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Interaction of Cultural Control with Biological Control of *Metopolophium dirhodum* (Walker) on Wheat

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Abstract: Wheat (*Triticum aestivum* L.) is an extremely important cereal crop: it is grown in almost all countries. Its spring and winter varieties, wide temperature tolerance and ability to grow under a variety of soil types and rainfall patterns, give this crop a wide range of adaptability. One of the factors limiting wheat production is attack by aphids. These cause damage by: extraction of plant sap; injection of toxic secretions; transmission of viral diseases and excretion of honeydew. Particularly in cereals, honeydew reduces quality by interfering in the milling process.

Key words: Aphids, wheat, biological control, *Metopolophium dirhodum*

Introduction

Wheat (*Triticum aestivum* L.) ranks next to rice in the world in importance as a food crop and is the principal food for about one third of the world population (NAS, 1972). The current average world production of wheat is around 576,317 million tons (FAO, 2000). The rose-grain aphid, *Metopolophium dirhodum* (Walker), the grain aphid, *Sitobion avenae* (F.), the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), the greenbug, *Schizaphis graminum* (Rondani) and Russian wheat aphid, *Diuraphis noxia* are the most serious aphid species (Carter *et al.*, 1982; Starks *et al.*, 1983; Dixon, 1987; Reed *et al.*, 1991). These aphid species cause damage the plants in different ways i.e., extraction of plant sap; injection of toxic secretions; while feeding, transmission of viral diseases and excretion of honeydew which fouls the plant and encourages the growth of sooty moulds. These species are also vectors of barley yellow dwarf virus (BYDV), which is a global problem (Plumb, 1983). This virus can cause a loss of over 30% of yield, especially when infections occur early in the season (Doodson and Saunders, 1970). In Britain, a moderate infestation due to aphids with a yield reduction of 10 %, without spraying, could cause losses of over £50 million (McLean *et al.*, 1977). Kolbe (1970) reported that spraying at the end of flowering, at a mean aphid population of 67 per stem and 17 per ear, resulted in a yield increase of about 14%. Kuorli and Nemeth (1987) reported that in Hungary during 1982 -1986 winters and spring wheat suffered losses due to cereal aphids to the extent of 50 and 36% respectively. The use of resistant varieties is an effective control for

cereal aphids (Starks *et al.*, 1983). In IPM, other control methods are also practiced along with resistant varieties, such as different cultural practices and use of biological agents (predators and parasitoids). The activity of natural enemies may be greater on resistant than on susceptible varieties (Gowling, 1989). Integrated use of all these methods not only reduces the use of chemicals but also may even eliminate the need for insecticides. Interaction of these different techniques needs to be studied in order to develop the most appropriate IPM strategy for a crop/pest. In this review paper the effects of: nutrients (nitrogen, potassium, calcium and phosphorus), plant/water relationships and intercropping wheat with peas (and how far host density accounted for intercropping effects) on the development of aphids and their parasitoids on wheat were studied.

The cereal aphids: Aphids are world-wide pests of agricultural importance. van Emden (1972) opined that aphids were probably the most important agricultural insect pest group. The greatest diversity of aphids occurs in the temperate regions and they are undoubtedly the most important insect pests of these regions (Harrewijn and Minks, 1988).

In South-east Asia, Lefroy (1909) was the first to report grain aphids on wheat. Das (1918) mentioned corn leaf aphid, *Melanaphis sacchari* (Zehntner), grain aphid and green bug on wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.) and sorghum (*Sorghum bicolor* L. Moench). Hamid (1983) surveyed Pakistan and reported *Forda formicaria* von Heyden and *M. sacchari* attacking sorghum, *R. maidis*

attacking wheat and sorghum, *R. padi* attacking wheat and corn, *S. graminum* attacking wheat, barley and sorghum and *S. avenae* attacking wheat and barley.

Since 1968 several severe outbreaks of cereal aphids have occurred in Britain and other European countries (Anglade, 1969; Fletcher and Bardner, 1969; Kolbe, 1969; Latteur, 1971, 1973) reaching pest status in many parts of Britain during 1970, 1975, 1976, 1977 and 1979 (Jones, 1976b, 1979; Vickerman and Wratten, 1979; Carter *et al.*, 1980). Aphids invade cereals in winter but the peak of their abundance is in June.

Aphids have considerable potential for survival. They are born alive, they have a high rate of reproduction, they are difficult to eliminate, they can survive on natural and cultivated plants and they can easily migrate because of winged flight. It is therefore necessary to have a range of techniques for controlling them by exploiting their limitations. One such weakness is that winged aphids have little control of direction and recognise their host only at close range. Because of their high energy needs to sustain reproduction, they soon die without food. Many perish though failure to find a host (Harrewijn and Minks, 1988).

The increase in abundance of cereal aphids in the UK has been associated with changes in agricultural practices in cereal crops. These include the switch from spring to winter varieties, the increased use of nitrogenous fertilizers, the introduction of selective herbicides and of new varieties which are more susceptible to aphids and the large areas of monoculture which are in general more favourable for the breeding of aphids than for their predators and parasitoids (Baranyovits, 1973; Potts, 1977). The influences of a maritime and continental climate produce different effects; the former encourages autumn migration, the latter makes control more difficult (Dedryver and Gelle, 1982).

Cereal losses due to aphid attack are reflected in reduced numbers of heads, reduced numbers of grains per head, reduced individual grain weight and impaired quality of grain (Wratten, 1978; Vickerman and Wratten, 1979; Lowe, 1982). Kolbe and Linke (1974) pointed out the need for controlling cereal aphids at flowering and grain formation stages, a time when 20-30 aphids per ear could cause yield losses of up to 10%.

***Metopolophium dirhodum* (Walker) (Plate 1.1):** *M. dirhodum* and *S. avenae* are the most common and important aphid species found on cereals in Europe, although their overall abundance varies from year to year (Heathcote, 1970; Latteur, 1973; Dean, 1974a; Dean *et al.*, 1981). *M. dirhodum* is also known as the rose-grain aphid



Plate 1.1: Rose grain aphid, *Metopolophium dirhodum*

because of its host alternation between Rosaceae and Graminae (Hille Ris Lambers, 1939; Hand and Williams, 1981). Yield losses due to feeding by this aphid have been reported to be 17% on spring barley (George, 1974) and 7% on winter wheat (Wratten, 1975). *M. dirhodum* feeds on the leaves of cereals and even after ear emergence tends to prefer young and flag leaves to the ear (Lowe, 1974; Watt, 1979). The grain-feeding *S. avenae* is therefore the more damaging to crop yield. However, Wratten (1975, 1978) found that *M. dirhodum*, though it did not affect grain weight, could affect grain quality. In combined attack with *S. avenae*, *M. dirhodum* can reduce seed number per head, seed weight, flag leaf area and plant height but not the number of heads per unit area (Carrillo and Mellado, 1975).

M. dirhodum is a host-alternating species. In autumn aphids migrate from cereals or grasses, where they fed on leaves during the summer, to spend the winter on roses, their primary host. During the summer, the aphids reproduce by parthenogenesis. Most aphids at this stage are wingless females (apterae). However, when overcrowding occurs, winged females (alatae) are produced to aid dispersion. In autumn, induced by a shorter day-length, females migrate to the primary host and give birth to sexual, egg-laying females (oviparae). Males are produced and migrate to the primary host to mate. The eggs overwinter and the females hatching in spring from these eggs (fundatrices) are the first individuals of a parthenogenetic line (clone). The fundatrix gives rise to one or more apterous generations on the primary host before winged aphids are born (spring migrants) which then colonise grasses and cereals (Carter *et al.*, 1980).

M. dirhodum, like other aphids, feeds on the phloem of plants. However, phloem sap is a nutritionally unbalanced diet, rich in sugars but comparatively poor in amino acids. Aphids have developed a symbiotic relationship with micro-organisms that enables them to exploit phloem sap (Dixon, 1987).

***Aphidius rhopalosiphi* (De Stephani Perez) (Plate 1.2):**

The Aphidiidae appear to be most common and abundant aphid parasitoids in the field (Starý, 1970, 1976; Dean, 1974b; Powell, 1986; Vorley, 1986). Dean *et al.* (1981) reported that most of the cereal aphid parasitoids found between 1973 and 1979 were *Aphidius picipes* Nees and species belonging to the *Aphidius uzbekistanicus* Luzhetskii complex. This complex is known to include *A. rhopalosiphi* and *A. ervi* Haliday. In spring and winter the dominant species are *A. rhopalosiphi* and *A. picipes* (Dean, 1974a; Powell, 1986; Vorley, 1986). The sporadic, rather than chronic, pest status of cereal aphids has been attributed to the action of natural enemies in certain years (Jones, 1979).

Female *A. rhopalosiphi* oviposit by piercing the cereal aphid with the ovipositor. The egg hatches and four larval instars can be distinguished (Starý, 1970). The developing parasitoid feeds on the host until the aphid is eventually killed and the fourth instar parasitoid spins a cocoon inside the empty aphid skin. At this stage the aphid skin becomes indurated and the typical 'mummy' develops. Prepupal, pupal and adult stages develop within the mummy (Chorney and Mackauer, 1979; Cloutier *et al.*, 1981). The adult parasitoid emerges through an emergence hole which is circular and bears an emergence lid that is easily broken (Starý, 1988). The newly emerged adults need a short time to mature. Males usually emerge somewhat earlier than females under the same conditions. Unfertilized eggs may be laid by unmated females and by mated females at the end of their reproductive life when the sperm supply has been exhausted (Mackauer, 1976). Unfertilized eggs give rise to males; fertilized eggs produce females (Starý, 1970).

A. rhopalosiphi has a high potential fecundity (Shirota *et al.*, 1983) which makes it a potentially important regulating factor in cereal aphid population dynamics. Unfortunately, parasitoids are also attacked by several hyperparasitoids of which the most commonly found on cereals are *Asaphes vulgaris* Wlk., *Dendrocerus carpenteri* (Curtis) and *Phaenoglyphis villosa* (Hartig) (Carter *et al.*, 1980). The impact of parasitoids on field cereal aphid populations is poorly understood and has been a major limiting factor for the development of accurate forecasting of pest outbreaks using simulation



Plate 1.2: Adult parasitoid, *Aphidius rhopalosiphi*

modelling (Carter *et al.*, 1982). Holler (1988) observed cereal aphid parasitoids in the field. He concluded that they were ineffective in controlling cereal aphid populations since their activity was curtailed by the action of hyperparasitoids. However, Vorley and Wratten (1985), with the aid of a simulation model, deduced that parasitoids were important during the early season when hyperparasitoids were less common. They found high rates of mortality due to parasitoids when the aphid population was developing.

Integrated pest management: Integrated pest management is a multi disciplinary, ecological approach to the management of pest populations, which utilizes a variety of control tactics compatibly in a single co-ordinated pest management system. It is based on the principle of optimum rather than maximum pest control and is a significant component of integrated crop management, which is intended to provide sustainable agricultural production with minimal deleterious effects on society. It does not attempt to eradicate pests, but rather to maintain pest populations below those that cause damage of economic significance. Its primary goal is not to eliminate the use of pesticides, but rather to use the best combination of control tactics to produce a stable and sustainable agroecosystem (Madder, 1986).

The natural enemies of pests are very important in the system and may provide adequate control when combined with other control methods which do not unduly disturb the biological agents (Soerjani and Morallo-Rejesus, 1980). It is also conceded that man's influence by way of cultural practices such as harvesting methods, fertilization, irrigation, intercropping, ploughing and other

forms of land preparation and the use of chemical pesticides have markedly reduced the effectiveness of various natural enemies (Stary, 1970). Cultivation of certain varieties, especially highly resistant ones, could also reduce the ability of parasitoids to attack phytophagous insects (Callahan, 1975; Price *et al.*, 1980; Vinson, 1986) and biological control may suffer (van Emden, 1986).

Nutritional effects on the plant/insect relationship: Crop nutrients are those elements or simple inorganic compounds, which are indispensable for the growth of crops and are not synthesized by the plant during the normal metabolic processes. Nitrogen, potassium, phosphorus and calcium are the key such elements. Unavailability of these nutrients often leads to serious nutritional stress to the plants which could subsequently affect the growth and development of the insects which feed on them, particularly sucking insects which are limited in their enzymatic capacity to modify their food and substrate.

Nutritional stresses occur in soils throughout the world (Dudal, 1976). Innumerable interactions of one element with another are known (Hewitt, 1963; Hiatt and Leggett, 1974) and these interactions could be of major significance (Clark, 1982). Fertilizers change metabolism and disrupt the relationships between plants and pests (Gurevich *et al.*, 1971). A poor nutrient sap offers a potent challenge to the viability of insects due to the deficiency of some of the amino acids in the plants (Boyd, 1970). Application of nitrogenous fertilizers within an optimum range can lead to a corresponding increase in insect populations as the amount of fertilizer is increased. But nitrogen either above or below this range may often be detrimental to phytophagous pests. Thus excess nitrogen supply causes significant biochemical changes in the plants and may lead to nutritional imbalances (Mills and Jones, 1979). The nutrition of the host plant can also influence the expression of host plant resistance to insect attack (Wiseman *et al.*, 1973; Leuck and Hammons, 1974). The importance of nitrogen in insect-plant interactions, particularly plant resistance to pests, has been reviewed (Jones, 1976a; McNeill and Southwood, 1978; Mattson, 1980). It is a general assumption that increased plant nitrogen increases insect performance. Scriber (1984) found 115 studies in which insect damage, growth, fecundity or numbers increased with higher levels of plant nitrogen and 44 studies that indicated a decrease in insect performance with high nitrogen or an increase in insect populations with low nitrogen. Nitrogen stress in the host plant during the reproductive phase of insects drastically

affects their populations (McNeill and Southwood, 1978). The digestion capacity of an insect increased with increase in nitrogen level in the food (Scriber, 1984) and the larval developmental period was shortened with increase of nitrogen level in the food (Al-Zubaidi and Capinera, 1984).

That enhanced supply of nitrogen in the soil was possibly a relevant factor in the increase in cereal aphids since the mid 1940s was first suggested by Baranyovits (1973). Schaefer *et al.* (1979) noted that the increase in the numbers of *M. dirhodum* in the UK in 1978 and 1979 was coincident with an increase in the application of nitrogen fertilizer and a noticeable increase in the greenness of leaves. Dewar (1980) found that wheat plants receiving high rates of nitrogen fertilizer had 48% more aphids than those receiving a lower rate. Honek (1991) studied the effects in the field of nitrogen treatments on the abundance of *M. dirhodum* and *S. avenae* in winter cereals over two years and concluded that the abundance of *M. dirhodum* increased with nitrogen input but that the numbers of *S. avenae* were little affected. Gash *et al.* (1996) studied the effects of five different rates of nitrogen fertilizer application on the abundance of the cereal aphids *M. dirhodum* and *S. avenae* in winter wheat over three years. At the time of peak aphid populations, higher densities of the two species were associated with plots, which received the highest spring applications of fertilizer. George (1975) found that cereals of poor nutrient status could also favour aphid reproduction. Similarly Henderson and Perry (1978) found that higher densities of three cereal aphids (including *M. dirhodum*) were associated with cereal crops having low nitrate concentrations in the plant sap, especially plants in the early growth stages. So it appears that there is no consistency in the effects of plant nutrient supply to cereals and the development of cereal aphid populations. Among other aphids, soluble nitrogen and certain amino acids have been shown to affect the growth and reproductive rates of *Myzus persicae* (Sulz.) and *Brevicoryne brassicae* (L.) on Brussels sprouts (van Emden, 1966; van Emden and Bashford, 1969, 1971). They also demonstrated that similar nutritional effects of Brussels sprouts on the two aphids could result from both host plant age and leaf position. Populations of leaf sucking pests were high on plants with a high level of total nitrogen, glutamine, glutamic acid and reducing sugars (Fritzsche *et al.*, 1957; Schwenke, 1964).

Hunt *et al.* (1992) found that higher nitrogen treatments resulted in higher nitrogen concentrations in the plants, greater plant yields and greater nitrogen uptake. They also found that Colorado potato beetles that developed

on plants receiving more nitrogen showed significantly higher survival from first instar to adult and also more rapid insect development and greater pupal weight. Zitzman and May (1989) reported that the nitrogen content of laboratory-reared Colorado potato beetle larvae and dry weight gain of greenhouse-reared larvae were both positively correlated with increasing concentration of nitrogen applied to potato plants while other performance parameters were not affected.

Deficiency of potassium can cause an increase in soluble nitrogen (van Emden, 1966) and an accumulation of amino acids and soluble sugars (Vaithilingam and Baskaran, 1982; Ismunadji, 1976). Increased potassium produced better proteogenesis (a physiological phenomenon correlated with deamination of the amino acids) and reduced sugars in the sap, thus lowering the favourability for sucking pests (Chaboussou, 1972). Some authors (Broadbent *et al.*, 1952; van Emden, 1966) have found that aphids are favoured by low and disadvantaged by high potassium supply to the plant, although there are also contradictory results (Barker and Tauber, 1951; Taylor *et al.*, 1952).

Phosphorus is an essential component of living matter. Second to nitrogen it is the most limiting element in soils (Yoshida, 1981). It is one of the prime examples of interactions with other elements especially the micronutrients (Clark, 1982). Phosphorus deficiency inhibits protein metabolism and so soluble nitrogen increases (Eaton, 1952). Sugars and auxins may decrease but osmotic pressure and plasma viscosity increase (Pirson, 1955). The effects on aphids have been little researched but such evidence as is available shows increased infestation by *M. persicae* and other aphids on plants given low or nil phosphorus.

Calcium is required in large amounts by plants for cell division, cell elongation and the detoxification of H⁺ ions (Pirson, 1955). Calcium also increases nitrogen availability (Burstrom, 1954) and potassium uptake by roots (Nielsen and Overstreet, 1955) but appears to have an antagonistic effect on potassium and manganese ions in enzymatic reactions (Kachmar and Boyer, 1953). El-Tigani (1962) reported that calcium-deficient plants are vulnerable to aphid attack. With calcium deficiency, larger amounts of manganese are taken up by plants and manganese deficiency may result.

Insect plant/water relationships: Conflicting results have been recorded about aphids in relation to the reduction of water available to host plants. The reproduction of aphids under water stress increases (Markkula, 1953) or decreases (Kennedy *et al.*, 1958). Wearing and van Emden

(1967) found that the effects of water strain on the fecundity of *M. persicae* and *B. brassicae* could be different according to the age of the leaves of Brussels sprouts on which they were confined and the two aphid species themselves responded differently to plant water strain. The effects are complex, with frequent contradictions in the literature (Kennedy, 1958) attributable to the direct antagonistic effects of water stress and the indirect improvement of the suitability of plant strata with water stress. On old brassica leaves, water stress is always detrimental to *B. brassicae* and sometimes even on mature and young leaves. Fecundity and the rate of development decline as water stress increases and the production of alatae increases as leaves age (Wearing, 1972a). Markkula (1953) noted an inverse relationship between the fecundity of *B. brassicae* and the amount of water supplied. Aphid survival is poor and the rate of reproduction is considerably reduced under conditions of severe wilt (Wearing, 1972a). The selection of plants by alatae was affected when three watering regimes; wet, medium and dry were applied to Brussels sprouts grown in pots. Wearing (1972b) noted an increase in acceptability to *B. brassicae* alatae from the wet to the medium regime, but a decline in acceptability from the medium to dry regime. There was a marked preference for turgid plants, possibly associated with the level of sinigrin and an indication that intermittent water stress was advantageous to the aphid. Under conditions of drought, the spindle (*Euonymus europaeus* L.) became less acceptable to *Aphis fabae* Scop. a feature attributed to changes in the quality and quantity of the sap involving such factors as reduced sap flow, decreased turgor pressure and increased sap viscosity (Kennedy, 1958; Kennedy and Booth, 1959).

Ansari (1984) studied the fecundity and biology of cowpea aphids on water stressed plants and reported that the fecundity of cowpea aphids was reduced significantly in a 10 ml per day water regime as compared to 100 ml and 200ml water regimes. These results were consistent at two plant ages and she was of the view that cowpea aphids are dependent on plant turgor pressure for feeding. Further, Wearing and van Emden (1967) showed that lower turgor pressure may be more important in reducing the frequency of feeding by aphids (increasing restlessness) than in directly reducing the rate of ingestion of sap. In another study Mittler (1957) presented evidence that turgor pressure in the phloem of the host plant played a major role in the rapid uptake of phloem sap by *A. fabae* and *Tuberolachnus salignus* (Gmelin).

Intercropping: The development of an insect population on a crop is affected by an array of factors relating to: host plants, non-host plants, the herbivore and its natural enemies. The plants involved may be those on which the biological control is occurring; they may be plants of other species in the same plant mosaic or they may be plants of other species growing at some distance. With reference to biological control of aphids, the three plant types are: the crop, weeds or intercropped species and plants outside the cultivated area. The host plants have a direct effect on the herbivore through their physical and chemical properties (van Emden and Wratten, 1990). This is because plants other than host plants of aphids may be relevant to a particular natural enemy and therefore may affect its distribution and abundance. The dispersal of aphids and natural enemies between cropped and non-cropped areas on farmland has been reviewed by Wratten and Thomas (1990). Vickerman (1982) reported that cereal aphid populations decreased 25% in weedy plots as compared to weed free plots.

Stability is not necessarily provided by the diversification of plants and insect communities, but mixed cropping in the tropics frequently reduces the losses from pest attack (Perrin, 1977). In 1976-1978 diversification of the cropping pattern in temperate zones was studied (Perrin and Phillips, 1978; Altieri and Whitcomb, 1979). Intercropping brassicas with French beans reduced infestations of the aphid *B. brassicae* and the rootfly *Delia brassicae* (Bohemann) by over 60% compared with those on brassicas grown in pure stand (Tukahirwa and Coaker, 1982). Tingey and Lamont (1988) studied the effect of intercropping beans with wheat on pests like *A. fabae* and *Empoasca fabae* (Harris). The population of both pests was lower in intercropped fields.

Smith (1976) investigated the effect of weed-covered and weed-free backgrounds on aphids on Brussels sprouts. She reported that certain phytophagous species, particularly aphids, are more attracted to crops without weeds. Most of the work was done on natural enemies of the cabbage aphid, *B. brassicae*. The Brussels sprouts grown in a background of bare soil were more attractive to colonising aphids than were Brussels sprouts grown in a background of weeds. Smith (1969) reported that yellow water-traps caught 10% more *B. brassicae* among sprout plants surrounded by bare soil than if there were weeds all around them. In autumn aphid populations were higher on sprouts in bare soil than on weed- surrounded ones.

Plant diversity tends to intensify the impact of natural enemies, thus contributing to the relatively infrequent pest outbreaks often associated with natural communities and mixed crop ecosystems (Huffaker, 1962). However,

higher natural enemy colonisation is expected in monoculture rather than multispecific vegetation if the response of specialist natural enemies to habitat diversification is similar to that of monophagous herbivores (Coll and Bottrell, 1996).

Potato plants in monocultural stands are more favourable to insect pest attack than in polycultures. McKinlay (1985) studied the effect of under-sowing potatoes with perennial ryegrass on aphid numbers and tuber yields. He found that the *Macrosiphum euphorbiae* (Thomas) count per leaf was 0.25 on potatoes not undersown but only 0.15 on potatoes undersown with grass.

Influence of population density on growth and development of insects:

The effect of population density on an insect population is complex. Populations in nature interact with such a variable environment that the influence of density, *per se*, is subject to analysis only through highly sophisticated techniques that separate the direct effects of density from the indirect effects that are concurrent with increased number per unit area (Peters and Barbosa, 1977). The influence of population density under laboratory conditions has been investigated repeatedly (Long, 1953; Albrecht *et al.*, 1958; Barbosa *et al.*, 1972). The population density influence on size or weight is either an immediate effect in which changes in population density are directly reflected in size or weight of resultant individuals (Long and Zaher, 1958; Leonard, 1968; Barbosa *et al.*, 1972) or a lag between differences in population density and changes in size or weight (Miller, 1964).

Leonard (1968) demonstrated the link between the effect of stress on body weight and on reproductive capabilities. He showed that pupal weights diminished for increasingly crowded *Lymantria dispar* L., the significance lying in the direct correlation between pupal size of females and their fecundity. Leonard reported a 20% reduction in male pupal weight and a 35% reduction for females. Miller (1964) showed a continued decrease in adult body weight of *Drosophila simulans* Sturtevant with increasing density (5 larvae to 300 larvae per vial) but a rebound effect for *Drosophila melanogaster* Meigen weights at high densities, so that adults from 300 larvae per vial had greater individual weights than adults from the 200 larvae per vial.

Some authors have used differences in size rather than weight as a parameter to judge density effects. Murdie (1969) showed that small aphids, produced from a crowded culture, were more fecund than similarly sized aphids that were small as a result of rearing at high temperature. The undersized first offspring from crowd-

induced small aphids had an increased growth rate over normal sized aphids. Successive offspring were progressively heavier at birth.

Dixon and Wratten (1971) demonstrated that high density affected the subsequent generations of aphids because the size of parents and their progeny at birth are directly correlated, with weight of the adult and number of progeny yielding straight positive regressions with a somewhat steeper slope for the apterae than for the alatae. Since the degree of crowding has been shown by Lees (1967) to increase production of alatae over apterae in *Megoura viciae* Buckton, the effect of parental crowding not only may be expressed as decrease in size of the aphid and its progeny but also as a lowered fecundity as a result of the production of alatae, which are less fecund than comparably sized apterae.

Ellis (1988) suggested that an ideal crop protection programme should be based on: the cultivation of resistant varieties, chemical, cultural and biological control measures. These are then integrated to achieve the desired level of crop protection. Cultural control is the deliberate alteration of the agroecosystem, either the cropping system or specific crop production practices, to reduce pest numbers and crop injury (Herzog and Funderburk, 1985). Some successful cultural control methods operate by enhancing the benefits derived from natural enemies. Conversely, successful biological control methods often require alteration of common cultural practices.

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