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General News

Reminded that it is a hundred years since the term 'parasitoid' was coined, we start 2014 with a 'feature' by Apostolos Kapranas and Ian Hardy of the University of Nottingham: a concise history of key areas of parasitoid research and a bibliography of key references. They highlight that although pure research uses parasitoids because they are good model insects, many results have been useful in developing better biological control. The remainder of the issue includes our usual mix of news but is weighted towards the use of parasitoids in biological control and we thank all our contributors for making this possible.

One Hundred Years of Parasitoids

The phenomenon of insect parasitism was first described around a thousand years ago by Lu Dian (China, 1042–1102) based on observations of the life cycle of tachinid flies[1]. Further descriptions of parasitism by insects are credited to European 16th and 17th century naturalists, including Jan Jacob Swammerdam (assisted by a painter, Otto Marsilius), and the better known work of Antoni van Leeuwenhoek[2]. It was not, however, until one hundred years ago that the term 'parasitoid' was coined: German entomologist Odo Morannal Reuter introduced it in his book[3] on insect habits and life histories, *Lebensgewohnheiten und Instinkte der Insekten*. He used the term 'parasitoidea' (parasitoid predators) to distinguish insects that live in close association with their host as immatures, killing it during their development and living freely as adults, from 'parasites' (true parasites) in which both adult and immature stages feed on the host. In defining parasitoids, Reuter had particularly in mind members of the Hymenoptera, such as ichneumonoid and chalcidoid wasps, and these also form our focus here. In reviewing Reuter's book, American entomologist William M. Wheeler[4] mostly downplayed the utility of the term although his criticisms were tempered due to the fact that Reuter has been blind for several years beforehand. Despite Wheeler's critique, the term has now become very widely used, especially in the last 30–40 years, and today a *Web of Science* search on 'parasitoid' returns well over 66,000 articles. We have not been able to cite let alone read all of these! Rather, we here provide a narrative overview of selected highlights of parasitoid research from just prior to Reuter's terminological advance to the present time.

Parasitoids were intentionally utilized as agents of biological pest control before they were so named. In 1883, Valentine Riley, a US Department of Agriculture entomologist, directed the first successful introduction of a parasitoid, the braconid wasp *Apanteles glomeratus*, from the UK to the USA for control of the imported cabbageworm[5]. Since then, research on parasitoids has thrived, broadening from the initial focus on agricultural applications to now include a vast array of topics within genetics, physiology, behaviour, ecology and evolutionary biology. The first comprehensive review of parasitoid biology was provided by Curtis Clausen in his classic *Entomophagous Insects*[6]. Later, Paul DeBach's book[5] *Biological Control of Pests and Weeds* and DeBach and Rosen's[7] *Biological Control by Natural Enemies* gave full descriptions of biocontrol programmes using parasitoids and a wealth of information on their general biology.

The first models of population dynamics of animals with discrete generations were put forward by Thomson[8] in the 1920s and by Nicholson[9] in the 1930s, both were entomologists working on parasitoids. Extensions to basic models proposed by Nicholson, working with V.A. Bailey, a physicist, continued throughout the rest of the century[10,11] indicating new areas of exploration including how parasitoid behaviour could affect influential model parameters, such as searching time. Meanwhile, George Salt's physiological and behavioural studies, from the early 1930s, set the stage for further advances on numerous topics such as superparasitism and within-host competition, host selection and the immunological and biochemical effects of hosts on parasitoid development and *vice versa*[12,13]. Towards the end of the century, the discovery that parasitoids search for hosts using chemical cues emanating directly from the host[14] and host-feeding induced plant volatiles[15] generated a comprehensive research programme on the chemical ecology of host–parasitoid interactions, which is ongoing today[16].

During the decades that parasitoids were increasingly deployed as biocontrol agents, important advances were also occurring in the fields of behavioural and evolutionary ecology. Ideas originating in studies on avian clutch size by David Lack[17], that selection maximizes the number of young produced per nest, were adopted for parasitoids by Klomp and Teerink[18] generating many productive extensions to clutch size theory and, more generally, optimal foraging theory[19–21]. Many further advances in evolutionary ecology can readily be traced back to W.D. Hamilton's 1960s' insights into how genetic relatedness influences the evolution of social behaviour and how sex ratios are influenced by population structure[22,23] plus John Maynard Smith's 1970s' developments of game-theoretic thinking, especially concerning contest behaviour[24]. Early developments in contest theory had little to do with the study of parasitoids, but numerous species of parasitoids exhibiting aggressive behaviour have since been used to test and develop contest research[25]. In contrast, parasitoid wasps and other hymenopterans were central to the stimulation and testing of some of the key developments in social behaviour and sex ratio theory: it is no accident that a parasitoid wasp, *Nasonia vitripennis*, is depicted on the cover of the volume collecting Hamilton's works from this period[26].

The extreme female bias of many parasitoid species is often explained by Hamilton's theory of Local Mate Competition[23]. Around a decade later the tendency for parasitoids to lay female eggs in larger (high-quality) hosts and male eggs on smaller (lower-quality) hosts, a phenomenon which had been commonly observed by biological control practitioners[27], was explained by Charnov and co-authors[28,29], borrowing concepts from mammal-oriented theory. These theories show how sex ratio bias arises from sexually differential returns from parental investment and, together with R.A. Fisher's frequency-dependent explanation for unbiased sex ratios, form the basis for arguably the most detailed and elegant area of understanding within evolutionary biology: parasitoids have played no small part in this[29–31]. Hamilton's Local Mate Competition paper[23] also laid the foundations for understanding the influence of symbiotic organisms on the sexual reproduction of their hosts. Parasitoids have played an important role in this, notably the discovery that *Wolbachia* bacteria cause parthenogenesis in *Trichogramma* wasps[32]. Today it is established that symbiotic organisms, either in hosts or in parasitoids, have enormous significance for ecological and evolutionary interactions[33–35].

From the early 1980s parasitoids increasingly captured the interest of evolutionary and population ecologists due to the many interspecific variations around the relatively simple core life history (it often seems possible to find a parasitoid to fit almost any set of modelling assumptions) and to the rather direct fitness and population dynamic consequences of parasitoid host handing decisions[11,21]. At the same time, biological control researchers became increasingly familiar with advances in evolutionary ecology; functional explanations for how decisions maximize reproductive success can be applied to enhance the mass rearing of parasitoids for release in biocontrol programmes and how to further conserve them in agroecosystems[36,37]. H.C.J. Godfray's 1994 monograph[21] on *Parasitoids: Behavioral and Evolutionary Ecology* was paramount in capturing and explaining a vast amount of literature accumulated up to that time. Various other landmark books on insect parasitoid biology, ecology and use in biological control appeared during the next decade and a half[10,38–40]. This was definitely the era in which parasitoid research bridged the gap between basic and applied science, as exemplified by a European research consortium explicitly focusing on applying parasitoid behavioural ecology to biological control and the associated book[41] *Behavioural Ecology of Insect Parasitoids: from Theoretical Approaches to Field Applications*.

One hundred years of parasitoid research have left us highly informed and yet somehow there is still so much left to discover and to achieve. In coming years it is anticipated that the use of biological control will increase as a sustainable alternative to chemical pesticides and, as parasitoids are among the most deployed natural enemies, parasitoid research should be the vanguard of this. Further, parasitoids will assuredly continue to serve as model systems for probing various questions in behavioural, evolutionary and population ecology. For instance, they remain ideal for researching the evolution of sex ratios, which connects to a number of general issues in evolutionary biology[31], and are currently being developed as genetic model organisms[42]. In conclusion, in defining the characteristics of parasitoids that mark them as distinct from predators and from parasites, Reuter, though blind, was far-sighted. For our part, we envisage no reason that research on insect parasitoids will lose its impetus in the century to come. This is because parasitoids are important for both pure and applied biology and for the synergistic interplay between the two.

Acknowledgements

This potted history inevitably overlooks many important details and some research areas entirely: we apologise. We thank our parasitoid research colleagues, past and present, and in particular those from the University of California Riverside, Silwood Park and the University of Leiden. We dedicate this article to the memory of Kees Hofker (13 May 1956 to 6 December 2013), a valued Leiden parasitoid research colleague and friend.

References

[1]Cai, W., Yan, Y. and Li, L. (2005) The earliest record of insect parasitoids in China. *Biological Control* 32, 8–11.

[2]van Lenteren, J.C. and Godfray, H.C.J. (2005) European science in the enlightenment and the discovery of the insect parasitoid life cycle in The Netherlands and Great Britain. *Biological Control* 32, 12–24.

[3]Reuter, O.M. (1913) *Lebensgewohnheiten und Instinkte der Insekten.* Friendlander, Berlin.

[4]Wheeler, W.M. (1914) Review of O. M. Reuter's "Lebensgewohnheiten und Instinkte der Insckten bis zum Erwachem der sozialen Instinkte". *Science* 39, 69–71.

[5]DeBach, P. (1964) *Biological Control of Insect Pests and Weeds*. Chapman and Hall, London.

[6]Clausen, C.P. (1940) *Entomophagous Insects*. McGraw-Hill, New York.

[7]DeBach, P. and Rosen, D. (1991) *Biological Control by Natural Enemies*, 2nd edn. Cambridge University Press, Cambridge, UK.

[8]Thompson, W.R. (1924) La theorie mathematique de l'action des parasites entomophages et le facteur du hasard. *Annales de la Faculté des Sciences de Marseille* 2, 69–89.

[9]Nicholson, A.J. and Bailey, V.A. (1935) The balance of animal populations. Part 1. *Proceedings of the Zoological Society of London* 3, 551–598.

[10]Hassell, M.P. (1978) *The Dynamics of Arthropod Predator–Prey Systems*. Princeton University Press, Princeton, New Jersey.

[11]Hassell, M.P. (2000) *The Spatial and Temporal Dynamics of Host-Parasitoid Interactions.* Oxford University Press, New York.

[12]Edson, K.M., Vinson, S.B., Stoltz, D.B. and Summers, M.D. (1981) Virus in a parasitoid wasp: suppression of the cellular immune response in the parasitoid's host. *Science* 211, 582–583.

[13]Bateson, P. (2003) George Salt. 12 December 1903 – 17 February 2003. *Biographical Memoirs of Fellows of Royal Society London* 49, 447–459.

[14]Jones, R.L., Lewis, W.J., Bowman, M.C., Beroza, M. and Bierl, B. (1971) Host-seeking stimulant for parasite of corn earworm: isolation, identification and synthesis. *Science* 173, 842–843.

[15]Turlings, T.C.J., Tumlinson, J.H. and Lewis, W.J. (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* 250, 1251–1253.

[16]Wajnberg, E. and Colazza, S. (2013) *Chemical Ecology of Insect Parasitoids.* Wiley-Blackwell, UK.

[17]Lack, D. (1947) The significance of clutch-size. *Ibis* 89, 302–352.

[18]Klomp, H. and Teerink, B.J. (1962) Host selection and number of eggs per oviposition in the egg parasite *Trichogramma embryophagum* Htg. *Nature* 195, 1020–1021.

[19]Iwasa, Y., Suzuki, Y. and Matsuda, H. (1984) Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. *Theoretical Population Biology* 26, 205–227.

[20]Hubbard, S.F. and Cook, R.M. (1978) Optimal foraging by parasitoid wasps. *Journal of Animal Ecology* 47, 593–604.

[21]Godfray, H.C.J. (1994) *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey.

[22]Hamilton, W.D. (1964) The genetical evolution of social behaviour II. *Journal of Theoretical Biology* 7, 17–52.

[23]Hamilton, W.D. (1967) Extraordinary sex ratios. *Science* 156, 477–488.

[24]Parker, G.A. (2013) A personal history of the development of animal contest theory and its role in the 1970s. In: Hardy, I.C.W and Briffa, M. (eds) *Animal Contests*. Cambridge University Press, Cambridge, UK, pp. xi–xx.

[25]Hardy, I.C.W., Goubault, M., Batchelor, T.P. (2013) Hymenopteran contests and agonistic behaviour. In: Hardy, I.C.W. and Briffa, M. (eds) *Animal Contests*. Cambridge University Press, Cambridge, UK, pp. 147–177.

[26]Hamilton, W.D. (1996) *Narrow Roads in Gene Land, Vol.1: Evolution of Social Behaviour*. W.H. Freeman, New York.

[27]Clausen, C.P. (1939) The effect of host size upon the sex ratio of hymenopterous parasites and its relation to methods of rearing and colonization. *Journal of the New York Entomological Society* 47, 1–9.

[28]Charnov, E.L., Los-den Hartogh, R.L., Jones, W.T. and van den Assem, J. (1981) Sex ratio evolution in a variable environment. *Nature* 289, 27–33.

[29]Charnov, E.L. (1982) *The Theory of Sex Allocation*. Princeton University Press, Princeton, New Jersey.

[30]Hardy, I.C.W. (2002) *Sex Ratios: Concepts and Research Methods*. Cambridge University Press, Cambridge, UK.

[31]West, S.A. (2009) *Sex Allocation*. Princeton University Press, Princeton, New Jersey.

[32]Stouthamer, R., Luck, R.F. and Hamilton, W.D. (1990) Antibiotics cause parthenogenetic *Trichogramma* (Hymenoptera: Trichogrammatidae) to revert to sex. *Proceedings of National Academy of Sciences USA* 87, 2424–2427.

[33]O'Neill, S.L., Hoffmann, A.A. and Werren, J.H. (1997) *Influential Passengers: Inherited Microorganisms and Arthropod Reproduction*. Oxford University Press, New York.

[34]Oliver, K.M. and Moran, N.A. (2009) Defensive symbionts in aphids and other insects. In: White, J.F. and Torres, M.S. (eds) *Defensive Mutualism in Microbial Symbiosis*. Taylor and Francis, London, pp. 129–148.

[35]Frago, E., Dicke, M. and Godfray, H.C.J. (2012) Insect symbionts as hidden players in insect–plant interactions. *Trends in Ecology and Evolution* 27, 705–711.

[36]Waage, J.K. and Greathead, D. (1986) *Insect Parasitoids: 13th Symposium of the Royal Entomological Society of London*. Academic Press, London.

[37]Ode, P.J. and Hardy, I.C.W. (2008) Parasitoid sex ratios and biological control. In: Wajnberg, E., Bernstein, C. and van Alphen, J.J.M. (eds) *Behavioral Ecology of Insect Parasitoids: from Theoretical Approaches to Field Applications*. Blackwell, Oxford, UK, pp. 253–291.

[38]Hawkins, B.A. (1994) *Pattern and Process in Host-Parasitoid Interactions.* Cambridge University Press, Cambridge, UK.

[39]Quicke, D.L.J. (1997) *Parasitic Wasps*. Chapman and Hall, London.

[40]Hochberg, M.E. and Ives, A.R. (2000) *Parasitoid Population Biology*. Princeton University Press, Princeton, New Jersey.

[41]Wajnberg, E., Bernstein, C. and van Alphen, J.J.M. (2008) *Behavioral Ecology of Insect Parasitoids: from*

Theoretical Approaches to Field Applications. Blackwell, Oxford, UK.

[42]Werren, J.H., Richards, S., Desjardins, C.A., Niehuis, O., Gadau, J., Colbourne, J.K., *et al.* (2010) Functional and evolutionary insights from the genomes of three parasitoid *Nasonia* species. *Science* 327, 343–348.

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Biological Control of Millet Head Miner in the Sahel

An innovative programme in the Sahelian zone of West Africa has shown that augmentative biological control using on-farm rearing of a parasitoid has potential for controlling the most serious insect pest of millet in the region. Pearl millet is the only cereal crop adapted to grow in this part of the Sahel but is heavily attacked by pests including the millet head miner (MHM), *Heliocheilus albipunctella*, with reported yield losses of 40–85%. There is potential for the parasitoid *Habrobracon hebetor* to control the univoltine pest but its impact occurs too late in the season to prevent damage.

A project implemented in Burkina Faso, Mali and Niger in 2007–09[1] developed on-farm parasitoid release 'kits', comprising small jute bags filled with millet grains and flour that was infested with the rice moth *Corcyra cephalonica* as a rearing host for mated *H. hebetor*. Villages in the project area, where millet occupies 68–80% of crop land, were supplied with 15 kits each; estimates suggested these could produce several thousand parasitoids within a few weeks, which could escape from the bags to parasitize MHM in surrounding fields. The method proved successful and the rate of parasitism of MHM increased at all sites – best illustrated in Niger where natural parasitism was initially negligible yet levels of up to 97% were recorded by the end of the project.

A project feature was farmer involvement and they proved extremely knowledgeable, citing soil fertility, drought and insect pests as the main constraints to millet production. They identified MHM as the most important pest, were familiar with its life cycle and the symptoms of its damage, and estimated that it cost them losses of 42–48%. They were not familiar with its natural enemies before the project, but interviews afterwards indicated they thought the implemented biological control was effective. Although the project itself did not set out to record increases in millet yield, farmers estimated up to 52% mortality of MHM larvae, and average yield gains of 42–57%. Their new-found understanding of biological control was reflected by the consistently expressed willingness to pay for parasitoid release kits, although this is one of the most impoverished parts of the world.

Large-scale extension of the programme is an exciting prospect, but the authors urge some caution: repeated releases could be necessary every two years, and ecological and economic assessments of the biological control achieved by the programme are needed. In addition, the development of a parasitoid-rearing cottage industry owned by private individuals or farmers' cooperatives will be needed to scale-up the technology.

[1]Ba, M.N, Baoua, I.B., N'Diaye, M., Dabire-Binso, C., Sanon, A. and Tamò, M. (2013) Biological control of the millet head miner *Heliocheilus albipunctella* in the Sahelian region by augmentative releases of the parasitoid wasp *Habrobracon hebetor*: effectiveness and farmers' perceptions. *Phytoparasitica* 41, 569–576.

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Biological Control of Papaya Mealybug in Asia

Papaya mealybug (PM), *Paracoccus marginatus,* is a native of Mexico and adjoining areas in the Central America. It was described by Williams and Granara de Willink in 1992. It spread to the Caribbean islands in 1994, Florida in 1998, South America in 1999, and the Pacific islands in 2002. In 2008, it was reported in Indonesia, India and Sri Lanka, and subsequently in several other countries in South and Southeast Asia. Surveys conducted in India and Sri Lanka proved the absence of effective natural enemies of this mealybug, leading to implementation of classical biological control by introducing the parasitoids *Acerophagus papayae*, *Anagyrus loecki* and *Pseudleptomastix mexicana.* These were originally collected in Mexico by US Department of Agriculture – Agricultural Research Service (USDA-ARS) entomologists and later cultured in a laboratory in Puerto Rico with the support of the USDA Animal and Plant Health Inspection Service (APHIS). The parasitoids were imported from Puerto Rico and released in Sri Lanka in 2009 and India in 2010. Within five months of the release of the parasitoids, the mealybug populations were controlled.

Surveys conducted in Java, Indonesia, in 2009 revealed the fortuitous introduction of *Acerophagous papayae,* negating the need for importation. Subsequent accidental introductions of PM to other islands in Indonesia and Timor-Leste resulted in the parasitoid fortuitously following, and it also trailed the mealybug in Pakistan and Oman. However, no fortuitous introduction of the parasitoid has been reported so far from Bangladesh, even though PM was recorded there in 2009.

PM was reported in Thailand (2008), Malaysia (2009), Cambodia (2010), and the Philippines (2010), where mealybug populations have been controlled by parasitoids. However, with a few exceptions, little or no work has been carried out to identify parasitoids. In Thailand, the parasitoids *Anagyrus* sp. and *Anasius* sp. were reported on PM[1], and *Acerophagus* *papayae* was recorded on it in Malaysia[2]. It is possible that *A. papayae* or *Anagyrus loecki* were introduced fortuitously into these countries. During my visit to Cambodia and the Philippines in 2010, I did find parasitoid mummies in the PM samples collected, but I did not have time to rear them out during my trip. A survey of PM and its natural enemies in Southern and Southeastern Asian countries would be valuable.

PM was first identified in India at Coimbatore in 2008, and by 2010 it had covered most of the southern part of India, killing papaya trees and seriously affecting the silkworm industry as it infested mulberry, a host plant of silkworm. In a collaborative effort between the Indian Council of Agricultural Research, the National Bureau of Agriculturally Important Insects, the Directorate of Plant Protection, Quarantine and Storage, Tamil Nadu Agricultural University, Krishi Vigyan Kendras (KVKs), the US Agency for International Development (USAID) mission in New Delhi, USDA-APHIS and the IPM Innovation Lab at Virginia Tech, the parasitoids *Acerophagus papayae*, *Anagyrus loecki*, and *P. mexicana* were imported from the laboratory in Puerto Rico in July 2010. These were multiplied and field released, achieving excellent control of PM within five months. Additionally, this method reduced the use of pesticides, increased the production of several crops such as eggplant/aubergine, cassava and mulberry, and restored cultivation of papaya. An economic analysis of the benefits derived from the classical biological control of PM in India was carried out by the IPM Innovation Lab, a project funded by USAID[3]. It was found that the farmers and consumers benefited greatly from this programme. In the first year of implementation alone, it saved Indian farmers and consumers $121 million to $309 million. Over a five-year period the benefit was $524 million to $1.34 billion.

In general, classical and fortuitous biological control of PM in the Caribbean, Florida, South America, South and Southeast Asia and Ghana has saved the environment and benefited farmers and consumers to the tune of several billions of dollars. Biological control is being pursued in countries that PM invaded recently and it will also be sought out when new countries are invaded by the pest.

[1]Saengyot, S. (2011) Biological control of papaya mealybug, *Paracoccus marginatus* (Hemiptera: Pseudococcidae) in Thailand. Thesis submitted to Kasetsart University.

[2]Mastoi, M.I., Azura, A.N., Muhammad, R., Idris, A.B. and Ibrahim, Y. (2011) First report of papaya mealybug *Paracoccus marginatus* (Hemiptera: Pseudococcidae) from Malaysia. *Australian Journal of Basic and Applied Sciences* 5, 1247–1250.

[3]Myrick, S., Norton, G., Selvaraj, K.N., Natarajan, K. and Muniappan, R. (2014) Economic impact of classical biological control of papaya mealybug in India. *Crop Protection* 56, 82–86.

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Classical Biological Control of Papaya Mealybug in West Africa

Papaya mealybug (PM), *Paracoccus marginatus*, was first detected on the African continent towards the end of 2009 when outbreaks were causing severe damage in papaya orchards near Accra in Ghana[1]. In a spectacular spread, PM had previously invaded most tropical regions of the world within only two decades. Although first samples had been collected in 1955 from its native range in Mexico and Central America, the species was only described in 1992 when it started to invade the Caribbean archipelago. From there it expanded to South America, the Pacific islands, Southeast Asia, the Indian subcontinent and by 2010 had reached Reunion in the Indian Ocean. Recent records indicate that PM is now found in more than 35 tropical countries around the globe. Since it was first observed on the African continent in Ghana, PM has spread more than 4000 km, primarily along the coast of West and Central Africa. To date its presence in the Afrotropics has been verified for at least nine further countries including Mauritania, Senegal, Sierra Leone, Burkina Faso, Togo, Benin, Nigeria, Cameroon and Gabon. The absence of natural enemies outside its native range has certainly been an important factor of the observed invasiveness of this species. Moreover, the pest is highly polyphagous attacking, beside its preferred host plant papaya, more than 80 species in 33 botanical families including other important tropical crops, fruits, and ornamentals.

Immediately following the accidental introduction of PM into Ghana, papaya orchards suffered alarming losses. In the main production areas of the country, 85% of all papaya farms averaged yield losses of 65%. In several tropical regions[2, 3], classical biological control campaigns against PM, using specific natural enemies such as the encyrtid endoparasitoids *Acerophagus papayae*, *Anagyrus loecki* and *Pseudleptomastix mexicana,* had been successful (see preceding article). In Ghana, a pilot project was therefore initiated in 2010 in the framework of an emergency FAO TCP (Food and Agricultural Organization of the United Nations – Technical Cooperation Programme) involving the Plant Protection and Regulatory Services Directorate (PPRSD) of Ghana and the International Institute of Tropical Agriculture (IITA). First releases of *Acerophagus papayae* originating from cultures maintained by the US Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) in Puerto Rico were made in commercial papaya orchards near Accra in July 2011.

Meanwhile the steady expansion of PM in West and Central Africa necessitated joint action among all affected countries, requiring scaling-up of activities at regional level. By the end of 2012, a new IITA-led project funded by the Swiss Agency for Development and Cooperation (SDC) was initiated to be implemented jointly with national partners from Benin, Cameroon, Gabon, Ghana, Nigeria and Togo. In addition to the release of natural enemies and a thorough assessment of their efficiency at regional scale, the project will document the socio-economic profitability of this intervention. It will also enhance national research and extension capacities for adequately responding to similar emerging pest problems in future.

Thus, in early 2013 stock colonies of *A. papayae* were transferred from PPRSD Ghana to rearing facilities of IITA-Benin at Cotonou for establishing a further steady supply source for project partners and other African countries. Since April 2013, more than 6000 parasitoids have been used for inoculative field releases in Benin. Preliminary field data indicate effective colonization by *A. papayae* in all 18 release sites, followed by a dramatic decrease of PM populations within two months. This high efficiency was achieved despite the presence of native hyperparasitoids, also known to attack previously released exotic parasitoids that are effectively controlling cassava mealybug (*Phenacoccus manihoti*) and mango mealybug (*Rastrococcus invadens*). Whether *A. papayae* will be able to adapt to a wide range of climatic conditions and ecologies while maintaining a high degree of efficiency will be determined from results of further releases and long-term monitoring in all project countries of West and Central Africa. In view of the current excellent prospects to permanently control the pest, the planned introduction of additional parasitoid species specific to PM has been put on hold.

[1]Muniappan, R., Shepard, B.M., Watson, G.W., Carner, G.R., Rauf, A., Sartiami, D., Hidayat, P., Afun, J.V.K., Goergen, G. and Ziaur Rahman, A.K.M. (2009, published 2011) New records of invasive insects (Hemiptera: Sternorrhyncha) in Southeast Asia and West Africa. *Journal of Agricultural and Urban Entomology* 26, 167–174.

[2]Meyerdirk, D.E., Muniappan, R., Warkentin, R., Bamba, J. and Reddy, G.V. (2004) Biological control of the papaya mealybug, *Paracoccus marginatus* (Hemiptera: Pseudococcidae) in Guam. *Plant Protection Quarterly* 19, 110–114.

[3]Muniappan, R., Meyerdirk, D.E., Sengebau, F.M., Berringer, D.O. and Reddy, G.V.P. (2006) Classical biological control of the papaya mealybug, *Paracoccus marginatus* (Hemiptera: Pseudococcidae) in the Republic of Palau. *Florida Entomologist* 89, 212–217.

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Parasitoid Reduces Gall Wasp Host Plant Range

According to the enemy release hypothesis, a species can attain much higher population levels in the absence of its natural enemies, and this can allow it to become invasive if it is introduced outside its native range. It may also, under heavy intraspecific competition, move into less-suitable ecological niches. In particular, a plant-feeding insect may extend its host range onto otherwise marginal hosts. A paper in *Biological Control*[1] describes a study of the impact of the parasitoid *Closterocerus chamaeleon* on the host range of the eucalyptus gall wasp, *Ophelimus maskelli*, following its arrival in the Mediterranean region.

The eucalyptus gall wasp, a native of Australia, was first recorded in the Mediterranean region in the early 2000s where it came to notice because of its high densities and the damage it was inflicting on *Eucalyptus* trees. As no local natural enemies were recovered from the gall wasp in its new range, a classical biological programme was initiated. The host-specific eulophid parasitoid *C. chamaeleon* was introduced from Australia to Israel, where it established, spread rapidly, and proved to be effective at reducing gall wasp populations.[2] The parasitoid's subsequent spread westwards through Mediterranean countries has given scientists an opportunity to investigate an invasive insect that had been freed from its natural enemies, and how it was affected by the introduction of one of its parasitoids.

In 2008 Branco and co-authors[1] sampled 50 *Eucalyptus* species at four sites in Tunisia and 37 *Eucalyptus* hybrids at a site in Portugal before *C. chamaeleon* was recorded in these countries, and again in 2012 and 2011 respectively, after its arrival, to capture information on what *Eucalyptus* species the gall wasp was attacking in the absence and then presence of the parasitoid. In both countries, there was a significant decline in the number of hosts between the two sampling dates: from 18 species to three (*E. camaldulensis, E. tereticornis* and *E. rudis*) in Tunisia, and from 37 hybrids to six in Portugal – all six of these hybrids had one of the three above *Eucalyptus* species as a parent. The authors speculate that the gall wasp did not attack all the sampled species/hybrids in the absence of the parasitoids because some hosts were not acceptable even under conditions of high intra-specific competition. With competition reduced by the natural enemy, the host range in Tunisia was reduced from 18 species in four sections of *Eucalyptus* to three closely related species. In practical terms, the authors conclude, successful biological control may reduce the realized host plant range of an invasive pest.

[1]Branco, M., Dhari, S., Santos, M. and Ben Jamaa, M.L. (2014) Biological control reduces herbivore's host range. *Biological Control* 69, 59–64.

[2]Protasov, A., Blumberg, D., Brand, D., La Salle, J. and Mendel, Z. (2007) Biological control of the eucalyptus gall wasp *Ophelimus maskelli* (Ashmead): Taxonomy and biology of the parasitoid species *Closterocerus chamaeleon* (Girault), with information on its establishment in Israel. *Biological Control* 42, 196–206.

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Using Genetic Analysis to Audit Biological Control

Identifying the optimum area to collect a classical biological control agent to introduce against a pest in its introduced range has been transformed by developments in biology. Techniques such as climate matching and genetic mapping have helped to turn exploration for natural enemies from something of an art into a more exact science. Researchers at the International Centre for Insect Physiology and Ecology (ICIPE) in Kenya and the North West University at Potchefstroom in South Africa have used genetic analysis to explore why the introduction 30 years ago of the same predator against a grain pest was an apparent success on one side of Africa but not on the other, and also whether increasing the genetic diversity of the predator in Africa might lead to better control throughout the continent[1].

The larger grain borer (LGB), *Prostephanus truncatus*, was accidentally and separately introduced to Togo and Tanzania some 30 years ago. It is now found in 21 countries in sub-Saharan Africa and is the most serious pest of post-harvest maize on the continent. It is therefore pertinent to assess whether current control measures could be improved.

Classical biological programmes in the 1980s led to the introduction of the histerid predator *Teretrius nigrescens* from central Mexico to East Africa, and from Costa Rica to West Africa. Although the size of the founding population alone is not necessarily an indicator of diversity, rearing colonies of *T. nigrescens* were founded by at least 200 individuals and the smallest releases were of 5000 individuals. The programmes have never been formally compared, but in West Africa introductions and subsequent biological control were reported as successful in Benin, Togo, eastern Ghana and Nigeria, while in East Africa the predator established only in Kenya and initial reductions in LGB populations did not persist. Both LGB and *T. nigrescens* have a very large range in the New World, from Ecuador to the southern USA, and occur in a wide range of agro-ecological conditions, so the questions were: what was the genetic diversity of *T. nigrescens* populations across its home range and in Africa, and could such information be used to improve LGB control?

Using microsatellite markers, authors Omondi *et al.* looked at the predator's population structure and demographic history, a process facilitated by the availability of independent populations and records of management strategies and releases. They found that *T. nigrescens* populations sampled at six sites in Mexico and Honduras vary, with differences broadly increasing with geographical distance. One site in southern Mexico showed the maximum diversity and the authors suggest that this could indicate either the area of origin of the predator from where it dispersed north and south, or the area where two distinct populations converged. In Africa, the introduced populations are most like the sampled Meso-American populations closest to the area of collection of their founding population. The Meso-American beetles are more genetically diverse than the populations they gave rise to in Africa, which contain only a fraction of the diversity found in the predator's home range. Interestingly, although the collection site for the material released in East Africa is much closer to the site of maximum diversity in southern Mexico, the West African material, originating from Costa Rica, has the higher diversity. Using colony management and release records, Omondi and co-authors showed that African populations have diminished further in diversity with each event in the biological control programmes (releases, establishment and subculturing/release elsewhere), and there is evidence of rapid genetic drift.

The authors acknowledge that it is not clear how loss of genetic diversity relates to ecological performance, but such a loss is likely to make a population less adaptable and lead to loss of genes related to fitness. As LGB has remained a significant post-harvest maize pest in Africa, they suggest that there is potential to select fresh material from Meso-America to try and enhance the efficacy of the predator as a biocontrol agent in Africa. Omondi Aman suggests that this could involve (i) assessing genetic diversity of the introduced pest to know which populations are invasive; (ii) assessing the ecological range and diversity of candidate natural enemies (or undertaking multiple isolations); (iii) keeping several quarantine populations in parallel; (iv) maintaining large culture sizes and making aggressively large natural enemy releases; and (v) auditing genetic diversity after establishment.

[1]Omondi, B.A., van den Berg, J., Masiga, D. and Schulthess, F. (2013 online) Molecular markers reveal narrow genetic base and culturing-associated genetic drift in *Teretrius nigrescens* Lewis populations released for the biological control of the larger grain borer in Africa. *Bulleting of Entomological* Research.
Web: http://dx.doi.org/10.1017/S0007485313000552

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IOBC Workshop Proceedings: Chromolaena, Mikania and Related Invasive Weeds

The Eighth International Workshop on Biological Control and Management of *Chromolaena odorata* and other Eupatorieae was held in Nairobi, Kenya, in November 2010. The workshop was held under the auspices of the Working Group on *Chromolaena odorata* of the International Organization for Biological Control (IOBC) and hosted by CABI's centre in Africa. The proceedings of this workshop were published by the Agricultural Research Council, South Africa, in late 2013[1], in both electronic and hard-copy format, with printing costs kindly provided by *Working for Water*, a Natural Resource Management programme of South Africa's Department of Environmental Affairs. The proceedings contain 18 full papers from participants at the workshop and several researchers who were unable to attend, and an additional 12 abstracts of papers that were presented. CABI's Arne Witt opens the proceedings with a paper emanating from his keynote address on alien plant invasions in sub-Saharan Africa.

Apart from *C. odorata*, there are several important invasive alien plants within the tribe Eupatorieae of the family Asteraceae, and this has led to an increasingly wide remit for the Working Group since it was founded in 1988. Other invasive Eupatoriae discussed at the workshop were *Mikania micrantha*, *Ageratina adenophora* and *Campuloclinium macrocephalum*. The scope of topics covered in the proceedings is broader than indicated by the title of the workshop. Five full papers discuss the distribution, spread and impacts of *Chromolaena odorata* in countries around Africa and in Bangladesh. These are followed by two papers each on aspects of the plant's physiology and ecology, and on management of the weed. Biological control of *C. odorata* in countries in Africa, Asia and Oceania is discussed in six papers, while a seventh examines the field host-range of a potential agent within the native range of *C. odorata*. The proceedings wrap up with a full paper on the biocontrol of *M. micrantha* in Papua New Guinea and Fiji, and abstracts on some promising candidate agents being investigated for the control of *A. adenophora* and *Campuloclinium macrocephalum* in South Africa.

Several conclusions can be drawn from these proceedings: *Chromolaena odorata* is certainly increasing its range in East Africa. Globally, biocontrol of *C. odorata* has made great strides, particularly in the wetter parts of Southeast Asia and Oceania, using the stem-galling fly *Cecidochares connexa* and the leaf-feeding moth *Pareuchaetes pseudoinsulata*. However, further work is needed on implementation of current agents, assessment of their efficacy, and the release of additional agents, particularly in seasonally drier areas and where the southern African biotype of the weed is present. With regard to other invasive Eupatorieae, considerable success has been achieved in Papua New Guinea on the biocontrol of *M. micrantha* using the rust fungus *Puccinia spegazzinii*. Should new agents on *A. adenophora* prove suitable for release, there is scope for their release in the many other parts of the world in which this species is a serious weed.

[1]Zachariades, C, Strathie, L.W., Day, M.D. and Muniappan, R. (eds) (2013) *Proceedings of the Eighth International Workshop on Biological Control and Management of Chromolaena odorata and other Eupatorieae*, Nairobi, Kenya, 1–2 November 2010. ARC-Plant Protection Research Institute, Pretoria, South Africa.

Electronic copies of the proceedings can be obtained from Costas Zachariades, (ZachariadesC@arc.agric.za), and will soon be available for download from the IOBC webpage at www.arc.agric.za/arc-ppri/Pages/WeedsResearch/Chromolaena/Chromolaena-odorata.aspx. A limited number of hard copies are also available from Costas.

Peter Neuenschwander: Fellow of the African Academy of Sciences

Our CABI staff remember Peter Neuenschwander when he was in Senegal in 1982/83 on an FAO-funded classical biological control project for the vegetable leaf-mining fly *Liriomyza trifolii*; CABI's centre in Trinidad was responsible for sourcing and supplying him with parasitoids from the New World. From there Peter moved to the International Institute for Tropical Agriculture where he was and still is a key figure in their biological control activities, ensuring scientific rigour in research and sharing his knowledge by training national programme staff in many countries. His contributions were fundamental to successes such as the cassava mealybug and mango mealybug biological control programmes. He became IITA's first Emeritus Fellow on retirement, and remains active in biological control and in conservation activities in Benin. Over the decades, CABI's staff have collaborated with him many times, in practical biological control and in publishing ventures – he has always been an effective advisory board member of *BNI*. We are therefore delighted to congratulate him on being elected a Fellow of the African Academy of Sciences.

China Special in *Biological Control*

The first 2014 issue of *Biological Control* (68, 1–144) is devoted to 'Biological control in China: past, present and future'. The special issue includes papers on the biological control of arthropods in China, covering development, implementation and future directions in ten major commodity crops (rice, cotton, maize, greenhouse crops, brassicas, litchi, citrus, apple, tea and forestry), and in the use of *Trichogramma* and entomopathogenic fungi, together with an overview of the taxonomy of Chinese parasitoids.

Web: www.sciencedirect.com/science/journal/10499644/68