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GUEST EDITORIAL

The contribution of Rothamsted to British entomology

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Entomological studies began at Rothamsted during the Great War, first in 1915 on the prevalence of house-fly larvae in farm manure heaps, and then in 1916 on the occurrence of wireworms in recently ploughed grassland. In 1918 A.D. Imms was appointed in charge of the new Entomology Department and it was from that position that he wrote his *General textbook of entomology* which persisted through ten editions as the standard text in most British and Commonwealth Universities. Over 70 years the scope of entomological studies evolved, changed and grew through four Departments to the present complement of about a hundred entomologists, chemists and virologists plus thirty post-graduate students and visiting workers. During that time some 1500 scientists have studied or been trained in aspects of entomology at Rothamsted. Six themes will serve as a reminder of the Station's impressive influence.

Soil dwelling pests

For the first 75 years of its existence Rothamsted was almost exclusively concerned with soil and plant nutrient studies, so it was natural that the first entomology should be soil-related. A.W. Rymer Roberts made some of the earliest observations in England on the biology and morphology of larvae of *Agriotes* spp. and *Athous* spp. (Coleoptera: Elateridae). Separation of insects from soil has always been a problem. The standard equipment for the last half a century has been the flotation system devised by W.R.S. Ladell at Rothamsted in 1935 in which soil samples are stirred in a strong solution of magnesium sulphate; the insects float and are skimmed off with the froth into a settling chamber. This technique led to some of the earliest indications of the enormous biomass and number of insects in arable soil which reach 1250 $10^6 ha^{-1}$ on parts of Broadbalk wheat field.

Classic work on soil pests was H.F. Barnes's study of the biology of gall midges of economic importance, begun in 1927 and continued for 26 years, particularly his demonstration that many larvae of the wheat midges *Contarinia tritici* (Kirby) and *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae) could remain diapausing in soil for at least four and 12 years, respectively. Most of his seven volume series documenting his lifetime's work has not been superseded.

More recently, in the 1970s and 80s, much work was done on the biology of a range of soil-dwelling insects, particularly wheat bulb fly *Leptohylemyia coarctata* (Fallen), its oviposition, population density and economic importance on wheat, and on the more general soil fauna in relation to arable farming practices. One very clear cut result was the demonstration that straw burning had little deleterious effect on true soil insects but it did drastically decrease the surface living micro fauna, especially Collembola.

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Movement, migration, and dispersal of airborne insects

In 1932, C.B. Williams began his studies on the migration of Lepidoptera. With a large group of amateur entomologists he organized the Insect Immigration Committee which observed and recorded, on standard record cards, the dates of arrival in Great Britain of immigrant butterflies and moths. These recordings continued for 30 years with the assistance of R.A. French and eventually led to collaborative work with G.W. Hurst of the Meteorological Office which showed convincingly that many species of moths regularly reach these islands from Spain, North Africa and eastern Europe, and occasionally from the Azores and North America.

Williams also started a series of investigations into the use of traps, devising the standard Rothamsted light trap and a primitive suction trap, as a means of sampling populations of flying insects and of relating activity to weather. The light trap was initially used to relate the total number of individuals to the total number of species in moth populations. Williams showed that the frequency distribution of catches traced a hollow curve and the expected number of species with 1, 2, 3, n individuals fitted a log series. This led to the use of α as an index of diversity, widely used and subsequently refined in a vast number of population studies on insects and other fauna and flora. These population diversity studies were further developed by L.R. Taylor and colleagues to form a unique long-term record of moth diversity throughout the UK, and one of the world's most comprehensive databases on any group of animals. With other long-term records of fauna, flora, weather and soil conditions, this information is one of the founding databases for the recently established national Environmental Change Network (ECN) initiated by the Natural Environment Research Council (NERC) in 1990.

While Williams concentrated on Lepidoptera, C.G. Johnson focused his attention after the Second World War on the small aerial fauna, especially aphids. The early work was on a grand scale using massive suction traps suspended on barrage balloon cables and flown from RAF Cardington, Bedfordshire. These studies plotted the detailed distribution of insect aerial density up to 615 m showing that while populations were always more concentrated near the ground, vast numbers of insects were nevertheless carried to greater heights, with serious implications for the spread of pests and virus vectors. Johnson's development of the disc-dropping segregation mechanism for suction traps enabled these vertical distributions to be related to time and duration of flight. These diurnal profiles of activity were recorded and plotted by T. Lewis and L.R. Taylor for several hundred taxa.

Taylor further developed the suction trap in the 1960s to produce the 12.2 m survey trap, the basis of the Rothamsted Insect Survey, now used so successfully over much of Europe to monitor aphid populations and for a range of studies on abundance and weather, dynamics, pest forecasting, virus spread and the development of resistance to insecticides. The data are now sufficiently long-term to be worthwhile investigating as possible indicators of global environmental change.

In the 1960s Lewis used the small suction traps nearer ground level to demonstrate to great effect the relationships between local wind movement, aerial density, distribution and damage in crops, showing for the first time the precision with which infestation patterns in fields were predictable from the physical characteristics of surrounding sheltering vegetation.

Behaviour

The first important stand in a complex web of behavioural studies can be traced back to the early work on the causes of swarming in honeybees by D.M.T. Morland in the 1920s and developed by J. Simpson in the 1940s and 50s.

A breakthrough in an understanding of colony control and cohesion occurred in 1954 when C.G. Butler proposed that worker bees normally obtain something called 'queen substance' from queens which inhibits them from rearing further queens and suppresses development of the ovaries. By 1959 he had extracted queen substance in solvents, showed it was produced in the mandibular glands, and with R.K. Callow, then at the National Institute of Medical Research and later at Rothamsted, he identified the active component as 9-oxo-2-decenoic acid, only the second insect pheromone to be identified.

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Much more bee pheromone work followed including the demonstration by R. Ribbands of the role of Nasonov pheromone in aiding orientation of workers at the hive entrance. Identification of further components in the pheromone by J.A. Pickett enabled I.H. Williams and colleagues to determine the roles of different compounds in foraging, nest-entrance marking and swarm clustering. A synthetic Nasonov pheromone was commercialized in 1984 and is used to attract swarms to hives or traps in many countries.

The collaboration between entomologists and chemists has enabled Rothamsted to initiate and develop a world lead in insect semiochemicals. Focus has switched to the Department of Biological and Ecological Chemistry, now headed by J.A. Pickett, in which L.J. Wadhams devised the first gas chromatograph/single cell link for detection and identification of pheromones. The recent isolation and identification of aphid sex pheromones constitutes a world 'first' for this family of insects. These multidisciplinary studies have opened up a new range of exciting prospects for pest control based on the use of semiochemicals combined with pathogens, or as agents to enhance the degree of natural parasitism in pests by attracting beneficial insects to crops.

Another behavioural strand centred on bees has been the whole subject of insect pollination largely pioneered by J.B. Free, who first came to Rothamsted in 1951 to study bumblebees. For over 25 years he contributed much to the practical aspects of enhancing pollination and thereby seed set and yield in fruit and field crops in Europe and the tropics.

A totally different behavioural and physiological activity, with profound consequences for agriculture, is the enormous topic of the vectoring of plant viruses by insects. In 1929 Marion Hamilton (M. Watson) was appointed to the Plant Pathology Department as a virus entomologist. Alongside F.C. Bawden, who, with N.W. Pirie, first identified virus nucleoproteins in tobacco mosaic virus, she showed that there was a specific relationship between the vector and the virus. This led to the description of the transmission of viruses as persistent, semi-persistent or non-persistent. Work developed in many areas, particularly in potatoes by L. Broadbent, one of the earliest users of yellow sticky traps for aphid monitoring. More recently R.T. Plumb has developed work on vector/virus relationships in studies on grass viruses, especially barley yellow dwarf virus; the present monitoring system used to predict the likely degree of infection in cereals, and the need to apply pesticides in autumn have resulted from this work.

Insect pathology

This is another area of work begun 70 years ago on bees, in which Rothamsted laid the foundations for a discipline which is still of great importance. Again management problems of beekeepers were the motivation, but the intellectual input was provided by L. Bailey from the early 1950s.

Controversy about the causative organism of European foulbrood existed for many years until the bacterium was first isolated at Rothamsted in 1956 and shown to cause infection when fed to larvae. Detailed epidemiological investigations followed to provide the basis of the present statutory control policy in this country. In 1982 taxonomic studies showed that the bacterium was sufficiently different from other *Streptococcus* spp. to be placed in its own genus, *Melissococcus*.

The early 1960s heralded a new era in insect pathology with the isolation and characterization of three non-occluded viruses of honeybees at Rothamsted. These were the first viruses of this type to be identified in insects. To date, a further 16 viruses have contributed much to our knowledge of invertebrate virology. The importance of virus diseases of honeybees has recently become more widely recognised with the spread of the parasitic bee mite *Varroa jacobsoni* Oudemans (Acari: Varroidae). Brenda Ball's work established that the mortality of infested colonies was primarily due to honeybee virus infections transmitted by the mite.

In the 1960s pathology studies were widened to other insects and to fungal pathogens. A good deal of the early work on the processes and epidemiology of fungal infection by *Entomophthora* spp. (Entomophthorales) and *Verticillium* spp. (Hyphomycetes) in field, as opposed to glasshouse, conditions was elucidated by N. Wilding and colleagues. Again, the opportunity to pursue a multidisciplinary approach has led to the existing development of combining sex pheromones to attract pests (e.g. *Plutella xylostella* (Linnaeus)

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(Lepidoptera: Yponomeutidae)) and pathogens not only to destroy the attracted individuals, but to use these to carry the pathogens to their mates and larvae feeding on the crop.

Pesticide development

At the same time as A.D. Imms began the embryonic entomology Department in 1918, F. Tattersfield began work on insecticides and fungicides with investigations of the possible chemical control of wireworms in soil. Under Tattersfield's guidance, studies began on the insecticidal activity of alkaloid plant products, derris root and pyrethrum. The concept of dosage response curves and LD_{50}s was developed through collaboration with no less a personage than the geneticist and statistician, R.A. Fisher, then a member of the Rothamsted Statistics Department. In 1925, the Ministry of Agriculture funded work to see whether pyrethrum flowers could be grown in this country and how the insecticidal properties of such plants compared with Japanese and Dalmatian grown plants. In 1931 Tattersfield's classical study, *Pyrethrum flowers – a quantitative study of their development*, set pyrethrum on its technically-based path. By 1935 Charles Potter was appointed to Rothamsted. It was he who developed the Potter Tower universally used for bioassays of pesticides, and who over a period of some 30 years, drove the pyrethrum programme ahead against much opposition and scepticism from the agrochemical industry and academe alike. His spearhead was a young organic chemist, M. Elliott, appointed in 1948, who headed a small team that eventually in the 1970s produced the synthetic pyrethroids. Deltamethrin, the most recent major Rothamsted compound is many times more toxic than the natural pyrethrin and yet is still safe to mammals and sufficiently field stable for very wide agricultural use. Rothamsted-derived compounds currently account for a quarter of all pesticides used world-wide.

The breadth of the insecticides programme is no better illustrated by the fact that alongside the search for new compounds, work was under way looking at the consequences of their misuse. R. Sawicki was for long a lone and unwelcome voice to the agrochemical industry in his contention that resistance to many classes of compounds, not least organophosphates and pyrethroids, had developed, and would spread to more species unless new strategies for the application and sequencing of insecticides were developed. How true his prophecies came, with over 500 pest species world-wide now resistant to current compounds and many major problems still unresolved. With immense foresight Sawicki recruited a biochemist, A. Devonshire, to his group and between them they undoubtedly established for Rothamsted a world lead in elucidating the biochemical mechanisms of resistance and the strategies to overcome it. For example, using an immunoassay for esterase, the detoxifying enzyme that destroys pesticides before they reach their target, Devonshire's group can now distinguish between susceptible, resistant and highly resistant aphids.

It would be remiss in this brief account of insecticide highlights if I did not return to the soil, where it all began, to draw attention to the important work on modelling the movement of soil pesticides, studies now so important from an environmental point of view.

National and international influence

Finally, mention should be made to some of the wider ripples emanating from Rothamsted. At the heart of entomology in this country, the Station has provided the Royal Entomological Society of London with four Presidents (C.B. Williams, R. Mellanby, C.G. Butler and T. Lewis) and many former students and staff who have attained high entomological distinction, including T.R.E. Southwood and M.J. Way.

The overseas input, somewhat beyond the remit of the editorial, is equally impressive and continuing. Indeed, one of the ways the Station is celebrating its 150th anniversary and perpetuating its influence, is to establish fellowships for post-graduate scientists from developing countries to come to Rothamsted for study and refreshment, under the sponsorship of 'Rothamsted International'. The Station has every intention of building on its illustrious contribution to entomology, not just in Great Britain, but world-wide!