Biological Control

27

Peter Tóth
Slovak University of Agriculture, Nitra, Slovak Republic

Introduction to Biological Control

There are many different means for controlling pests but this chapter is concerned only with methods using living organisms to control pests, a strategy called biological control. Biological control is a rapidly growing area which brings together ecologists, entomologists, weed scientists, plant pathologists, insect pathologists and microbiologists. The modern concept of biological pest control has been developed primarily by entomologists and in practice is normally taken to mean the use of living natural enemies to control pest species. Biological control has been defined many times but a commonly accepted definition was provided by Eilenberg et al. (2001):

> *'The use of living organisms to suppress the population density or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be'.*

In this way, biological control is, generally, human use of a specially chosen living organism (including viruses) to control a particular pest. This chosen organism might be a predator, parasite, or pathogen which will attack the harmful species.

The predators, parasites and pathogens of pests that are used in biological control are a large component of world biodiversity. These natural enemies are of enormous value to sustainable agriculture, where they can often eliminate the need for pesticide input. They are also of value to the control of invasive alien species, which threaten natural ecosystems.

Biological control is a form of manipulating nature to increase a desired effect. Certain biological control approaches definitely have the potential to conform to the sustainable agricultural philosophy and can be effective in all types of agricultural systems, including organic, sustainable and conventional. The method represents an alternative to continued reliance on pesticides.

Use of biological control requires much more background information about the biology and ecology of pests than for the use of chemical pesticides. For all types of biological control, it is necessary to demonstrate that natural enemies are effective at controlling pests. Life tables are used to document the effects of natural enemies on pest populations of different ages.

Biological control has several advantages over other types of control. These advantages include:

- Long-term management of the target pest (valid for conservation and introduction).
- Limited side-effects.
- Attack of only one or a few related pests.
- Self-perpetuating agents.
- Non-recurring costs (valid for conservation and introduction).
- Known levels of risks identified and evaluated before agent introduction.

The most important disadvantage of biological control is that it takes more intensive management and planning. It can take more time, require more record keeping, more patience, and sometimes more education or training. Other disadvantages are:

- It often takes many years for the populations of the introduced biological control agents to increase to levels that permanently decrease the pest population (valid for conservation and introduction).
- Agents may be subject to natural enemies.
- Environmental conditions often exclude some agents from certain locations.
- Agents usually do not eradicate the pest population.

There are three overlapping strategies of biological control, each clearly separated from the other, and they are: **Classical biological control**, **Augmentation** and **Conservation**. Historically, most emphasis has been placed on classical biological control although more recently a great deal more effort has been directed at augmentative control.

Biological Control Agents

The types of natural enemy used in biological control of insects include parasitoids, predators and pathogens.

The major uses of biological control agents are: (1) biological control of invertebrate pests using predators, parasitoids and pathogens, (2) biological control of weeds using herbivores and pathogens, and (3) biological control of plant pathogens using antagonistic micro-organisms and induced plant resistance.

Parasitoids

Parasitoid is a term derived from the more general term parasite. Parasites are organisms living in (endoparasites) or on (ectoparasites) other organisms. The term parasitoid specifically refers to insects that parasitise on other insects when they are immature (larval stage) but free-living when adult. Parasitoids are taxonomically restricted to Hymenoptera and Diptera. Parasitoids are ‘parasitic’ as larvae only (but some parasitoids may also kill many pests by direct host feeding on the pest eggs or larvae). Parasitoids are usually smaller than the hosts upon which they develop and typically only attack one stage of host (egg/larva/nymph/pupa/adult). Different species of parasitoids attack different life stages of the pest. Thus, *Trichogramma* spp. which attack the egg stage of insects are known as egg parasitoids, Braconidae such as *Cotesia glomerata* which attack larvae are larval parasitoids and so on for adult or nymphal parasitoids. Parasitoid larvae kill their hosts near the end of the parasitoid’s larval development. Adult parasitoids are free-living and usually feed on pollen, nectar, honeydew or even the body fluids of their host. Parasitoids exhibit a number of different life habits and are themselves parasitised by secondary hyperparasites.

Parasitised immature stages of pests are usually differently coloured. For example stages of immature whiteflies parasitised with parasitic wasp, *Encarsia formosa* (Encyrtidae) are darker or black when late in the parasite development compared with yellowish to creamy healthy ones. Aphids are hosts for species in the subfamily *Aphidiinae* (Braconidae) such as *Aphidius* spp. and others in the family *Aphelinidae* (Chalcidoidea). Parasitised aphids, called ‘aphid mummies’, appear puffed up, brown and hardened (Figure 27.1). The adults chew a round hole in the abdomen to emerge. Hymenoptera parasitoids are generally known as parasitic wasps.

Host-specific parasitoids are considered the most suitable for biological control. Many are commercially available with detailed guides on how ‘to use’ them.

Predators

A predator is an animal (invertebrates or vertebrates) that overpowers, kills and consumes other animals (the prey).

Figure 27.1. Mummies – aphids in the advanced stages of parasitism by internal parasitoids. Photo: P. Toth.

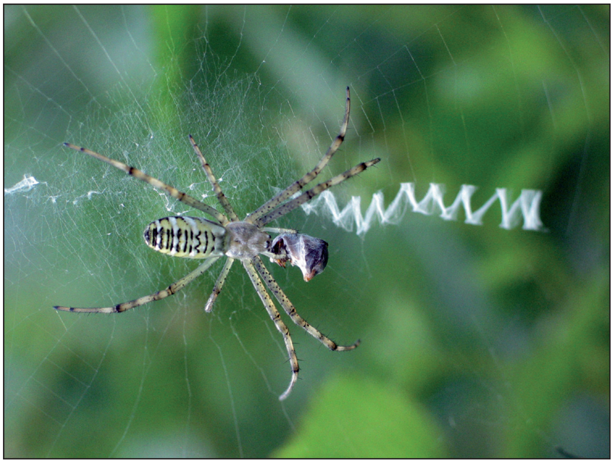

Figure 27.2. Spiders are predaceous primarily upon insect. Photo: P. Toth.

Figure 27.3. Many wasps are predatory, using other insects as food for their larvae. Photo: P. Toth.

Invertebrate predators are found among Coleoptera, Neuroptera, Hymenoptera, Diptera, Hemiptera and Odonata, but more than half of all predators are coleopterans. The most important families within Coleoptera for biological control are Coccinelidae and Carabidae. Other arthropod natural enemies include predatory mites and spiders (Figure 27.2). Adults and immatures are often generalists rather than specialists. They consume large numbers of prey (adult or immature) during their lifetime and are generally larger than their prey. Some of the adults feed on pollen if prey is not available. Invertebrate predators actively capture prey using several very different methods (Figure 27.3). Some mobile predators have good vision, such as ground beetles (Carabidae) and jumping spiders (Salticidae), and they chase their prey. Others with poor vision use a combination of vision and chemical cues to find their prey.

Vertebrate predators (especially birds, e.g. Ring-necked Pheasant, *Phasianus colchicus*) are better known to the general public than most invertebrate predators. However, the days for use of vertebrates for biological control are largely over, as the prey of vertebrate predators is too unpredictable.

Most beneficial invertebrate predators will consume many pest insects during their development, but some predators are more effective at controlling pests than others. Some species may play an important role in the suppression of some pests. Others may provide good late season control, but appear too late to suppress the early season pest population. Many beneficial species may have only a minor impact by themselves but contribute to overall pest mortality.

The predators specifically used for biological control include:

a) Predatory mites (Order Acari), which play an important role in biological control both in orchards (mainly *Typhlodromus pyri*) and glasshouses (e.g. *Phytoseiulus persimilis*) by feeding on phytophagous mites and thrips.
b) True bugs (Order Hemiptera), which are often general feeders (e.g. *Orius* spp.), both immatures and adults eating eggs, immatures and adults of a diversity of insects and mites.
c) Lady beetles (Order Coleoptera, family Coccinelidae), adults and larvae feed on soft-bodied prey, mainly aphids but also whiteflies, mites, mealybugs and scale insects. For example *Stethorus punctillum* feeds on mites in glasshouses.
d) Lacewings (Order Neuroptera), e.g. Green Lacewing, *Chrysoperla carnea*, adult lacewings can be predaceous; some feed on pollen or do not feed. Larvae

Figure 27.4. Larvae of lacewings (Neuroptera) inhabit foliage where they attack aphids, mites, soft-bodied insects and eggs. Photo: P. Toth.

Figure 27.5. Hover fly (Syrphidae) feeding on flower nectar and pollen. Females lay white, oval eggs near colonies of aphids. Photo: P. Toth.

prefer to feed on aphids but also eat other small insects as well as mites (Figure 27.4).

e) Predatory flies (Order Diptera), mostly hover flies (family Syrphidae), aphid flies (family Chamaemyiidae) and predaceous midges (Cecidomyiidae). While adults feed on pollen (Figure 27.5), nectar or do not feed, the larvae are predatory (Figure 27.6). Many of the species mentioned above are commercially available with a detailed guide on how 'to use' them.

Figure 27.6. Magot like larvae of hover flies (Syrphidae) are active predators on aphids. Photo: P. Toth.

Among the invertebrate predators that provide a naturally occurring biological control are praying mantises (Order Mantodea), ground beetles (Order Coleoptera, family Carabidae), ants (Order Hymenoptera, family Formicidae), and spiders (Order Araneae).

Pathogens

A pathogen is any disease-producing microorganism. In principle, pathogens include bacteria, viruses, fungi and nematodes. Pathogens represent one of three principal categories of natural enemies used in applied biological control. Most insect pathogens are relatively specific to certain groups of insects and certain life stages. Unlike chemical insecticides, microbial insecticides can take longer (several days) to kill or debilitate the target pest. Although they kill, reduce reproduction, slow growth, or shorten the life of pests, their effectiveness may depend on environmental conditions or host abundance. The degree of control by naturally occurring pathogens may be unpredictable. Microbial insecticides are compatible with the use of predators and parasitoids, which may help to spread some pathogens through the pest population.

The most important pathogen used in biological control as a biopesticide is the rod-shaped soil bacterium *Bacillus thuringiensis* (Bt). Bt can be found worldwide on plants, in insects and in soil, surviving in the environment as resistant spores. It is only rarely found to cause epizootics in insect populations under natural conditions. Yet, Bt has the power to control numerous chewing-insect pests, particularly Lepidoptera larvae with alkaline pH in the gut (Figure 27.7). It has been developed extensively for pest control in a variety of habitats, and it is applied to virtually all tree, field and vegetable crops. Bt is photosensitive, with its life limited to a few days at most and only effective when ingested by insects, where it acts as a stomach poison. Insects that eat leaves treated with Bt die from hunger or infections. Insects are most sensitive to Bt during early larval instars (stages).

There are different strains (subspecies) of Bt, each with specific toxicity to particular types of insects: Bt *kurstaki* and Bt *azaiwai* are used against lepidopteran larvae; Bt *israelensis* is effective against dipteran larvae and Bt *tenebrionis* is active against coleopteran larvae.

Another species of *Bacillus*, *B. popilliae*, infects coleopteran larvae causing 'milky disease' of larvae and *B. sphaericus* is active against mosquito larvae.

There are six main groups of insect viruses but only three are sufficiently different from human viruses to be considered safe and these are: the nuclear polyhedrosis virus (NPV), the granulosis virus (GV) and the cytoplasmic polyhedrosis virus (CPV). These viruses produce an occlusion body, a structure that protects virus particles or virions.

Figure 27.7. Impact of the most important biopesticide, *Bacillus thuringiensis* (Bt), on larvae of *Helicoverpa armigera*. Photo: P. Toth.

The occlusion body is resistant to environmental insults and could be considered analogous to a bacterial spore.

Viruses can be highly effective natural regulators of several lepidopteran larvae especially. Different strains of naturally occurring NPV and GV are present at low levels in many insect populations. Epizootics can occasionally devastate populations of some pests, especially when insect numbers are high.

Insect viruses need to be eaten by an insect to cause infection. They invade an insect's body via the gut and replicate in many tissues where they can disrupt components of the insect's physiology, interfering with feeding, egg laying and movement. On the other hand viruses may also spread from insect to insect during mating or egg laying.

Different viruses cause different symptoms. In general, infested larvae stop feeding, turn white (NPV) or very dark (GV), climb to the top of the crop canopy, the body contents are liquefied and within three to eight days they die. However, especially with NPV strains that are commercially produced, the number of commercially successful products is limited.

Some insect species, including many pests, are particularly susceptible to infection by naturally occurring, entomopathogenic fungi. Those with the most potential as biopesticides are fungi from the Deuteromycetes (imperfect fungi), namely species of *Beauveria*, *Metarhizium*, *Verticilium*, *Nomuraea* and *Hirsutella*. These fungi are often very specific to insects. Fungal growth is favoured by moist conditions but fungi also have resistant stages that maintain an infection potential under dry conditions. Fungi have a considerable epizootic potential and can spread quickly through an insect population and cause its collapse. Entomopathogenic fungi do not need to be consumed by insects, because they penetrate the insect body through the cuticle and can infect in this way, also infesting insects such as aphids and whiteflies that are not susceptible to bacteria and viruses. The fungus proliferates in the host's blood and invades the host's organs shortly before the host dies, or kills the insect more quickly, possibly through use of fungal toxins. It generally takes several days for a fungus-infested host to die.

The only insect-parasitic nematodes that kill their hosts in a relatively short time are entomopathogenic nematodes from the families Steinernematidae and Heterorhabditidae. These two families have very similar life histories. The nematodes have searching ability. The infective stage of the nematode (third stage larva) can detect its host by responding to chemical and physical cues. When a host has been located, the nematodes penetrate into the insect body cavity, usually via natural body openings (mouth, anus, spiracles) or areas of thin cuticle. The third-stage infective larva carry symbiotic bacteria in their guts and, after invading a host, release the bacteria (*Xenorhabdus* for steinernematids, *Photorhabdus* for heterorhabditids). The bacteria are responsible for killing hosts very rapidly, within 2-3 days. The nematodes feed upon the bacteria and liquefy the host, and mature into adults. Nematode generations continue to develop within the same cadaver and infective larvae exit when density of nematodes is high and nutrients are low.

The most important species are *Steinernema carpocapsae* against Lepidoptera and Coleoptera (Curculionidae and Chrysomelidae), *S. feltiae* against dipteran pests, *Heterorhabditis bacteriophora* against Lepidoptera and Coleoptera and *Phasmorhabditis hermaphrodita* against slugs and snails.

Classical Biological Control

> *'The intentional introduction of an exotic, usually co-evolved, biological control agent for permanent establishment and long-term pest control' (Eilenberg et al. 2001)*

Biological control through introduction is most frequently used against introduced pests which arrive in a new area and become permanently established without an associated natural enemy complex. Thus, classical biological control involves travelling to the country or area from which a newly introduced pest originated and returning with some of the natural enemies that attacked it and kept it from being a pest there. New pests are constantly arriving accidentally or intentionally. Sometimes they survive. When they come, their enemies are left behind. If they become a pest, introducing some of their natural enemies can be an important way to reduce the amount of harm they can do. The search for suitable natural enemies (parasitoids, predators, pathogens) should in principle include all organisms closely related to the target pest, with special consideration to those organisms that affect pest density and distribution.

The first example of classical biological control dates back to the end of nineteenth century, when Californian citrus orchards had suffered attacks from the Australian scale, *Icerya purchasi*. This scale was successfully controlled with the introduction of its natural enemy, the coccinellid cardinal ladybird, *Rodolia cardinalis*. The most famous example of this technique within Europe is control of woolly apple aphid, *Eriosoma lanigerum*, through the introduction of its specific parasitoid *Aphelinus mali* and that of San José scale, *Quadraspidiotus perniciosus*, through the introduction of the parasitoid *Prospaltella perniciosi*.

When a natural enemy is introduced, it should (if established) reduce the pest's abundance to a level below the pre-introduction population size. After an initial phase of rapid reduction of the pest population and equally rapid growth of the natural enemy population, a long period of equilibrium generally follows. In successful introduction, the new population level will be well below the economic damage threshold. When successful, this traditional use of biological control offers permanent levels of control with few risks and leads to a very cost-effective solution.

Classic biological control is most successful with environmental pests and pests in orchards and forests, where the perennial nature of the crop permits continuous interaction between its natural enemy and host without the agroecosystem disturbance associated with annual crops.

Augmentation

Augmentation is a method of increasing the population of a natural enemy which attacks a pest. This can be done by mass-producing a pest in a laboratory and releasing it into the field at the proper time. Another method of augmentation is breeding a better natural enemy that can attack or find its prey more effectively. Mass rearings can be released at special times when the pest is most susceptible and natural enemies are not yet present, or they can be released in such large numbers that few pests go untouched by their enemies. The augmentation method relies upon continual human management and does not provide a permanent solution, unlike the introduction or conservation approaches. There are two basic approaches of augmentation: Inoculation and Inundation.

Inoculation biological control

> *'The intentional release of a living organism as a biological control agent with the expectation that it will multiply and control the pest for an extended period, but not permanently' (Eilenberg et al., 2001)*

Inoculation is used in cases where a native natural enemy is absent from a particular area, or an introduced species is unable to survive permanently. Inoculative releases are made at the beginning of the season to achieve seasonal control, i.e. to colonise the area for the duration of the season or crop and thus prevent pest build-up.

Inundation biological control

> *'The use of living organisms to control pests when control is achieved exclusively by the released organisms themselves' (Eilenberg et al., 2001)*

Releases made with biological control through inundation involve very large numbers of native or introduced natural enemies, in a way similar to the application of chemical pesticides. The natural enemy is usually a pathogen and is often formulated so that it can be applied using conventional pesticide spraying equipment. Sometimes used as substitutes for chemical pesticides, inundative control agents are applied for short-term control when pest populations reach damaging levels.

This technique is specifically used in greenhouses because of its relatively elevated costs. In addition, greenhouses are circumscribed places in which control of exogenous factors determining the success of the intervention is easier. The most successful agent in this category is the bacterium *Bacillus thuringiensis* used to control pests such as lepidopterans, dipterans and coleoptera, although other entomopathogens based on fungi and viruses have also found niches.

Conservation

> *'Modification of the environment or existing practices to protect and enhance specific natural enemies or other organisms to reduce the effect of pests' (Eilenberg et al., 2001)*

Conservation is an important part of any biological control effort. This involves identifying any factors that limit the effectiveness of a particular natural enemy and changing them through environmental modifications to help the beneficial species. Conservation of natural enemies involves either reducing factors which interfere with the natural enemies or providing needed resources that help natural enemies.

Many environmental modifications are designed to both preserve and enhance natural enemies and thus lie at an intermediate point on this continuum. In certain situations biological control of insect pests through environmental modification has inherent advantages over either classical biological control or augmentative releases. Conservation relies on naturally occurring enemies that are well adapted to the target area. Natural enemies occur from the backyard garden to the commercial field. Therefore, conservation is probably the most important and readily available biological control practice available to growers. The method is generally simple and cost-effective. With relatively little effort the activity of these natural enemies can be observed. For example lacewings, lady beetles, hover fly larvae, and parasitised aphid mummies are almost always present in aphid colonies. Fungus-infected adult flies are often common following periods of high humidity.

The usage of pesticides has a side-effect on natural enemies. When a pesticide kills the pest, the natural enemies disappear too. They migrate from the agroecosystem or die. Certain cultural practices can also damage the natural enemies or their habitats, e.g. removal of uncultivated areas, field margins, weedy areas, roadsides, etc.; soil cultivation; crop establishment; fertilisation, growth regulators, or harvesting especially at the critical periods of beneficial organism's life cycle.

To conserve natural enemies, pest management decisions must be carefully planned. Conservation involves planning a programme for the whole farm, including the non-farmed land, to enhance biodiversity and landscape features. This may include developing and maintaining a network of hedges, ditches, field margins, beetle banks and conservation headlands, which enable wild species to establish and migrate. A greater diversity of broadleaved weed species may be left within crops to provide food sources for birds and insects, so long as the numbers of aggressive, crop-damaging weeds are contained.

Conservation, creation and improvement of habitats for parasitoids and predators of crop pests may regulate pest populations by increasing the natural level of biocontrol, thereby reducing the need for insecticidal intervention. Often the best we can do is to recognise that beneficial organisms are present and minimise negative impacts on them. If an insecticide is needed, every effort should be made to use a selective material in a selective manner.

One of the best examples of conservation biological control is the practice of strip-harvesting hay alfalfa in California. When an entire field of alfalfa is moved during hot weather, the native Western tarnished plant bug, *Lygus hesperus*, migrates within 24 hours, often to cotton where it is a key pest. However, when fields are harvested in alternating strips up to 120 m wide (=strip cut), lygus bugs move from the cut strips to the remaining strips rather than migrating to cotton. This cultural practice can conserve natural enemies in cotton (due to reduced chemical control of *Lygus*) and in hay alfalfa, where mobile natural enemies can disperse from cut strips to half-grown strips. Another method for conserving natural enemies in cotton is to interplant alfalfa (a preferred host of *Lygus*) at regular intervals to hold *Lygus* bugs and prevent them from dispersing into the adjacent cotton.

Other Non-chemical Control Strategies

In addition to the above-mentioned examples, there are nowadays many other non-chemical control strategies of pests, such as semiochemicals for mass trapping, mating disruption, etc.; insect hormones to manipulate development and sterile insect technique for 'birth control of insects'.

Conclusion

Biological control offers an environmentally friendly, safe and cost-effective pest management option. The above examples highlight important bio-tools. Successful biological control requires not only a better understanding of biological control agents but also a more comprehensive picture of the whole agro-environment. The key has to be an area-wide pest management, which differs from traditional pest management in that the primary focus is on creating an environment unfavorable for pest establishment, growth and reproduction. This management is supported with pest-to-pest specific control tactics. The best approach may be to integrate plant growing and knowledge of ecology with all available biological control strategies into comprehensive pest management system. Enhanced research acting in this area in recent years has greatly augmented our knowledge. This progress could be translated into new and innovative concepts for biological pest control.

Sigvald, R. 1989. Relationship between aphid occurrence and spread of potato virus Yo (PVYo) in field experiments in southern Sweden. In: *J. Appl. Ent*. 108, p. 34-43.

Sigvald, R. 1990. Aphids on potato foliage in Sweden and their importance as vectors of potato virus Yo. In: *Acta Agric. Scand*. 40: pp. 53-58.

Sigvald, R. 1992. Progress in aphid forecasting systems. In: *Neth. J. Pl. Path*, 98, Supplement 2: pp. 55-62.

Twengström, E. and Sigvald, R. 1993. Forecasting sclerotinia stem rot using meteorological and field specific data. *Workshop on Computor-based DSS on Crop Protection, Parma, Italy, 23-26 November 1993*.

Twengström, E., Sigvald, R., Svensson, C. and Yuen, J. 1998. Forecasting Sclerotinia stem rot in spring sown oilseed rape. In: *Crop Protection*, 17:5, pp. 405-411.

Wiik, L. 1993. Väderleken och Septoria Spp. Sambandet mellan några klimatparametrar och skördeförlusten orsakad av Septoria Spp. In: *34e svenska växtskyddskonferensen, Uppsala, 1993*.

Wiik, L. 2009a. Yield and disease control in winter wheat in southern Sweden during 1977-2005. In: *Crop Protection* 28 (1), pp. 82-89

Wiik, L. and Ewaldz, T. 2009b. Impact of temperature and precipitation on yield and plant diseases of winter wheat in southern Sweden 1983-2007. In: *Crop Protection*, (Article in Press).

Wiktelius, S. 1981. *Studies on aphid migration with special reference to the bird cherry oat aphid Rhopalosiphum padi (L.)*. Växtskyddsrapporter avhandlingar 5. Sveriges Lantbruksuniversitet, Uppsala.

Yuen, J., Twengström, E. and Sigvald, R. 1996. Calibration and verification of risk algorithms using logistic regression. In: *European Journal of Plant Pathology* 102:847-854.

Chapter 26

Chulkina, V.A., Toropova, E.U., Chulkin, U.I. and Stetsov, G.J. 2000. *Agrotechnical methods in plant orotection*. – Moscow.: (in Rus).

Encyclopedia Britannica, 1999.

Soroka, S.V. (ed.) 2005. *Integrated Pest Management in agriculture*. Minsk.: 2005 (in Rus)

Chapter 27

Eilenberg, J., Hajek, A., Lomer, C. 2001. Suggestions for unifying the terminology in biological control. In: *BioControl* 46, 387-400.

Chapter 28

Alakukku, L. 2000. Response of annual crops to subsoil compaction in a field experiment on clay soil lasting 17 years. In: Horn, R., van den Akker, J. J. H. and Arvidsson, J. (eds.) *Subsoil compaction. Distribution, processes and consequences*. Advances in Geoecology 32: pp. 205-208.

Alakukku, L. 1999. Subsoil compaction due to wheel traffic. In: *Agricultural and Food Science in Finland*. 8: 333-351.

Alakukku, L., Ahokas, J. and Ristolainen, A. 2002. Response of clay soil macroporosity to stress caused by tracked tractors. In: Pagliai, M. and Jones, R. (eds.) *Sustainable land management. Environmental protection. A soil physical approach*. Advances in Geoecology 35: 319-330.

Alakukku, L., Weisskopf, P., Chamen, W.C.T., Tijink, F.G.J., Van Der Linden, J.P., Pires, S., Sommer, C. and Spoor, G. 2003. Prevention strategies for field traffic-induced subsoil compaction: a review, Part 1. Machine/soil interactions. In: *Soil & Tillage Research* 73: pp. 145-160.

Ansorge, D. and Godwin, R.J. 2007. The effect of tyres and a rubber track at high axle loads on soil compaction, Part 1: single axle-studies. In: *Biosystems Engineering* 98: pp. 115-126.

Arvidsson, J. 1998. Influence of soil texture and organic matter content on bulk density, air content, compression index and crop yield in field and laboratory compression experiments. In: *Soil Tillage Research* 49: pp. 159-170.

Arvidsson, J. 2001. Subsoil compaction caused by heavy sugarbeet harvesters un southern Sweden. I. Soil physical properties and crop yield in six field experiments. In: *Soil Tillage Research* 60: pp. 67-78.

Arvidsson, J. 1999. Nutrient uptake and growth of barley as affected by soil compaction. In: *Plant and Soil* 2008: pp. 9-19.

Arvidsson, J. and Håkansson, I. 1996. Do effects of soil compaction persist after ploughing? Results from 21 long-term field experiments in Sweden. In: *Soil Tillage Research* 39: 175-197.

Arvidsson, J., Trautner, A., Van den Akker, J.J.H. and Schjønning, P. 2001. Subsoil compaction caused by heavy sugarbeet harvesters in southern Sweden II. Soil displacement during wheeling and model computations of compaction. In: *Soil Tillage Research* 60: 79-89.

Ball, B.C., Scott, A. and Parker, J.P. 1999. Field N2O, CO2 and CH4 fluxes in relation to tillage compaction and soil quality in Scotland. In: *Soil Tillage Research* 53: 29-39.

Blackwell, P.S., Graham, J.P., Amstrong, J.V., Warc, M.A., Howse, K.R., Dawson, C.J. and Butler, A.R. 1986. Compaction of a silt loam soil by wheeled agricultural vehicles. I Effects upon soil conditions. In: *Soil Tillage Research* 7: 97-116.

Blake, G.R., Nelson, W.W., Allmaras, R.R., 1976. Persistence of subsoil compaction in a Mollisol. In: *Soil Science Society American Journal* 40: 943-948.

Chamen, T., Alakukku, L., Pires, S., Sommer, C., Spoor, G., Tijink, F. and Weisskopf, P. 2003. Prevention strategies for field traffic-induced subsoil compaction : a review, Part 2.Equipment and field practices. In: *Soil Tillage Research* 73: 161-174.

Chamen, W.C.T., Chittey, E.T., Leede, P.R., Goss, M.J. and Howse, K.R. 1990. The effect of tyre/soil contact pressure and zero traffic on soil and crop responses when growing winter wheat. In: *Journal of Agricultural Engineering Research* 47: 1-21.

Commision of the European Communities 2006. *Proposal for a Directive of the European Parliament and of the Council establishing a framework for the protection of soil and amending Directive 2004/35/EC*. COM (2006) 232 final http://ec.europa.eu/environment/soil/pdf/com_2006_0232_en.pdf).

Ehlers, W. 1982. Die Bedeutung des Bodengefüges für das Pflanzenwachstum bei moderner Landbewirtschaftung. In: *Mitteilungen Deutsche Bodenkundliche Gesellschaft* 34: 115-128.