

# Non-invasive techniques for investigating and modelling root-feeding insects in managed and natural systems

Scott N. Johnson, John W. Crawford\*, Peter J. Gregory, Dmitry V. Grinev\*, Richard W. Mankin†, Gregory J. Masters‡, Philip J. Murray§, Diana H. Wall¶ and Xiaoxian Zhang\*

Scottish Crop Research Institute, Invergowrie Dundee, DD2 5DA, U.K., \*SIMBIOS Centre, University of Abertay, Bell Street, Dundee DD1 1HG, U.K., †Center for Medical, Agricultural & Veterinary Entomology, 1700 SW 23rd Drive, Gainesville, Florida 32608, U.S.A., ‡CABI Bioscience, Bakeham Lane, Egham, Surrey TW20 9TY, U.K., §Institute of Grassland & Environmental Research, North Wyke Research Station, Okehampton, Devon EX20 2SB, U.K. and ¶Natural Resource Ecology Laboratory, NESB, B203, Colorado State University, Fort Collins, CO 80523-1499, U.S.A.

- Abstract**
- 1 Root-feeding insects are now considered to play a greater role in ecosystem processes than previously thought, yet little is known about their specific interactions with host plants compared with above-ground insect herbivores. Methodological difficulties associated with studying these insects in the soil, together with the lack of empirical and theoretical frameworks, have conventionally hindered progress in this area.
  - 2 This paper reviews recent empirical and theoretical developments that have been adopted for studying root-feeding insects, focusing on the non-invasive techniques of X-ray tomography and acoustic field detection and how these can be integrated with new mathematical modelling approaches.
  - 3 X-ray tomography has been used for studying the movements of several insects within the soil and has helped to characterize the host plant location behaviour of the clover root weevil, *Sitona lepidus*. Acoustic detection of soil insects has been used in various managed systems, ranging from nursery containers to citrus groves.
  - 4 Mathematical modelling plays a complementary role for investigating root-feeding insects, illustrated by a number of published models. A model is presented for the movement of *S. lepidus* in the soil, which suggests that these insects undergo Lévy movements, similar to those recently demonstrated for above-ground organisms.
  - 5 The future directions and challenges for investigating root-feeding insects are discussed in the context of the wider ecosystem, incorporating both above and below-ground organisms.

**Keywords** *Agriotes* spp., *Diaprepes abbreviatus*, non-invasive techniques, *Otiorhynchus sulcatus*, *Phyllophaga crinita*, roots, *Sitona lepidus*, soil fauna, white clover, wireworms.

## Introduction

One of the more recent developments in entomology has been the realization that root-feeding insects play a much greater role in ecosystem processes in both managed and natural systems than previously thought (Blossey & Hunt-Joshi, 2003; Wardle *et al.*, 2004; Bardgett, 2005; Bezemer & van

Dam, 2005). It has been known for some time that root-feeding insects can severely reduce agricultural yields (Chiang *et al.*, 1980; Spike & Tollefson, 1991), but more recent studies have shown how root-feeding insects can significantly shape communities of plants (Schadler *et al.*, 2004), microbes (Treonis *et al.*, 2005) and above-ground insect herbivores (van Dam *et al.*, 2005).

Research into insect root herbivory has largely taken place in the fields of agricultural and forest pest entomology, illustrated by the variety of studies on the black vine weevil

Correspondence: Scott Johnson, Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, U.K. Tel.: +44 (0)1382 560016; fax: +44 (0)1382 568502; e-mail: scott.johnson@scri.ac.uk

(*Otiorynchus sulcatus*), which is a pest of both types of system (van Tol *et al.*, 2001; Lola-Luz *et al.*, 2005; Son & Lewis, 2005). Indeed, *O. sulcatus* has become the most serious pest of ornamental nursery stock and soft fruit production in Europe (Labuschagne, 1999). At the same time, researchers are considering some root-feeding insects as biocontrol agents of invasive plant species, with Blossey & Hunt-Joshi (2003) reporting a favourable 54% success rate against target plants, compared with only 34% for above-ground insect herbivores tested; but see also Thelen *et al.* (2005).

Despite the recent interest in research involving below-ground insect herbivores, progress has been sporadic compared with studies of above-ground insect herbivores. Two seminal reviews (Brown & Gange, 1990; Villani & Wright, 1990) called for greater attention to be paid to root-feeding insects but, when revisiting the subject a decade later, Hunter (2001) concluded that subsequent progress had been comparatively slow. Methodological difficulties associated with studying these interactions in the soil have clearly hampered progress, but it is probable that empirical progress has also been hindered by the lack of theoretical and mathematical modelling frameworks that are so common for above-ground insect–plant interactions. For example, areas such as optimal defence allocation by plants remain largely focused on above-ground plant parts because detailed data are not available for how insects interact with the roots (Bouma *et al.*, 2001; Yanai & Eissenstat, 2002).

The present review aims to widen participation in this topical area of entomology and enable researchers to consider new approaches to existing questions. We focus on two examples of empirical techniques that have recently been developed to study root-feeding insects (X-ray microtomography and acoustic detection in soil). We then discuss a recent example of a mathematical model that has been developed for below-ground insect herbivores and how it can be refined using new empirical techniques and by drawing on parallels with theory for above-ground organisms. Finally, we consider the challenges that lie ahead and how a better understanding of below-ground insect herbivory could improve models for understanding ecosystem processes as a whole.

## X-ray tomography

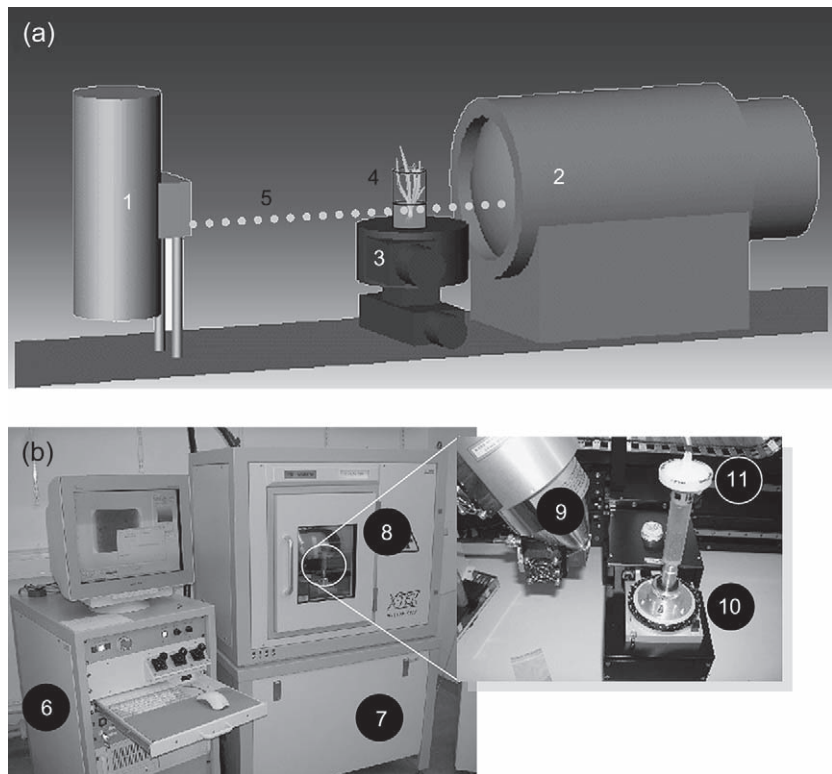
Soil is an opaque, tri-phasic medium making the investigation of subterranean insect–plant interactions very difficult. Studies of subterranean insects usually involve destructively dismantling the experimental system to recover insects, which has a number of inherent restrictions. These ‘black box’ approaches are insensitive to subtle spatio-temporal aspects of insect–root interactions and only allow the final consequences of the interaction to be measured. Attempts to overcome this have conventionally involved observing insects at a transparent interface (e.g. slant boards used by Murray & Clements, 1992), rhizotrons or using telemetric techniques (Reynolds & Riley, 2002). The former tend to restrict insect movements, whereas the latter are only suitable for very large invertebrates or small mammals.

X-ray computer tomography has become of interest to plant researchers over recent years, in particular for measuring root growth and development (Asseng *et al.*, 2000). The technique relies on biological tissue (e.g. roots) attenuating X-rays less than the surrounding soil. X-rays are passed through a soil microcosm containing a living plant and root-feeding insects and detected at the other side (Fig. 1A). Each cubic unit (or voxel) within the soil microcosm is assigned a value based on the extent to which the X-rays have been attenuated. This information can be used to reconstruct an image of the contents of the microcosm (i.e. insects and plant roots). However, the comparatively low resolution of such systems has conventionally only allowed very large soil insects to be visualized (e.g. > 25 mm in body length; Harrison *et al.*, 1993), whereas the younger instars (approximately 1–3 mm in body length) that first interact with the plant tend to be of more interest to researchers. Perhaps because of this, X-ray tomography has not conventionally been exploited by entomologists.

However, with the advent of X-ray microtomography, obtaining higher resolution images has become possible, enabling a range of insect instars and sizes to be visualized. For example, a recently installed facility (Fig. 1B) at the SIMBIOS Centre at the University of Abertay has been used to visualize soil-dwelling insects. Figure 2 shows cross sections of reconstructed and rendered images of a soil containing a mature wireworm, *Agriotes* sp. (approximately 20 mm in body length) (Fig. 2A–D) and a neonatal black vine weevil, *O. sulcatus*, larva (approximately 1 mm in body length) (Fig. 2E–F). In particular, the internal body cavity of the wireworm can clearly be distinguished in Fig. 2(C). The bench-top apparatus used to obtain these images (X-TEK Group, U.K.) has a 5- $\mu$ m focal spot reflection target and an X-ray source with an operating regime of 25–160 kV and 0–1000  $\mu$ A (noncontinuous). Feature recognition limit is approximately 1 mm, and different targets (e.g. tungsten, molybdenum, copper and silver) can be used to scan a maximum area of soil of 20  $\times$  20 cm, weighing up to 2 kg. The images in Fig. 2 were obtained by reconstructing datasets in Hounsfield units (Rogasik *et al.*, 1999), which was accomplished using the filtered backprojection algorithm and ramp filter. In particular, we found that reconstructing in Hounsfield units was best for visualizing and distinguishing insects in the soil. Hounsfield units increase with increasing density of material; for example, for the scan of the wireworm, the Hounsfield unit values were in the range of 1000–1500 for insect tissue, whereas they were between 2500 and 3000 for the surrounding soil particles.

This technique has begun to be used to answer applied questions, for example how pests such as the clover root weevil (*Sitona lepidus* Gyllenhal) locate host plants (Johnson *et al.*, 2004a, b). The X-ray microtomography system used for these studies with *S. lepidus* ensured that the insects received minimal doses of radiation (0.1 Gy), but this inevitably restricted the size of the microcosm (2.5 cm in diameter) that permitted X-ray penetration when retaining high resolution imaging of its contents. Indeed, this trade-off between scanning time, radiation dosage and the size of the microcosm must be considered by researchers when addressing

**Figure 1** (A) Schematic diagram of generalized X-ray tomography apparatus. (1) X-ray source; (2) X-ray detector; (3) rotating turntable; (4) soil microcosm containing living plant; (5) path of X-ray beam through soil microcosm. (B) X-TEK Benchtop X-ray microtomography apparatus: (6) Image acquisition and processing module consisting of a personal computer and manipulation joysticks; (7) X-ray microtomography module consisting of an X-ray gun, computer tomography (CT) chamber, vacuum pumps, detector and CCD camera; (8) CT chamber with sample inside. Enlarged image shows the interior of the CT chamber: (9) X-ray gun consisting of a high voltage power supply, vacuum chamber, beam tube, cooling unit and ultra focus target; (10) high precision sample manipulation table; (11) soil sample in the sample holder.



specific experimental aims. For example, more rapid scans reduce resolution whereas larger microcosms require higher dosages to penetrate the soil column, which may be deleterious to the insects. Researchers are now looking at how these systems can be improved for studying root growth, and there is a clear advantage for entomologists to exploit and where possible to drive these developments in X-ray microtomography. X-ray microtomography units can be custom-made (Fig. 1A), but bench-top apparatus can now be purchased relatively inexpensively (Fig. 1B). Moreover, their ease of operation and the inevitable developments in resolution (Asseng *et al.*, 2000) should allow this technique to become more widely used for studying below-ground insect–plant interactions.

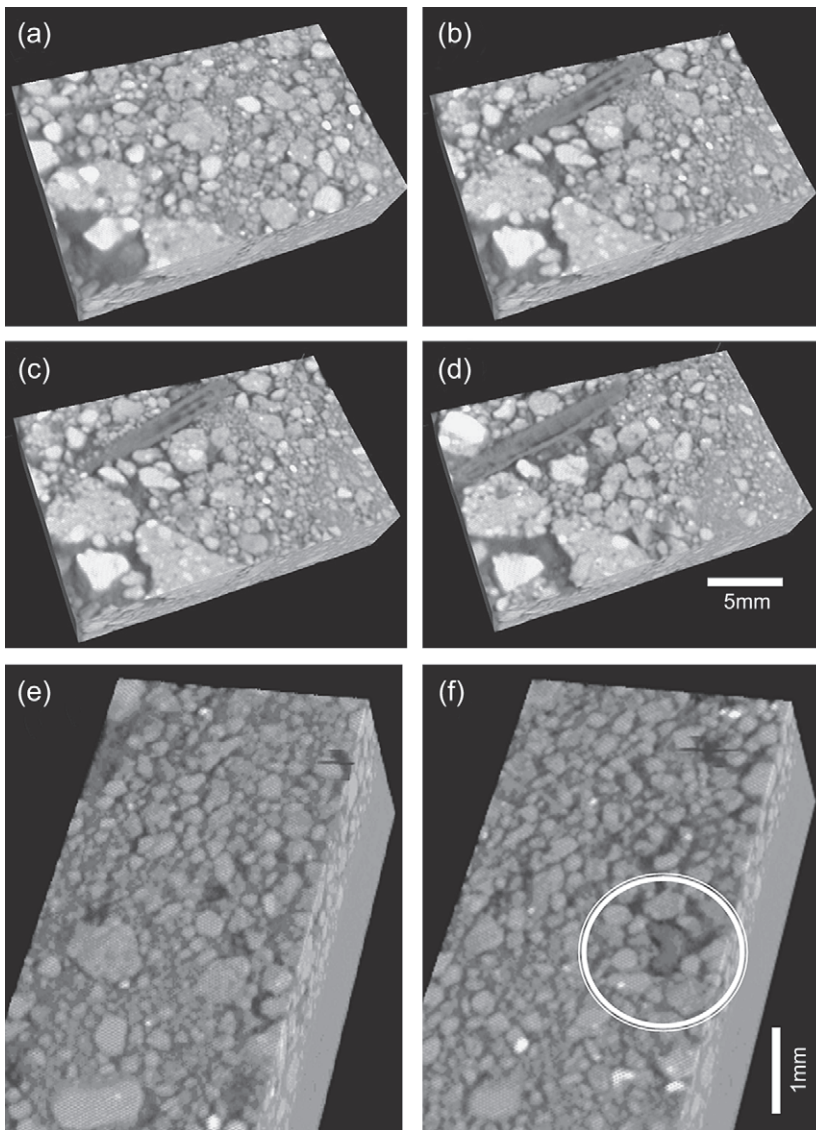
### Acoustic detection

Although X-ray microtomography offers a novel laboratory based approach, advances have also been made in development of field techniques based on acoustic detection. Acoustic technology has been considered in multiple applications for its potential to detect hidden infestations of insects in food (Brain, 1924; Adams *et al.*, 1953; Vick *et al.*, 1988), wood (Fujii *et al.*, 1990; Scheffrahn *et al.*, 1993; Lemaster *et al.*, 1997) and, more recently, in the soil (Mankin *et al.*, 2000, 2001; Zhang *et al.*, 2003a). Several different microphone and accelerometer systems have been used successfully to detect sounds generated by subterranean larvae in citrus groves (Mankin *et al.*, 2001), forage fields (Brandhorst-Hubbard

*et al.*, 2001) and nursery containers (Mankin & Fisher, 2002a, 2002b). Researchers have begun development of techniques to identify different types of sounds and relate them to larval behavioural activities (Zhang *et al.*, 2003b). The occurrence of short (< 10 ms), variable-amplitude pulses may be associated with feeding, based on similarities with sounds observed from above-ground insects involved in biting and chewing activities. Longer (500–1000 ms), moderate- to weak-intensity ‘rustles’ are suggestive of general rubbing or dragging movements, or digging activity. An oscillogram with several snaps and a rustle produced by a *Diaprepes abbreviatus* (L.) larva feeding on citrus tree roots is shown in Fig. 3(A).

Acoustic sensors can detect insects over distances of only 10–30 cm in soil, but the range can be extended by attaching a sensor to a metal probe that is inserted near where the insects are expected to be present. Spatial distribution of soil insect sounds and larval populations has been assessed by use of regularly spaced, multiple probes or by monitoring multiple sites over brief, 180–300-s periods (Mankin & Lapointe, 2003). The movement and feeding activity detected by the sensor can be monitored with headphones as the output is amplified and saved (without data compression) on a digital audio tape or other high-quality storage medium for subsequent computer or oscilloscope analyses. Some insects become quiescent when they are disturbed, but will usually resume their activities within 3–5 min.

Insects produce a wide variety of sounds in the soil, many of which can be readily distinguished from background noise by an experienced listener or a computer program. Larval-produced sounds typically are low intensity (< 80 dB) pulses



**Figure 2** X-ray reconstructed and rendered images of (A–D) successive transverse sections of soil, with (B–D) containing a mature wireworm (*Agriotes* sp.) that had been immobilized and (E–F) a neonatal black vine weevil larva (*Otiorynchus sulcatus*) (circled when fully visible in F). These data were acquired at 90 kV, 125 mA using a tungsten target and angular positions numbering 720 (*O. sulcatus*) and 1008 (*Agriotes* sp.). Each image has been averaged over 32 frames and is geometrically corrected. Ring artefacts, whereby increases or decreases in X-ray attenuation along a circle, or portion of a circle, cause image distortions were minimized. Isotropic voxel sizes are 0.29038 mm for *O. sulcatus* and 0.041337 mm for *Agriotes* sp. Three-dimensional volume renderings have been created in VGStudioMax, version 1.2 (Volume Graphics, Germany). Scale bars given for both images.

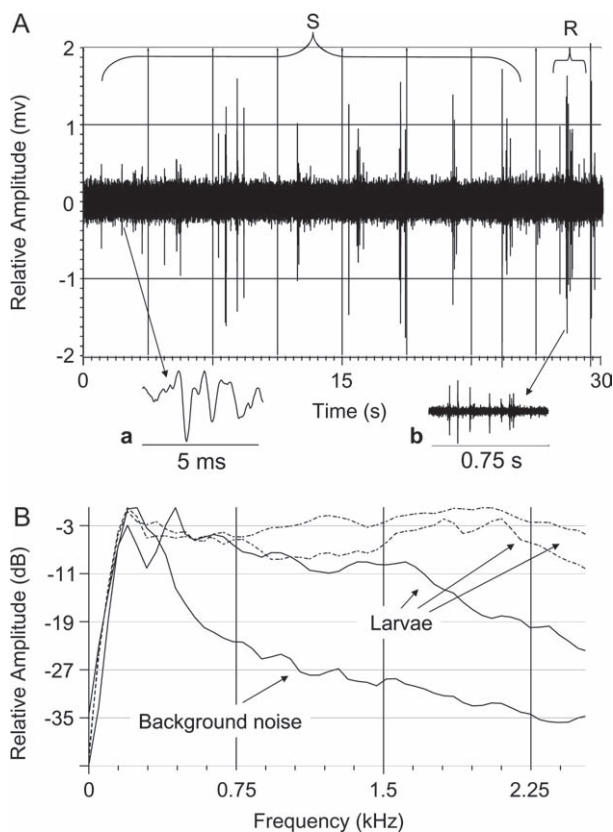
with a preponderance of spectral energy between 500 and 1800 Hz (Mankin *et al.*, 2000). Examples of average spectra of *Phyllophaga crinita* (Burmeister) larvae recorded at three different locations in a forage field at Auburn University, Alabama, U.S.A. are shown in Fig. 3(B).

The most recent refinements in acoustic techniques have primarily been in reductions of cost and in development of signal processing techniques to distinguish insect signals from noise (Mankin *et al.*, 2000) and identify temporal patterns (Zhang *et al.*, 2003b) and spatial distributions (Mankin *et al.*, 2002; Zhang *et al.*, 2003a) of insect activity. Originally, most of the software implementing the new techniques was written in efficient, but technically difficult C or C++ code, but higher-level, user friendly tools such as Matlab (MathWorks, Inc., Natick, Massachusetts) have become available that enable more rapid progress in development of soil insect detection and monitoring applications.

## Mathematical models

X-ray tomography and acoustic techniques represent significant experimental advancements in the study of subterranean insects, but mathematical modelling can play a complementary role for predicting aspects of their ecology that otherwise remain unseen. A recent example of a mathematical model for a specific part of the life-cycle of a root feeding insect comprises the location of host plants in the soil using chemical cues exuded from the roots.

A small number of mathematical modelling studies have been conducted in this area, mostly based on the diffusion–chemotaxis partial differential equation (Murray, 2002), in which the organism’s movement is assumed to consist of a pure random Brownian motion prior to detecting chemical root exudates, followed by a determinant motion towards roots along the gradient of these host location signals. In common with studies of soil nematodes (Anderson *et al.*,



**Figure 3** (A) Acoustic signals recorded from fifth-instar, *Diaprepes abbreviatus* larvae feeding on citrus tree roots. Most of the sounds in the recording were classified as snaps (S) based on their short durations and variable amplitudes (see text). A group of closely spaced, medium-amplitude snaps at the end of the record were classified as a rustle (R). Inset (A) shows an expanded trace of a low-amplitude snap, and inset (B) shows an expanded trace of the rustle. (B) Average spectra in three recordings of *Phyllophaga crinita* larvae in a forage field. The spectra of all three larvae had significantly greater energy between 0.5–1.8 kHz than background noise recorded in the same field.

1997; Hunt *et al.*, 2001), this concept has recently been extended to model the movement of soil-dwelling insects (Wiktorsson *et al.*, 2004) and, in particular, the clover root weevil *S. lepidus* (Zhang *et al.*, 2006).

Although these models remain useful for subterranean insect foraging behaviour, they are based on experiments that were not conducted in the soil (usually arenas) and tend to oversimplify movement patterns. For example, recent findings for above-ground organisms suggest that movement prior to the detection of host location cues is more complicated than that described by Brownian movement. These studies suggest that this movement is better described by fractal and/or multiple-fractal distributions (Doerr & Doerr, 2004; Seuront *et al.*, 2004). This is particularly true when resources are scarce (as is the case for suitable roots or root parts in the soil) and where the organism is seen to travel long distances between periods of intensive searches; so-called Lévy flights (Viswanathan *et al.*, 1996). These move-

ment strategies were found to be more efficient for locating scarce resources compared with Brownian movements (Viswanathan *et al.*, 1999).

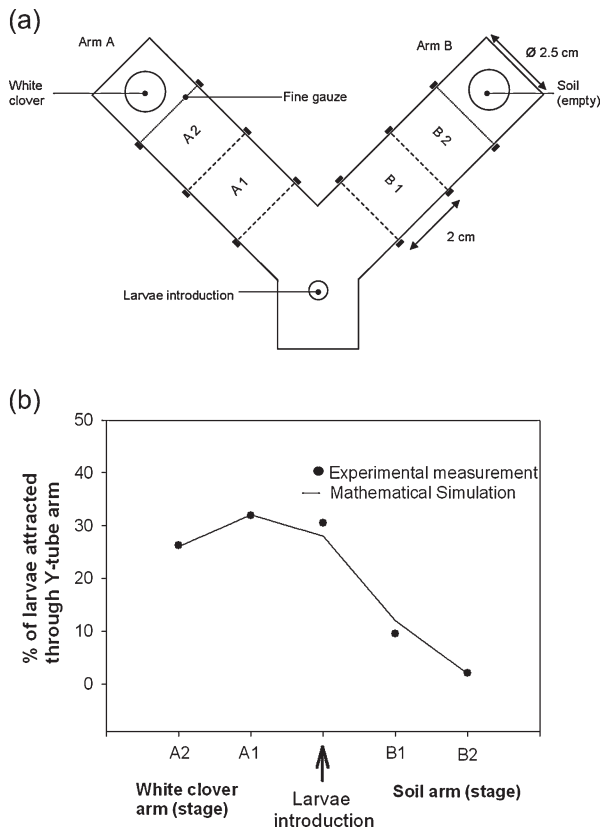
Taking this into account, a more general model for soil-dwelling insect movement in a two-dimensional plane can be derived. The movement of an individual insect can be seen as consisting of active burrowing movements and inactive 'rest periods' where the insect remains stationary, both being treated as random variables and characterized by their joint probability. The classical diffusion model (Murray, 2002) describes movement patterns where 'resting' periods are exponentially distributed and the burrowing distances between two periods of inactivity has a Gaussian distribution. Experimental data regarding these probability distributions are not available for below-ground insects, but the empirical observations of the above-ground organisms consistently show that both 'resting' time and movement distance have power-law distributions. If this is also true for the below-ground insects, insect movement can be modelled by the more general model:

$$\frac{\partial^\beta P}{\partial t^\beta} = D \left( \frac{\partial^\alpha P}{\partial x^\alpha} + \frac{\partial^\alpha P}{\partial y^\alpha} \right) - \left[ \frac{\partial}{\partial x} \left( \gamma \frac{\partial c}{\partial x} P \right) - \frac{\partial}{\partial y} \left( \gamma \frac{\partial c}{\partial y} P \right) \right] \quad (1)$$

where  $P$  is the probability of finding an individual insect at position  $(x, y)$  at time  $t$ ,  $0 < \beta \leq 1$  is a parameter characterizing the 'resting' time distribution,  $1 < \alpha \leq 2$  and  $D$  are parameters characterizing how often the insect makes long-distance burrowing movements,  $c$  is the concentration of root exudates exploited for host location (Johnson & Gregory, 2006), and  $\gamma$  represents the sensitivity of the insect to such root exudates. Overall, the term on the left-hand side describes the 'resting' time pattern, the first term on the right-hand side describes the random burrowing pattern in the absence of host location cues (e.g. root exudates), and the last term on the right-hand side represents the attractiveness of root exudates to the insects.

Testing Eq. (1) as a refinement to the model proposed by Zhang *et al.* (2006) is difficult because, to our knowledge, there are no detailed experimental studies of insect herbivore searching strategies that were conducted in realistic soil conditions. However, Eq. (1), assuming Lévy motion, can be applied to a recent study of the movements of the clover root weevil that incorporated X-ray tomography (Johnson *et al.*, 2004a). In that study, the distribution of larvae within a soil-filled Y-tube (Fig. 4A) was measured after 3 days.

Equation 1 was used to simulate the distribution of larvae in Y-tubes in which  $0 < \beta \leq 1$  and  $\alpha = 2$  (in recognition that the larvae were unlikely to make long continual burrowing movements as there were no fissures or big pores in the soil). The parameters  $D$  and  $\beta$  in Eq. (1) were determined from a calibration based on a control in which both arms of the Y-tubes were filled with soil alone. In modelling the larval movement towards the roots, we combined  $\gamma \delta c / \delta x$  as single parameter to characterize the attractiveness of roots to the larvae; its value also being determined from the calibration. A numerical and experimental comparison can be made (Fig. 4B), demonstrating good agreement between the prediction and experimental measurements. This suggests that Lévy motion



**Figure 4** (a) Y-tube apparatus used to investigate the dispersal of *S. lepidus* larvae towards plant roots, as described in Johnson *et al.* (2004a). (b) Simulation of dispersal of larvae in the soil-filled Y-tubes using equation 1 (see text), compared with experimental results.

might be usefully included in future models of subterranean insect movement. By incorporating new empirical techniques and drawing parallels from studies for above-ground organisms, novel mathematical modelling clearly has the potential to provide better insight into below-ground insect herbivory.

### Future directions: an ecosystem perspective of root-feeding insects

There is growing recognition that interactions between above- and below-ground organisms are more important in shaping ecosystem processes than previously thought. Therefore, to fully understand ecosystem processes, a holistic approach must be adopted to link the various components of a given system. For example, Schroter *et al.* (2004) provide a qualitative model that includes key feedbacks and interactions that link above- and below-ground organisms associated with a single plant. These include microbial symbionts, pathogens, decomposers and grazers, in addition to root and shoot herbivores, and their respective parasites and predators. Although root herbivores are just one component of this model, their interactions with a host plant and other organisms in the ecosystem are amongst the least understood and need to be addressed if these models are to be validated.

Studies suggest that multiple interactions across trophic levels for below-ground organisms are equally complex as those involving above-ground organisms. For example, it has recently been demonstrated that root herbivory can induce the plant to recruit natural enemies of both above- (Wackers & Bezemer, 2003) and below-ground insect herbivores (Rasmann *et al.*, 2005). This complexity represents a significant challenge, and experimental work will undoubtedly produce nonlinear feedbacks and counterintuitive dynamics. This challenge is compounded by uncertainty and the paucity of empirical data on root-feeding insects. However, mathematical modelling could assist with this, as modelling is an iterative process that represents the current best understanding of a system. Independent consequences that are predicted from models will provide new testable hypotheses that will either support or disprove the latest iteration of understanding and lead to further refinement.

A further challenge is concerned with scaling. The spatio-temporal dynamics of root-feeding insects are likely to differ in scale from many of the other organisms in the ecosystem (Schneider, 1994). At the smallest scale, a subterranean insect herbivore interacts with a single root, yet the impact of this interaction is at the scale of the plant community. Between those scales, there is considerable spatial and temporal heterogeneity that will affect the emergent structure of the community. It will therefore be necessary to look for natural scales where patterns, or 'laws' become apparent. Modelling could assist with this, and spatio-temporal statistical models in particular could play an important role.

The approaches and techniques discussed in this review are timely given the recent interest in below-ground insect herbivory and its wider consequences throughout managed and natural ecosystems. With the inevitable advances in empirical and theoretical approaches that will take place in the coming years, ecological and applied researchers may be able to re-address how they investigate the fundamentally important 'black box' aspect of below-ground systems.

### Acknowledgements

This article was originally formulated during the workshop, *Integrative approaches for investigating root herbivory in agricultural and managed systems*, held at the University of Reading on 25–26 October 2004. This workshop was funded by the Biotechnology and Biological Sciences Research Council (BBSRC) of the U.K. (grant reference ISIS 1310). J.W.C. and D.V.G. also acknowledge funding from the BBSRC (grant reference BBS/B/01294). The authors are grateful for the constructive comments made by anonymous referees of this paper.

### References

- Adams, R.F., Wolfe, J.E., Milner, M. & Schellenberger, J.A. (1953) Aural detection of grain infested internally with insects. *Science*, **118**, 163–164.
- Anderson, A.R.A., Sleeman, B.D., Young, I.M. & Griffiths, B.S. (1997) Nematode movement along a chemical gradient in a structurally heterogeneous environment. 2. Theory. *Fundamental and Applied Nematology*, **20**, 165–172.

- Asseng, S., Aylmore, L.A.G., MacFall, J.S., Hopmans, J.W. & Gregory, P.J. (2000) Computer-assisted tomography and magnetic resonance imaging. *Root Methods* (ed. by A. L. Smit, A. G. Bengough, C. Engels, M. van Noordwijk, S. Pellerin and S. C. van de Geijn), pp. 343–364. Springer, Germany.
- Bardgett, R.D. (2005) *The Biology of Soil: A Community and Ecosystem Approach*. Oxford University Press, U.K.
- Bezemer, T.M. & van Dam, N.M. (2005) Linking aboveground and belowground interactions via induced plant defences. *Trends in Ecology and Evolution*, **20**, 617–624.
- Blossey, B. & Hunt-Joshi, T.R. (2003) Belowground herbivory by insects: influence on plants and aboveground herbivores. *Annual Review of Entomology*, **48**, 521–547.
- Bouma, T.J., Yanai, R.D., Elkin, A.D., Hartmond, U., Flores-Alva, D.E. & Eissenstat, D.M. (2001) Estimating age-dependent costs and benefits of roots with contrasting life span: comparing apples and oranges. *New Phytologist*, **150**, 685–695.
- Brain, C.K. (1924) Preliminary note on the adaptation of certain radio principles to insect investigation work. *Annals of the University Stellenbosch, Series A*, **2**, 45–47.
- Brandhorst-Hubbard, J.L., Flanders, K.L., Mankin, R.W., Guertal, E.A. & Crocker, R.L. (2001) Mapping of soil insect infestations sampled by excavation and acoustic methods. *Journal of Economic Entomology*, **94**, 1452–1458.
- Brown, V.K. & Gange, A.C. (1990) Insect herbivory below ground. *Advances in Ecological Research*, **20**, 1–58.
- Chiang, H.C., French, L.K. & Rasmussen, D.E. (1980) Quantitative relationship between western corn rootworm population and corn yield. *Journal of Economic Entomology*, **73**, 665–666.
- van Dam, N.M., Raaijmakers, C.E. & van der Putten, W.H. (2005) Root herbivory reduces growth and survival of the shoot feeding specialist *Pieris rapae* on *Brassica nigra*. *Entomologia Experimentalis et Applicata*, **115**, 161–170.
- Doerr, V.A.J. & Doerr, E.D. (2004) Fractal analysis can explain individual variation in dispersal search paths. *Ecology*, **85**, 1428–1438.
- Fujii, Y., Noguchi, M., Imamura, Y. & Tokoro, M. (1990) Using acoustic emission monitoring to detect activity in wood. *Forest Products Journal*, **40**, 34–36.
- Harrison, R.D., Gardner, W.A., Tollner, W.E. & Kinard, D.J. (1993) X-Ray computed-tomography studies of the burrowing behavior of 4th-instar Pecan weevil (Coleoptera, Curculionidae). *Journal of Economic Entomology*, **86**, 1714–1719.
- Hunt, H.W., Wall, D.H., DeCraeppe, N.M. & Brenner, J.S. (2001) A model for nematode locomotion in soil. *Nematology*, **3**, 705–716.
- Hunter, M.D. (2001) Out of sight, out of mind: the impacts of root-feeding insects in natural and managed systems. *Agricultural and Forest Entomology*, **3**, 3–9.
- Johnson, S.N. & Gregory, P.J. (2006) Chemically-mediated host-plant location and selection by root-feeding insects. *Physiological Entomology*, **13**, 1–13.
- Johnson, S.N., Gregory, P.J., Murray, P.J., Zhang, X. & Young, I.M. (2004a) Host plant recognition by the root-feeding clover weevil, *Sitona lepidus* (Coleoptera: Curculionidae). *Bulletin of Entomological Research*, **94**, 433–439.
- Johnson, S.N., Read, D.B. & Gregory, P.J. (2004b) Tracking larval insect movement within soil using high resolution X-ray microtomography. *Ecological Entomology*, **29**, 117–122.
- Labuschagne, L. (1999) Black vine weevil – the millennium bug? *Bulletin of the Royal Entomological Society*, **23**, 213–220.
- Lemaster, R.L., Beall, F.C. & Lewis, V.R. (1997) Detection of termites with acoustic emission. *Forest Products Journal*, **47**, 75–79.
- Lola-Luz, T., Downes, M. & Dunne, R. (2005) Control of black vine weevil larvae *Otiorynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae) in grow bags outdoors with nematodes. *Agricultural and Forest Entomology*, **7**, 121–126.
- Mankin, R.W., Brandhorst-Hubbard, J., Flanders, K.L. *et al.* (2000) Eavesdropping on insects hidden in soil and interior structures of plants. *Journal of Economic Entomology*, **93**, 1173–1182.
- Mankin, R.W. & Fisher, J.R. (2002a) Acoustic detection of the black vine weevil, *Otiorynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae) larval infestations in nursery containers. *Journal of Environmental Horticulture*, **20**, 166–170.
- Mankin, R.W. & Fisher, J.R. (2002b) Current and potential uses of acoustic systems for detection of soil insect infestations. *Proceedings of the Bouyocous Conference on Agroacoustics, Fourth Symposium*. National Center for Physical Acoustics, Oxford, Mississippi.
- Mankin, R.W. & Lapointe, S.L. (2003) Listening to larvae. Acoustic detection of *Diaprepes abbreviatus* (L.). *Proceedings of the Florida State Horticultural Society*, **116**, 304–308.
- Mankin, R.W., Lapointe, S.L. & Franqui, R.A. (2001) Acoustic surveying of subterranean insect populations in citrus groves. *Journal of Economic Entomology*, **94**, 853–859.
- Mankin, R.W., Osbrink, W.L., Oi, F.M. & Anderson, J.B. (2002) Acoustic detection of termite infestations in urban trees. *Journal of Economic Entomology*, **95**, 981–988.
- Murray, J.D. (2002) *Mathematical Biology. I. An Introduction*. Springer, New York, New York.
- Murray, P.J. & Clements, R.O. (1992) A technique for assessing damage to roots of white clover caused by root feeding insects. *Annals of Applied Biology*, **121**, 715–719.
- Rasmann, S., Köllner, T.G., Degenhardt, J. *et al.* (2005) Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature*, **434**, 732–737.
- Reynolds, D.R. & Riley, J.R. (2002) Remote-sensing, telemetric and computer-based technologies for investigating insect movement: a survey of existing and potential techniques. *Computers and Electronics in Agriculture*, **35**, 271–307.
- Rogasik, H., Crawford, J.W., Wendroth, O., Young, I.M., Joschko, M. & Ritz, K. (1999) Discrimination of soil phases by dual energy X-ray tomography. *Soil Science Society of America Journal*, **63**, 741–751.
- Schadler, M., Alpehi, J., Scheu, S., Brandl, R. & Auge, H. (2004) Resource dynamics in an early-successional plant community are influenced by insect exclusion. *Soil Biology and Biochemistry*, **36**, 1817–1826.
- Scheffrahn, R.H., Robbins, W.P., Busey, P., Su, N.Y. & Mueller, R. (1993) Evaluation of a novel hand-held acoustic detector to monitor termites (Isoptera: Rhinotermitidae) in wood. *Journal of Economic Entomology*, **86**, 1720–1729.
- Schneider, D.C. (1994) *Quantitative Ecology. Spatial and Temporal Scaling*. Academic Press, San Diego, California.
- Schroter, D., Brussaard, L., De Deyn, G. *et al.* (2004) Trophic interactions in a changing world: modelling aboveground–belowground interactions. *Basic and Applied Ecology*, **5**, 515–528.
- Seuront, L., Schmitt, F.G., Brewer, M.C., Strickler, J.R. & Souissi, S. (2004) From random walk to multifractal random walk in zooplankton swimming behavior. *Zoological Studies*, **43**, 498–510.
- Son, Y. & Lewis, E.E. (2005) Modelling temperature-dependent development and survival of *Otiorynchus sulcatus* (Coleoptera: Curculionidae). *Agricultural and Forest Entomology*, **7**, 201–209.
- Spike, B.P. & Tollefson, J.J. (1991) Yield response of corn subjected to Western corn rootworm (Coleoptera, Chrysomelidae) infestation and lodging. *Journal of Economic Entomology*, **84**, 1585–1590.
- Thelen, G.C., Vivanco, J.M., Newingham, B. *et al.* (2005) Insect herbivory stimulates allelopathic exudation by an invasive plant and the suppression of natives. *Ecology Letters*, **8**, 209–217.

- van Tol, R., van der Sommen, A.T.C., Boff, M.I.C., van Bezooijen, J., Sabelis, M.W. & Smits, P.H. (2001) Plants protect their roots by alerting the enemies of grubs. *Ecology Letters*, **4**, 292–294.
- Treonis, A.M., Grayston, S.J., Murray, P.J. & Dawson, L.A. (2005) Effects of root feeding, crane fly larvae on soil microorganisms and the composition of rhizosphere solutions collected from grassland plants. *Applied Soil Ecology*, **28**, 203–215.
- Vick, K.W., Webb, J.C., Weaver, B.A. & Litzkow, C. (1988) Sound detection of stored-product insects that feed inside kernels of grain. *Journal of Economic Entomology*, **81**, 1489–1493.
- Villani, M.G. & Wright, R.J. (1990) Environmental influences on soil macroarthropod behavior in agricultural systems. *Annual Review of Entomology*, **35**, 249–269.
- Viswanathan, G.M., Afanasyev, V., Buldyrev, S.V., Murphy, E.J., Prince, P.A. & Stanley, H.E. (1996) Lévy flight search patterns of wandering albatrosses. *Nature*, **381**, 413–415.
- Viswanathan, G.M., Buldyrev, S.V., Havlin, S., da Luz, M.G.E., Raposo, E.P. & Stanley, H.E. (1999) Optimizing the success of random searches. *Nature*, **401**, 911–914.
- Wackers, F.L. & Bezemer, T.M. (2003) Root herbivory induces an above-ground indirect defence. *Ecology Letters*, **6**, 9–12.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science*, **304**, 1629–1633.
- Wiktorsson, M., Ryden, T., Nilsson, E. & Bengtsson, G. (2004) Modelling the movement of a soil insect. *Journal of Theoretical Biology*, **231**, 497–513.
- Yanai, R.D. & Eissenstat, D.M. (2002) Coping with herbivores and pathogens: a model of optimal root turnover. *Functional Ecology*, **16**, 865–869.
- Zhang, M.L., Crocker, R.L., Mankin, R.W., Flanders, K.L. & Brandhorst-Hubbard, J.L. (2003a) Acoustic estimation of infestations and population densities of white grubs (Coleoptera: Scarabaeidae) in turfgrass. *Journal of Economic Entomology*, **96**, 1770–1779.
- Zhang, M.L., Crocker, R.L., Mankin, R.W., Flanders, K.L. & Brandhorst-Hubbard, J.L. (2003b) Acoustic identification and measurement of activity patterns of white grubs in soil. *Journal of Economic Entomology*, **96**, 1704–1710.
- Zhang, X., Johnson, S.N., Gregory, P.J., Crawford, J.W., Young, I.M., Murray, P.J. & Jarvis, S.C. (2006) Modelling the movement and survival of the root-feeding clover weevil, *Sitona lepidus*, in the root-zone of white clover. *Ecological Modelling*, **190**, 133–146.

Accepted 10 August 2006

First published online 31 October 2006