agents. It is

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likely that an integrated approach to pest control will be required to maintain *O. sulcatus* populations below their economic threshold level.

Key words: *Otiorhynchus sulcatus*, vine weevil, horticultural pest, pest biology, pest control, review

Introduction

Members of the genus *Otiorhynchus* (occasionally misspelt as *Otiorrhynchus* and referred to as *Brachyrhinus* in earlier literature) are polyphagous pests in many parts of the world. The genus is considered to be primarily of European origin and Hustache (cited by Wilcox, Mote & Childs, 1934) estimated that there were over 1000 species in Europe with a fossil record dating back to the Pleistocene (Feytaud, 1918). The most important pest species in the UK is the vine weevil, *O. sulcatus* (F.). Other important species of this genus are the clay-coloured weevil, *O. singularis* (L.); red-legged weevil, *O. clavipes* (Bonsd.); pig weevil, *O. porcatus* (Herbst); strawberry root weevils, *O. ovatus* (L.) and *O. rugifrons* (Gyll.) and the rough strawberry root weevil, *O. rugosostriatus* (Goeze) (Anon., 1981; Foster, 1982). Descriptions and keys of the adults and larval stages of the species are provided by Warner & Negley (1976) and May (1977) respectively.

Damage to greenhouse plants by *O. sulcatus* was first reported in 1834 in Germany (Smith, 1932), in 1837 in the UK (Westwood, 1837) and in 1831 in the USA, where it was originally described as *Curculio apiculatus* (Warner & Negley, 1976). There have been a number of publications on the biology and control of *O. sulcatus* since these initial observations, but no detailed reviews of this species since Feytaud (1918) and Smith (1932).

A number of common names have been applied to *O. sulcatus*, such as 'cyclamen borer' (Mote & Wilcox, 1927) and 'strawberry root-weevil' (Feytaud, 1918). Most recent American literature refers to 'black vine weevil' as the common name for *O. sulcatus*, although the accepted British common name is 'vine weevil' (Seymour, 1979).

Distribution

The vine weevil is endemic to the temperate areas of Europe extending from northern Italy to the southern parts of the Baltic states (Fig. 1). The eastern boundary of the distribution extends well into central Russia (Anon., 1974). The distribution of this species is strongly influenced by temperature. Stenseth (1987) observed that the vine weevil population in Norway was concentrated in areas having a mean air temperature above −4°C in January. The upper temperature limits restricting *O. sulcatus* distribution have not been quantified in the field, although Stenseth (1979*a*) found that pupal development ceased at a constant 27°C.

The movement of *O. sulcatus* from Europe to other regions in the world such as Australia and USA was associated with shipments of plants (Smith, 1932). In the USA and Canada *O. sulcatus* is most common in eastern and western areas (Fig. 1; Warner & Negley, 1976). One of the earliest observations of *O. sulcatus* in Australasia was made in New Zealand by Kingsley (1898). Since then it has also been reported from south eastern Australia and Tasmania. *O. sulcatus* recently arrived in Japan and attempts have been made to prevent further spread (Masaki, Ohmura & Ichinohe, 1984). There has also been a recent report of *O. sulcatus* in Chile (Prado, 1988).

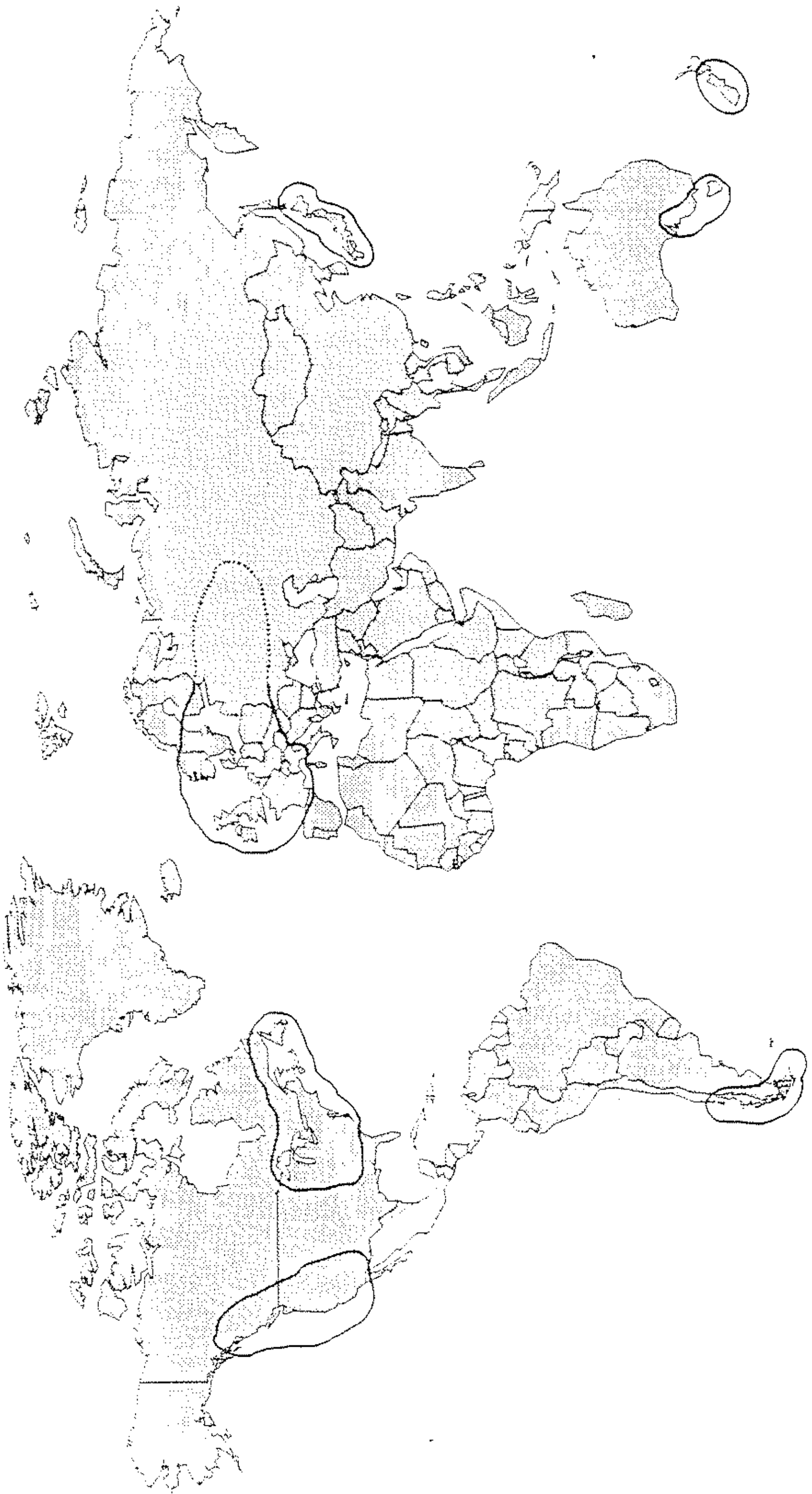

Fig. 1 Approximate global distribution of *Otiorhynchus sulcatus*.

Host Range

The larval stages of *O. sulcatus* feed on plant roots and are relatively immobile. Therefore the selection of oviposition sites by the leaf-feeding adult largely determines their diet. The polyphagous nature of adult vine weevils was demonstrated by Smith (1932) who compiled a list of 77 host plant species. Another 70 species were added to this list from the USDA Plant Pest Survey Files (Warner & Negley, 1976). In tests on economically important Japanese plants the adults fed on 101 out of 108 species tested (46/49 families), a further indication of the very wide host range (Masaki *et al.*, 1984).

Pest Status

Infestations of the vine weevil can result in substantial levels of crop damage and significant economic loss for the grower. Serious damage has been reported on a wide range of plant species, such as *Cyclamen*, *Taxus* and *Fragaria*. The damage reported on most species results from larvae feeding on the roots (Fig. 2). The damage threshold in certain situations is very low and *Cyclamen* plants have been frequently killed in glasshouse trials by a single mature larva (Moorhouse, 1990), while as few as three larvae can be lethal to a *Rhododendron* plant (La Lone & Clarke, 1981). Established crops are more resistant to weevil damage than young plants and recently transplanted cuttings, because their larger root systems can withstand some feeding without adverse effects on growth (Neiswander,

Fig. 2. Damage to the root system of *Viburnum plicatum* by *O. sulcatus* larvae. One larva was recovered from the plant on the right compared with twelve from the plant on the left.

1953; Foster, 1982). The position of the larvae within the root system will also have a significant effect on damage level (Evenhuis, 1978). One larva can do more damage at the base of the stem than several around the periphery of the root system. Penman & Scott (1976*a*) obtained a positive correlation between larval numbers and damage to strawberry plants. They estimated that the economic damage threshold was between two and eight larvae plant^{-1}. Damage caused by adults was only important on plants already severely damaged by high larval populations.

The damage to mature grape vines mainly results from the feeding activity of the adults on developing fruit (Cone, 1963). Cone (1968) observed complete defoliation from 11 adults vine^{-1}, and calculated an economic threshold of 1–3 adults plant^{-1}. Root injury resulting from larval feeding over a three year period did not significantly reduce yields. Both adults and larvae also damage vines by ring barking and this often results in plant death (Smith, 1932). The activity of adult vine weevils in vineyards has also been associated with the spread of plant viruses (Ochs, 1960). Leaf notching by adult *O. sulcatus* can cause economic loss to nurserymen as a result of rejection of plant consignments rather than serious physical damage. The presence of adult weevils in the foliage of soft fruit can also lead to berry contamination if the crop is harvested mechanically (Shanks, 1981*a*).

A number of modern husbandry practices, such as the widespread use of peat based potting mixes and black polythene mulches, as well as the expansion of horticultural production, are likely to have been partially responsible for the increased frequency of weevil infestations (Stenseth, 1979*b*; Nielsen & Roth, 1985; Stimmann, Kaya, Burlando & Studdert, 1985). It has also been suggested that the extensive use of insecticides has disrupted the balance between *O. sulcatus* and its natural enemies.

Life Cycle

There is one generation per year, but there may be considerable overlap between the different stages (Schread, 1972). The life cycle may be advanced by as much as two months under heated glass (Foster, 1982) and all stages can be present at the same time (Evenhuis, 1982). The life cycle of an outdoor population of *O. sulcatus* is shown in Fig. 3. The timing of the appearance and duration of the different stages is only approximate and is influenced by a number of factors which are discussed below.

Descriptions of the Stages

a) The egg

The eggs of *O. sulcatus* are generally subspherical with a maximum diameter of 0.8 mm (Smith, 1932; Foster, 1982). Eggs laid by the adults in cracks and crevices may become flattened and wedged shape, but this does not appear to influence viability (Smith, 1932). When first laid, the eggs are glistening white and relatively soft. Melanisation of the egg chorion occurs after 20–80 h (depending on temperature) and the shells become rigid and chestnut-brown in colour. The melanised eggs are more resistant to fungal infections and less sensitive to environmental extremes (Shanks & Finnigan, 1973). The melanisation process is an essential part of egg development and all eggs which did not become melanised were found to be non viable.

The mandibles and the head capsule of the developing larva can be seen through the egg shell approximately 2–3 days before hatching occurs. Hatching larvae use their mandibles

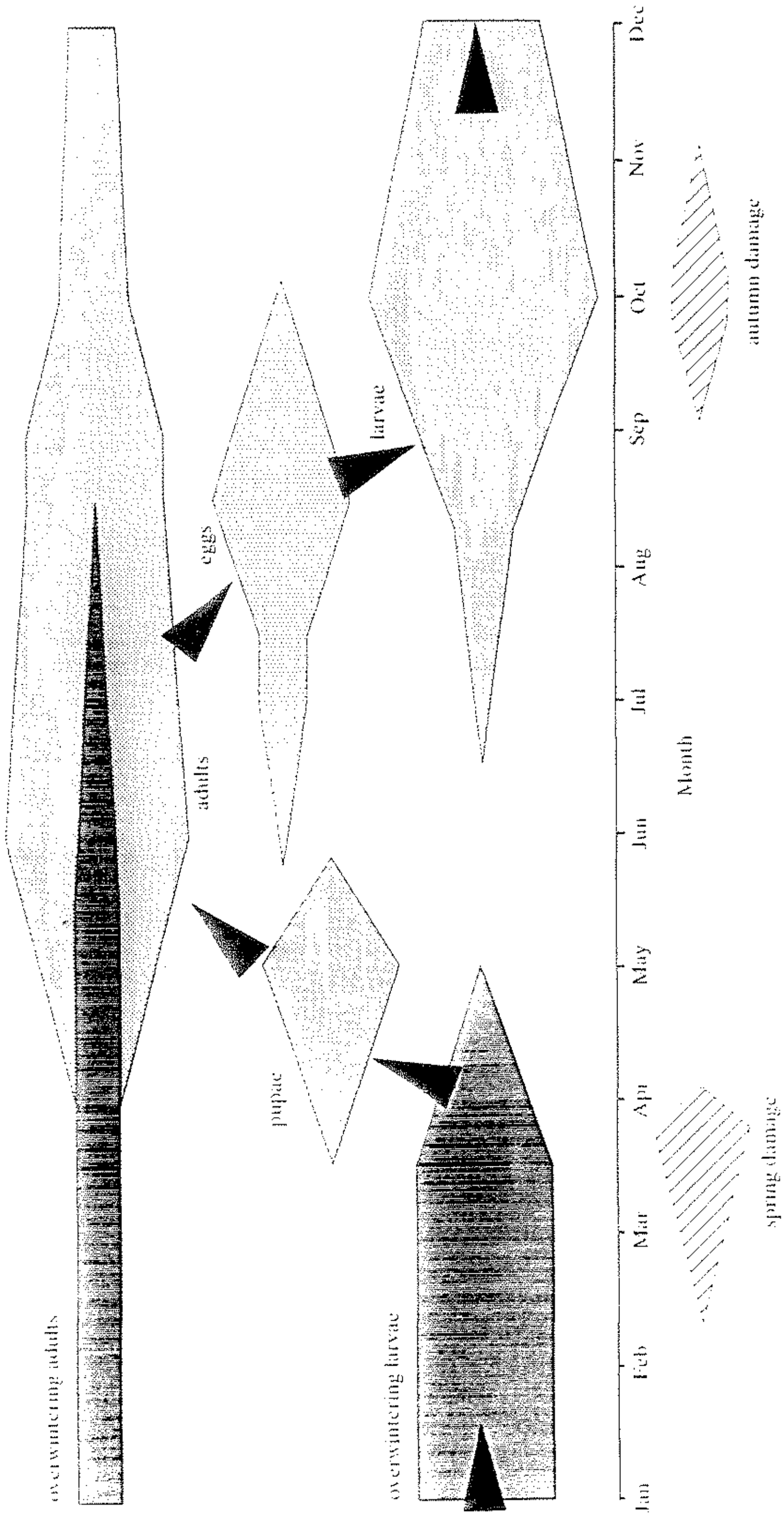

Fig. 3. Life cycle of *Otiorhynchus sulcatus* and periods of economic damage (modified from Foster, 1982) (the duration of each stage and the number of individuals present (shown by the bar widths) are approximations of the normal activity in the field).

to cut and tear a hole in the egg shell through which they emerge. The neonate larvae are negatively phototropic and rapidly burrow into the soil leaving the egg shell on the surface.

The development time of *O. sulcatus* eggs is highly dependent on temperature. Hatching occurs after 8.4 days at 27°C, but takes 56 days at 9°C (Stenseth, 1979*a*). The upper and lower temperature thresholds for egg development are 30°C and 5°C respectively (Moorhouse, 1990). Montgomery & Nielsen (1979) demonstrated that *O. sulcatus* could not overwinter as eggs in Ohio because of the cold temperatures. They observed fungal growth on the eggs in the laboratory at 10°C and suggested fungi may have contributed to egg mortality during winter.

Egg development is also influenced by moisture availability. Montgomery & Nielsen (1979) and Mason (1960) found the embryonic development was retarded at low humidities and egg desiccation increased. However, Garth & Shanks (1979) found no significant difference under field conditions between the larval survival from eggs placed in watered soil compared with those placed in dry soil.

b) The larva

The white, legless vine weevil larvae are found throughout the plant root zone down to a depth of several centimetres (Evenhuis, 1978). There is some variation in larval colour and it is mainly influenced by host species, for example, larvae feeding on strawberry plants are often a reddish-orange colour. All the larval instars have chestnut-brown heads and the larval cuticle is covered with small hairs (Fig. 4). The older larvae normally adopt a typical 'C' shaped posture as a result of the thickening of the thoracic segments (Smith, 1932). A full description of *O. sulcatus* larvae is provided by May (1977)

The neonate larvae are very sensitive to moisture levels and survival can be greatly reduced when the r.h. falls below 85% (Shanks & Finnigan, 1973). Death of the neonate larvae can also occur in soils where there is a hard crust that restricts penetration (Smith,

Fig. 4. Mature *O. sulcatus* larva (approximately 10 mm long).

1932). The compost surface in potted plants is often loose in comparison to field soils and this may partially explain the greater survival of neonate larvae in these conditions.

The larvae of *O. sulcatus* are polyphagous and will readily consume material from a wide range of plant species. The younger larvae tend to feed on the finer plant roots, whereas older larvae will eat larger membranous roots. After many of the roots have been destroyed, the larvae begin to burrow into the corms, rhizomes and stem bases of different plant species. Larvae have often been observed feeding above the soil surface inside the stems of species, such as *Begonia* and *Impatiens* and also in strawberry fruit that are in contact with the soil surface. Late instar larvae will frequently feed on the cortex of larger roots and stem bases of woody plants causing extensive damage (La Lone & Clarke, 1981). High populations of weevil larvae frequently destroy plants under field conditions and there is some evidence that larvae can be attracted over 15–20 cm to fresh plant roots (Klingler, 1957). The ability to find fresh plant material is obviously important to the completion of the larval life cycle and Klingler (1957) suggested that larvae located new hosts by following carbon dioxide gradients from the roots.

The exact number of larval instars is uncertain and may be variable; La Lone & Clarke (1981) distinguished six different instars whereas Smith (1932) identified two groups of larvae with six or seven larval instars. The larvae moult inside soil cells which they build inside hard pieces of organic matter or soil. The inside wall of the cell is fairly smooth and lined with the contents of the alimentary tract (Smith, 1932). The larva moults after one to three days in the cell by splitting the head capsule and thoracic segments along the median dorsal line (Fig. 5). The head of the freshly moulted larva is initially white, but it turns brown after one to three days and then the larva resumes feeding.

The rate of larval development is highly dependent on temperature. Schread (1972) considered that a soil temperature of 21°C was ideal for larval activity. Stenseth (1979*a*)

Fig. 5. Freshly moulted *O. sulcatus* larva.

calculated the development time from egg to pupa at 198, 130 and 110 days at 12°C, 15°C and 24°C respectively. Similar temperature effects were noted by La Lone & Clarke (1981) when they observed that larval development took 211 and 84 days on outdoor and glasshouse *Rhododendron* plants respectively. These glasshouse results suggest that vine weevil larvae do not have an obligatory diapause.

O. sulcatus mainly overwinters as larvae in overwintering cells at varying depths (normally 15 – 25 cm deep) in soil (Smith, 1932). S. Hockland (personal communication) considers that in order to survive the larvae must have reached the third instar (60–90 days) at the onset of winter. The development threshold temperature for larvae was estimated by Stenseth (1979*a*) to be between 2°C and 6°C. In later work, Stenseth (1987) demonstrated that larvae could survive at a constant 2°C for 150 days with only 7% mortality. The survival rate declined at lower temperatures, with an LT_{90} of 90 days at −3°C and 9 days at −6°C.

Increasing weevil activity in the spring is associated with rising temperatures. The larvae break out of their overwintering cells and feed voraciously for a short period prior to pupation (Evenhuis, 1978). Smith (1932) reported that pupal cells were never more than 10–12 cm deep and the usual depth was 2–5 cm. However, Schread (1972) found that the majority of the pupal cells were between 7.5 and 10 cm deep, and work in the UK suggested that pupation occurred at depths of between 15 and 20 cm (Anon., 1981). The differences between the observations may result from factors such as soil type, temperature conditions and host species. The larva will form a new pupal cell if the existing one is damaged shortly after formation, but later damage often results in mortality. Once the cell has been formed the larva voids its gut contents and appears creamy-white in colour. The prepupal phase of development may last from 3 to 34 weeks depending on temperature (Smith, 1932).

c) The pupa

The pupa is creamy-white in colour after it emerges from the prepupal exuviae. As it matures the eyes change colour from white to brown and then black. The wing pads begin to elongate at the same time and the body appendages take on a rusty-brown appearance. A full description of the pupal stage of *O. sulcatus* is provided by Barrett (1930).

Pupation in the field normally occurs between mid May and mid June (Schread, 1972; Garth & Shanks, 1978), although there are reports of pupation at other times. Large numbers of pupae were collected from a trial in California during mid April (Parrella & Keil, 1984) and newly emerged adults have occasionally been recovered in the autumn under field conditions in the UK (Anon., 1981). Stenseth (1979*a*) concluded that the pupa was the most temperature-sensitive of the pre-adult stages. Pupal development took 10 and 50 days at 24°C and 15°C respectively. Pupation also occurred at 12°C, but the process was aborted and no adults emerged. There have been some reports of relatively high levels of weevil mortality during this critical period of metamorphosis, for example, Garth & Shanks (1978) only recovered 36 adults from 50 mature larvae (28% mortality).

d) The adult

Adult vine weevils are all parthenogenetic females and no males have been found in spite of intensive examinations of natural populations (Feytaud, 1918). It has been suggested that the males of the ancestral parthenogenic Yugoslavian species of the genus *Otiorhynchus* died out during the ice age (Kovačević, 1981) and it is possible that *O. sulcatus* males might have died at the same time. Quasi mating behaviour ('pseudocopulation') has been observed in insectary populations of adults (Moorhouse, 1990; S. Hockland, personal communication). 'Pseudocopulation' has also been observed in other species of this genus and Pardi

(1987) suggested that it was connected with dominance and crowded conditions in *O. pupillatus cyclophtalmus* (Sol.).

Garth & Shanks (1978) reported peak adult emergence from the end of May until the third week of June, whereas emergence in Norway occurred between mid June and mid August (Stenseth, 1976). The young, teneral adult has a white body, black eyes and snout and rusty-brown appendages. The elytra expand shortly after transformation and the abdomen is covered within a hour (Smith, 1932). The adult changes colour from white to brown over the following one or two days. Further colour changes take place and eventually the whole body is a dull black and small tufts of yellow hair become visible on the elytra. All these changes take place within the pupal cell and the adult does not break out of the cell until approximately 7–8 days after transformation (Smith, 1932; Klingler, 1959).

Adult feeding begins on the night following emergence and the most extensive feeding occurs during the preoviposition and early oviposition periods (Doss & Shanks, 1985; Stenseth, 1976). The weight increase during the preoviposition period ranged from 8.5–32.3% on four different ornamental species (Maier, 1981). The adults are nocturnal feeders and maximal adult activity and peak oviposition rate occurs 3 to 4 h after sunset (Sol, 1981; Stimmann *et al.*, 1985). Adult vine weevils have a well-developed habit of catalepsy and will often fall to the ground if disturbed whilst feeding. The adults are negatively phototropic and they hide during the day in various locations such as cracks in the soil and around the base of leaf petioles. There have been isolated reports of adult activity during the day, for example Haegermark (1979) collected adults from strawberry foliage during a period of hot weather. This abnormal behaviour may have resulted from more suitable temperature and humidity conditions in the canopy compared to the ground. Smith (1932) also observed behavioural responses to unfavourable environmental conditions, in that the adults hid beneath the bark of host trees rather than in the moist leaf litter.

Adults are more polyphagous than larvae (Nielsen & Dunlap, 1981) and will readily consume a range of weed species if the desired host plant is absent. This means that some adults may survive insecticide treatments by feeding on unsprayed hedgerow plants (Cram & Pearson, 1965). Adult vine weevils normally feed on the margins of leaves and also on the petals of species such as *Cyclamen*. Damage to the plant foliage is rarely very severe and growers are often not aware that adult weevils are active on their crops.

The length of the preoviposition feeding period is variable and dependent on factors such as temperature (Stenseth, 1979*a*) and host plant (Nielsen & Dunlap, 1981). A strong inverse correlation has been shown between preoviposition period and total number of eggs laid (Maier, 1981). There have been reports of oviposition occurring about 2 wk after emergence (Mote & Wilcox, 1927), but the normal preoviposition period is approximately 4–9 wk. A small number overwinter and lay their first eggs the following spring (Klingler, 1959). The viability of the eggs laid within the first week of oviposition is relatively low (Garth & Shanks, 1978) and subsequent viability may vary from 59% (Mason, 1960) to over 88% (Maier, 1981).

Peak oviposition occurred one to three weeks after initial oviposition (Garth & Shanks, 1978; Nielsen & Dunlap, 1981). The oviposition duration appears to vary between populations and cyclic activity has been observed in the laboratory (Moorhouse, Fenlon, Gillespie & Charnley, 1992). Stenseth (1979*a*) found three cycles lasting 70, 90 and 60 days, whereas Penman & Scott (1976*b*) reported shorter, host-dependent cycles. Environmental factors have a significant effect on total egg production. For example, 1211 and 525 eggs adult^{-1} were collected from laboratory and outdoor populations (Cram, 1965*a*).

The factors that control oviposition in *O. sulcatus* remain unclear, however a number of likely components have been identified. Temperature is important because of its influence on adult activity and feeding. The upper and lower temperature thresholds for oviposition were estimated by Evenhuis (1978) at 26°C and 11°C respectively, with an optimum of 20–23°C. Evenhuis (1982) also observed that oviposition occurred throughout the summer and continued until the end of September when lower temperatures began to reduce adult activity. The overwintering period represents a period of temperature-induced quiescence, rather than true diapause (Cram, 1965*a*).

The sensitivity of adult vine weevils to high moisture levels was shown by Smith (1932). Feeding and oviposition by adults were both reduced on primroses that were sprinkled with water each evening compared with the dry plants. These results conflict with those of Cram (1965*a*) who found that constant high humidity increased oviposition except at the lowest temperature regime examined (8–15°C). Shanks (1980) observed that depriving the adults of water rapidly resulted in lower egg productivity. A link between oviposition and photoperiod was also demonstrated by both Nielson & Dunlap (1981) and Garth & Shanks (1978).

The host plant has been shown by many workers to have a major effect on oviposition and egg viability (Shanks, 1980; Maier, 1981; Nielsen & Dunlap, 1981; E. R. Moorhouse & D. Gay, unpublished observations). Maier (1981) and Hanula (1988) found that adults chose to oviposit on *Taxus cuspidata* in preference to alternative species and it was suggested that *Taxus* foliage contained an oviposition stimulant. The mechanisms of recognition are unclear, but it is thought that the antennae play a role in chemoreception.

The nutritional quality of the food source also influences the reproductive biology of *O. sulcatus*, particularly preoviposition period, oviposition and egg viability (Cram, 1965*b*). This may (Hesjedal, 1984) or may not (Cram, 1965*c*) result from reduced consumption of less nutritious food. Cram (1965*b*) concluded that protein N in leaves was critical.

There have been a number of conflicting reports regarding the ovipositional behaviour of *O. sulcatus*. Neiswander (1953) and Breakey (1959) report that adults drop eggs at random onto the soil from the feeding sites. Adults in other situations carefully selected an oviposition site such as a leaf vein or the junction between the leaf lamina and petiole (Moorhouse, 1990) or, as on vines, at the base of the stem, under the bark and in the soil (Klingler, 1959). In outdoor strawberries most eggs were laid at varying depths in the soil underneath the foliage (Garth & Shanks, 1978). The careful placement of the eggs at the base of the plant or in the soil has obvious advantages for larval survival and development.

There have been many different reports concerning the ability of *O. sulcatus* to overwinter as adults. Survival rates ranged from 90% in a sheltered outdoor site in Holland (Evenhuis, 1982) to as little as 25% and 1% in Vancouver (Garth & Shanks, 1978) and Ohio (Nielsen & Dunlap, 1981) respectively. Stenseth (1987) also found that temperature was a critical factor in the survival of adult weevils. Reduced survival rates of adults compared to larvae has been observed at low temperatures in laboratory experiments and this would be further exacerbated in the field because the adults hibernate in more exposed positions nearer the soil surface (Stenseth, 1987).

Oviposition is resumed as the spring temperatures increase and S. Hockland (personal communication) reported that the first eggs were laid 10–14 days after emergence from hibernation in the UK. Oviposition in a group of overwintered adult weevils in Vancouver began on 26 April and continued until late August with a peak in early August (Garth & Shanks, 1978). Overwintered females in Norway did not recommence oviposition until May/June and most were dead by mid July (Stenseth, 1976). Under laboratory conditions the oviposition period is extended and adults have a potential life span in excess of two years (Moorhouse *et al.*, 1992), but survival for such lengthy periods has not been reported in natural populations.

Adult vine weevils are flightless and consequently migration is limited compared with other insect species. Over a 57 day period the maximum movement from a release site was

85 m (Maier, 1978). The mean distance travelled following release increased with time, although the majority of adults still remained less than 10 m from the release site after 57 days. Nielsen & Dunlap (1981) also observed limited migration and noted that oviposition often occurred near to the site of emergence. There was a tendency for the adults to accumulate on plants at the ends or on the corners of beds and hedges. It is assumed that corridors of host plants facilitate migration and barriers such as areas of grass restrict further movement. The causes of migration are uncertain, but host plant quality and the physiological condition of the adults are thought to be important. Temperature is another important factor and large numbers of adult weevils have been known to move into a glasshouse in the autumn in search of hibernation sites (Foster, 1982). *O. sulcatus* is currently spreading across the United States at over 15 km year^{-1} (Maier, 1978), and it is suggested that this rapid migration is facilitated by the movement of infested plant material. This hypothesis is supported by the 'island' nature of a number of *O. sulcatus* populations.

Natural Enemies

O. sulcatus has a number of natural enemies, but the relative contribution of the individual agents to total mortality is uncertain.

a) Mammals

Feytaud (1918) listed three types of insectivorous mammals (hedgehogs, moles and shrews) that fed on *O. sulcatus*. He stated that hedgehogs were prolific predators and on some occasions their diets were composed entirely of vine weevil adults. Moles were also recorded as predators of *O. sulcatus* by Breakey (1959), but they tend to prefer moister areas than vine weevil. In the USA, Smith (1932) observed predation by skunks and deer mice. Significant levels of adult mortality were recently observed in a number of blackcurrant crops with large indigenous rodent populations (A. Winfield, personal communication).

b) Birds

Theobald (1911) listed flycatchers, finches, starlings, several different warblers and tits as being predatory on vine weevil in the UK. Feytaud (1918) reported that poultry were good scavengers of larvae and adults which were exposed during the cultivation of vineyards and small flocks of bantams used to be kept on tree nurseries in Boskoop, Holland to destroy adults and larvae (Evenhuis, 1978).

c) Reptiles and amphibians

Feytaud (1918) identified a number of different lizard species as predators. Toads and frogs were also considered to be very important and effective natural control agents due to their nocturnal foraging activity in vineyards.

d) Insects

Carabid (Feytaud, 1918) and staphylinid (Smith, 1932) beetles may be important in the regulation of *O. sulcatus* populations. The importance of carabid predation was further emphasised by Evenhuis (1982) who found reduced carabid and higher *O. sulcatus* populations in plots treated with the insecticide, ethoprophos compared to the untreated plots. Larger carabids tend to eat larvae, whereas the smaller species, such as *Bembidion tetracolum* (L.) are voracious egg predators (Evenhuis, 1983). Carabid species and the common earwig

Forficula auricularia (L.) were also recorded as predators of eggs and larvae in glasshouse trials in the USA (Garth & Shanks, 1978).

There are a limited number of records of dipteran and hymenopteran parasites of *O. sulcatus*. Theim (cited by Evenhuis, 1978) reported *Pandelleia sexpunctata* (Pand., Diptera: Tachinidae) to be a major parasite of larvae and adults in German vineyards. The braconid, *Blacus* sp. and the digging wasp, *Cerceris arenaria* (L.) were reported to be occasional parasites by Smith (1932). He also observed predation of eggs and small larvae by ants (*Formica* sp.) in the laboratory. In a more recent study, a colony of pavement ants, *Tetramorium caespitum* (L.) killed 29 *O. sulcatus* adults over a 3 day period (Maier, 1978).

e) Arachnids

Adult vine weevils have been recovered from the soil surface of field trials in Kent and Hereford wrapped up in silk (Fig. 6), although the significance of spider predation on the mortality of *O. sulcatus* is uncertain. Spiders have been seen attacking adults of *O. ovatus* and mite predation on eggs of the same species has also been recorded (Wilcox *et al.*, 1934).

f) Entomogenous fungi

There are many reports of mortality in all stages as a result of fungal infection. Saprophytic or weakly parasitic fungi are the probable causal agents in a number of these infections, such as the growth of *Fusarium* on weevil pupae observed by Smith (1932). Feytaud (1918) observed entomogenous fungi, such as *Isaria destructor* (*Metarhizium anisopliae* (Metsch.) Sor.) on other Curculionidae and recognised that species such as *O. sulcatus* might also be killed by similar fungi. A number of scientists working with *O. sulcatus* have observed

Fig. 6. Adult *O. sulcatus* wrapped up in spider's silk.

natural infection by various entomogenous species, such as *M. anisopliae* (Mason, 1960), *M. flavoviride* Gams & Rozsypal, *Beauveria bassiana* (Bals.) Vuill., *B. brongniartii* (Sacc.) Petch and *Paecilomyces fumosoroseus* (Wize) Brown & Smith (Marchal, 1977) and *P. farinosus* (Holm ex S. F. Gray) Brown & Smith and *Verticillium lecanii* (Zimm.) Viégas (Zimmermann, 1981).

Marchal (1977) quantified the natural occurrence of the different fungal species and found that *M. anisopliae* was the most widespread, causing up to 28% mortality. The potential of *M. anisopliae* as a natural control agent was further demonstrated in a trial in France when 72% of the larvae in an untreated control plot became infected (Soares, Marchal & Ferron, 1983).

g) Entomogenous bacteria, nematodes and viruses

There have been few reports of natural bacterial infection or nematode parasitism of vine weevil. Marchal (1977) examined 644 larval cadavers and isolated *Bacillus cereus* from 15% of them, however this work was not continued. Three nematode species (*Rhabditida*) were also isolated during these examinations and it was estimated that nematodes occasionally killed around 90% of the larvae. Simons (1981) also isolated a *Heterorhabditis* species from a dead *O. sulcatus* larva in Holland. Viral infections in populations of weevil adults or larvae have never been reported.

Control

A range of different strategies have been employed to control an existing *O. sulcatus* infestation or to prevent one developing.

a) Plant resistance

Utilisation of inherent plant resistance has considerable potential for reducing *O. sulcatus* damage. Shanks & Doss (1986) observed less feeding, a longer preoviposition period and lower fecundity in weevil adults that were fed on leaves from a resistant strawberry clone. It was concluded that resistance was due to the presence of hairs on the abaxial leaf surface (Doss, Shanks, Chamberlain & Garth, 1987; Doss & Shanks, 1988).

Resistance to vine weevil adults has also been demonstrated within the genus *Rhododendron* (Antonelli & Campbell, 1981; Nielsen & Dunlap, 1981). *Rhododendron* resistance to another Curculionid, the obscure root weevil (*Sciopithes obscurus* Horn), was correlated with the presence of leaf scales (lepidote) and curled leaf edges (Doss, 1980, 1984). A potent hexane-soluble feeding inhibitor was also identified in extracts from lepidote species. The sensitivity of other plant species and clones may be due to the presence of phagostimulants, such as sucrose, and lipids, such as sitosterol, in the leaves (Doss & Shanks, 1984).

b) Physical control

At the end of the 19th century growers occasionally resorted to collecting adult weevils by hand in an attempt to reduce high populations. In 1914 over one million adults were collected in vineyards on a small French island (l'Ile d'Oléron) between the end of May and mid July (Feytaud, 1918).

Some success was achieved using sticky bands on the stems of shrubs. This provides an effective barrier restricting the movement of the adults to and from their feeding sites (Antonelli & Campbell, 1981). Control was reduced where the plants were closely spaced because the adults could move freely within the crops using 'green bridges'. Smith (1932) also advocated the use of physical barriers such as mesh screens to inhibit the migration of *O. sulcatus* adults into small glasshouses and cold frames. The use of chemical barriers such as ash soaked in kerosene or carbolic acid (Kingsley, 1898) is impractical in most situations.

c) Cultural control

In Vancouver, Garth & Shanks (1978) found that removal of strawberry foliage by mowing after harvest could reduce adult weevil numbers by up to 60%. Penman & Scott (1976*b*) also suggested that the removal of white clover as ground cover would reduce the adult population by increasing environmental exposure and reducing food supply. Different cover crops also had a significant effect on the population of adult weevils in vineyards (Cone, 1963).

Wood & Fox (1982) recommended that good control of vine weevil in cranberry bogs could be achieved by flooding for at least two weeks whilst the host plant was dormant. However, this approach may be more detrimental to the host plants than to the insects (Smith, 1932).

The use of crop rotation has been suggested as a possible way to reduce *O. sulcatus* infestations (Wilcox *et al.*, 1934). Early ploughing was advocated by Shanks (1981*a*) to kill both adults and larvae and reduce migration. In the UK, growers are advised to destroy rather than compost dead plants, to clean growing areas prior to restocking and to check new stock for vine weevil contamination (Anon., 1981). It is also advisable that plants on fresh ground should be located at least 100 m from a crop of infested host plants.

d) Chemical control

The economic damage caused by larvae is normally severe and consequently control of this stage is critical. This can either be achieved directly by soil treatments or indirectly by controlling the adults before eggs are laid. A number of early attempts to control *O. sulcatus* involved the use of a range of arsenical insecticides. These were incorporated into the soil, mixed into baits or applied as foliar sprays and dusts (Smith, 1932). Good control was reported with many of the chemical treatments, but phytotoxicity and safety were major problems. Eventually they were replaced by more effective insecticides such as the organochlorines.

i) Development of larvicides

Application of larvicides (especially as high volume drenches) is currently causing some concern because of the risks of ground water contamination. The options for soil treatment are incorporation prior to potting or planting, drench application and soil sterilisation. The effectiveness of each treatment is severely limited by a number of factors.

The prophylactic control of *O. sulcatus* by soil incorporation of insecticides has many advantages provided that a persistent and cost effective chemical is available. Sufficient persistence is a prerequisite for all incorporated products in order to protect the crop throughout the oviposition period. The persistence of organochlorine insecticides in the soil was initially demonstrated by Eide (1955). Later work by Breakey (1959) demonstrated that aldrin and heptachlor were still very effective in controlling larvae after five years, whereas the efficacy of lindane was greatly reduced. Soil treatment with aldrin and dieldrin reduced the weevil problems dramatically in a number of areas. For example, Cram & Andison (1959) found that aldrin reduced the number of *O. sulcatus* larvae by 100% and increased strawberry yield by 1.9 tons acre^{-1} (270%). Aldrin was used extensively as a routine soil and compost treatment, but it has now been banned because of its prolonged environmental persistence.

A number of potential replacements for aldrin have been examined. Chlorpyrifos (Dursban) was effective for 16–20 wk when mixed into compost (Blackshaw, 1984*a*). Chlorpyrifos also performed well as a high-volume drench treatment (Blackshaw, 1984*b*). However, the potential of this product on certain ornamental species is limited because of phytotoxicity (Anon., 1985). Microencapsulation has been examined as a potential way of extending the persistence of certain insecticides. The larval control recorded using slow release formulations of fonofos and chlorpyrifos was lower than for granular formulations, although the difference was not significant (Blackshaw, 1985). Microencapsulated fonofos is currently marketed as 'Cudgel' in the UK for control of vine weevil larvae and a controlled release chlorpyrifos formulation ('suSCon Green') is being developed. The performance of incorporated products (and also drenches) will be influenced by potting media or soil type (Evenhuis, 1978; Nielsen & Boggs, 1985; Nielsen & Roth, 1985).

The option to use a soil drench gives growers more flexibility in their pest control strategy. The potential product range is expanded because prolonged persistence is not essential provided that good control can be guaranteed. The timing of drenches which have limited persistence is obviously critical. In most cases the grower is unaware of the size of the larval population and its potential threat to the crop. Dead plants are often the first signs of larval activity and losses can mount rapidly even if the drench is applied at the first sign of damage. Single drench applications in the field can sometimes be made in the autumn once the adults have stopped laying. In the glasshouse, the situation is more complicated due to the longer oviposition period and repeat applications may be necessary. In both cases the grower needs to be aware of adult activity on the crop in order to time applications effectively. Antonelli & Campbell (1981) recommended that drench applications of acephate ('Orthene 75 S') should be made against the larvae on glasshouse and outdoor stock during mid September and mid October respectively. Younger larvae tend to be more sensitive to pesticides and control levels of 100% and 64% were recorded against young and old instars respectively following drenches of bendiocarb (Stimmann *et al.*, 1985).

The performance of a number of pesticides which were either incorporated into compost or drenched onto plants was examined by Blackshaw (1983). Only aldrin gave 100% control as a compost additive, whereas bendiocarb, chlorfenvinphos, gamma-HCH, permethrin and triazophos gave complete control as drenches. Good control has also been recorded using carbofuran (Saunders, 1970) and diazinon as soil drenches (Schread, 1972). In the latter case, total mortality occurred after 9 days.

A major problem with soil drenches is penetration and this can usually only be achieved using very high-volume sprays (Nielsen, Dunlap & Boggs, 1978). Some strawberry growers in the UK have improved penetration of chlorpyrifos (Dursban) by injecting the drench under the plant. It is also possible to improve penetration by irrigation following application or by defoliating the plants before treatment (Shanks, 1981*b*).

An alternative approach to soil drenches is the use of insecticidal dips for treating containerised nursery stock (Nielsen & Dunlap, 1990). Good control for weevil larvae has also been achieved on field strawberries using soil fumigants, such as ethylene dibromide (Eide, 1959). This method of treatment has many practical difficulties associated with it and is only feasible in certain situations.

ii) Development of adulticides

Adult vine weevils can be controlled more effectively than larvae (Neiswander, 1953). The effective use of adulticides involves targeting the adults during the preoviposition periods (Bogs & Braasch, 1988). This will normally involve a minimum of two spray applications to control the overwintering adults and emerging adults in the spring and early summer respectively. Control of the latter is a particular problem on soft fruit because adult emergence often coincides with the beginning of the fruit harvest. The harvest interval of many of the effective chemical insecticides is long and consequently applications have to be delayed until after harvest, by which time eggs have been laid.

Careful monitoring of adult activity is an obvious prerequisite for optimum spray timing. This can be achieved by simple techniques such as the provision of artificial day-time resting sites (Maier, 1983; Phillips, 1989) and searching foliage after dark using a torch. Antonelli & Campbell (1981) recommended that applications of acephate should be made at the first signs of adult activity on rhododendron and azalea. They also advised repeat applications at monthly intervals until the first frost.

Nielsen *et al.* (1978) concluded that the minimum effective persistence for a foliar spray was at least 48 h because adults do not feed every night. Nielsen & Montgomery (1977) found that fenvalerate remained active on foliage for up to 8 wk, whereas the residues of bendiocarb and acephate were relatively inactive after 2 wk. In more recent work, Nielsen & Dunlap (1988) showed that bifenthrin ('Talstar') provided residual effectiveness for 35 days on *Taxus* foliage, whereas acephate ('Orthene 75 SP') was ineffective after 1 day.

Gordon & Woodford (1986) demonstrated that control of *O. singularis* was improved by night spraying and it is likely that this strategy would be advantageous in the control of *O. sulcatus*. A thorough coverage is also necessary to achieve good control and this can only be obtained using high-volume sprays (Neiswander, 1953).

A comparison of insecticidal toxicity via contact and ingestion by Nielsen (1983) showed that adult weevils were more sensitive to ingestion of both carbofuran and bendiocarb. He also found that acephate had no contact or topical activity, but ingestion of foliage treated with a 0.1% spray resulted in 90% mortality. In this study chlorpyrifos and carbaryl were non-toxic.

Dieldrin resistance was reported by Nielsen, Niemczyk, Balderston & Purrington (1975) in a population of adult vine weevils in Ohio. The mortality of the resistant population was only 7–8% when exposed to 1.0% dieldrin, whereas another population from Ohio had 70% mortality following treatment with 0.01% dieldrin. The resistant population was sensitive to carbofuran but not to carbaryl or fensulfothion. A number of workers have also shown that *O. sulcatus* has a relatively low sensitivity to some organophosphate insecticides (Shanks, 1970; Nielsen *et al.*, 1975), though parathion-methyl, methamidophos and pirimiphos-methyl have given acceptable control (Bogs & Braasch, 1988).

Shanks & Chamberlain (1988) demonstrated that the host plant could have a significant effect on the toxicity of pyrethroid insecticides. Adult weevils feeding on yew were much more sensitive to fenvalerate, permethrin and fluvalinate compared with those feeding on either strawberry or cranberry. They demonstrated that the increased sensitivity resulted from a chemical factor in the yew needles. In further work on pyrethroids, Nielsen & Montgomery (1977) and Nielsen (1983) found that exposure to permethrin residues on the leaves resulted in rapid knockdown (< 2 h) resulting from contact toxicity. The adults that were only exposed for 24 h recovered, whereas 54% mortality was recorded in those exposed to 5 wk old residues for 5 days.

Studies have recently been conducted on the activity of diflubenzuron ('Dimilin') against vine weevil adults. Oviposition and egg viability were adversely affected, but only when the adults were feeding on treated foliage; there was no adult mortality (Zepp, Dierks & Sanders, 1979; Sol, 1985) and oviposition was only temporarily reduced. A second application of diflubenzuron resulted in total egg mortality for the following 8 wk. However, the effects were transient and egg viability returned to its pre-treatment level when the adults received untreated foliage.

e) *Biological control*

Many of the considerations for the development of effective chemical control agents (described above) are equally as applicable to the development of biological agents. The additional factor of temperature must also be considered and this may determine the success or failure of a number of biological agents.

i) *Entomogenous fungi*

The first attempts to control *Otiorhynchus* sp. using entomogenous fungi were reported by Decaux nearly 100 years ago (cited by Feytaud, 1918). Larvae were inoculated with *Entomophthora plusiae* and *E. saccharina*, but infection failed to develop. Entomogenous fungi were examined more recently in Sweden (Giege, 1975) and encouraging results were obtained with *B. bassiana*. There have been a number of other studies conducted over the last 15 years on the potential of the entomogenous fungi for vine weevil control in Europe (Marchal, 1977; Prado, 1979; Zimmermann, 1981; Moorhouse, Gillespie & Charnley, 1990).

All stages of the insect life cycle are prone to infection (Moorhouse, 1990; Fig. 7), however the best results have been obtained against larvae. Prado (1979) compared *M. anisopliae* with *B. bassiana* and found that they were pathogenic to weevil larvae when applied at 4×10^6 and 1×10^6 conidia cm^{-3} soil respectively. Prophylactic applications of *M. anisopliae* conidia to potted azalea and strawberry plants in glasshouse trials resulted in 94% and 81% larval mortality respectively (Zimmermann, 1981). High levels of weevil control have also been recorded in field trials using *M. anisopliae* (Moorhouse, 1990). A microbial insecticide based on a mycelial formulation of *M. anisopliae* is currently being developed for control of *O. sulcatus* and other soil insects (Andersch, Hartwig, Reincke & Stenzel, 1990).

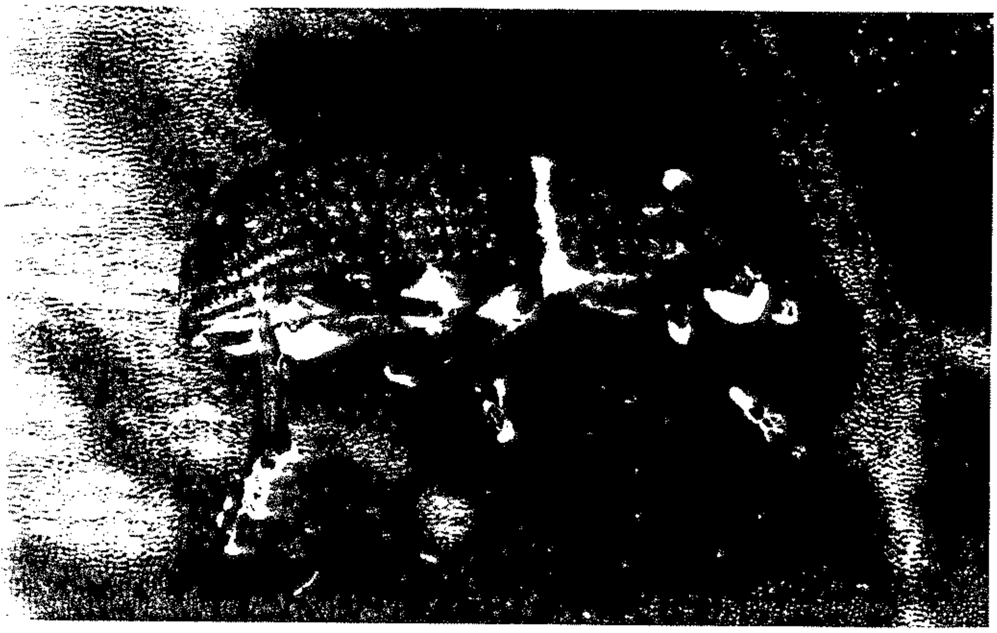

Fig. 7. Development of mycosis on the cadaver of an adult *O. sulcatus* infected with *M. anisopliae*.

ii) Entomogenous bacteria

Strains of *Bacillus thuringiensis* Berliner active against Coleoptera have shown, at best, only moderate activity against vine weevil larvae (Herrnstadt, Soares, Wilcox & Edwards, 1986; P. Jarrett, personal communication). No significant control of *O. sulcatus* was achieved using *B. thuringiensis* in a series of trials in Northern Ireland (Blackshaw, 1984*b*; Anon., 1987).

iii) Entomopathogenic nematodes

The development of entomopathogenic nematodes as control agents for *O. sulcatus* has advanced rapidly over the last few years. The nematodes parasitise all larval stages, pupae and also newly-emerged adults (Bedding & Miller, 1981). The performance of nematodes has been shown to be significantly influenced by many factors including temperature, application time, dose and host plant (Simons, 1981; Evenhuis, 1982; Stimmann *et al.*, 1985). In particular, younger larvae are more difficult to control than older larvae and performance of nematodes in the field is not equal to that under glass. Heterorhabditid nematodes are more effective control agents for *O. sulcatus* than steinernematids, but the former are more difficult to mass-produce and have limited field persistence (unpublished observations). This is unfortunate, as at least in one trial *Heterorhabditis heliothidis* (Khan, Brooks & Hirschmann) reduced the population of older larvae by up to 90% and out-performed all chemical treatments (Stimmann *et al.*, 1985). Nematodes are now sold commercially in many parts of the world for the control of *O. sulcatus* larvae.

iv) Viruses

Treatment of *O. sulcatus* larvae either directly or indirectly (via a compost drench) with a commercial formulation of a nuclear polyhedrosis virus had no effect on larval mortality (Anon., 1987).

Conclusions

There is now an urgent need to develop effective and environmentally-sound control products. Many modern insecticides have been tested against *O. sulcatus*. However, none is as effective as aldrin. The development of novel chemical agents has shown some potential for future control. Biological control based on nematodes and fungi is of particular interest because it combines efficacy and safety. However, nematodes are expensive and lack the necessary persistence for effective control of *O. sulcatus*. Fungi are not so constrained, but they must be registered prior to use. This adds to their cost, which may slow, if not prohibit commercialisation. Exploitation of natural host plant resistance to *O. sulcatus* would improve the prospects of long-term control and could possibly be developed as part of an integrated control programme.

The current understanding of the biology and behaviour of *O. sulcatus* is rather weak in certain areas. The challenge over the next few years will be to improve our understanding of a number of key areas and this will facilitate the development of effective and acceptable control strategies.

Acknowledgements

The authors would like to acknowledge the funding for this work from the University of Bath, the Horticultural Development Council and the Ministry of Agriculture, Fisheries and Food. We would also like to thank Keith Sunderland for his helpful comments on the manuscript.

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(Received 14 November 1991)