

## REVIEW ARTICLE

**The ecology of *Bactrocera tryoni* (Diptera: Tephritidae): what do we know to assist pest management?**A.R. Clarke<sup>1,2</sup>, K.S. Powell<sup>3</sup>, C.W. Weldon<sup>4</sup> & P.W. Taylor<sup>5</sup>

1 Discipline of Biogeoscience, Faculty of Science and Technology, Queensland University of Technology, Brisbane, QLD, Australia

2 Cooperative Research Centre for National Plant Biosecurity, Bruce, ACT, Australia

3 Biosciences Research Division, Department of Primary Industries, Rutherglen, VIC, Australia

4 Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

5 Department of Brain, Behaviour &amp; Evolution, Macquarie University, Sydney, NSW, Australia

**Keywords**

Applied ecology; area-wide management; Dacinae; tropical fruit fly.

**Correspondence**

A.R. Clarke, Discipline of Biogeosciences, Faculty of Science and Technology, Queensland University of Technology, GPO Box 2434, Brisbane, QLD 4001, Australia. Email: A.clarke@qut.edu.au

Received: 28 January 2010; revised version accepted: 19 September 2010.

doi:10.1111/j.1744-7348.2010.00448.x

**Abstract**

The distribution, systematics and ecology of *Bactrocera tryoni*, the Queensland fruit fly, are reviewed. *Bactrocera tryoni* is a member of the *B. tryoni* complex of species, which currently includes four named species, viz. *B. tryoni* ssp., *B. neohumeralis*, *B. melas* and *B. aquilonis*. The species status of *B. melas* and *B. aquilonis* is unclear (they may be junior synonyms of *B. tryoni*) and their validity, or otherwise, needs to be confirmed as a matter of urgency. While Queensland fruit fly is regarded as a tropical species, it cannot be assumed that its distribution will spread further south under climate change scenarios. Increasing aridity and hot dry summers, as well as more complex, indirect interactions resulting from elevated CO<sub>2</sub>, make predicting the future distribution and abundance of *B. tryoni* difficult. The ecology of *B. tryoni* is reviewed with respect to current control approaches (with the exception of sterile insect technique (SIT) which is covered in a companion paper). We conclude that there are major gaps in the knowledge required to implement most noninsecticide-based management approaches. Priority areas for future research include host–plant interactions, protein and cue-lure foraging and use, spatial dynamics, development of new monitoring tools, investigating the use of natural enemies and better integration of fruit flies into general horticultural IPM systems.

**Introduction**

*Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) is one of Australia's worst horticultural pest insects, attacking most fruit and many vegetable crops (Drew *et al.*, 1978; Bateman, 1991; Hancock *et al.*, 2000). Its native distribution is considered to be tropical and subtropical coastal Queensland and northern New South Wales (Gilchrist *et al.*, 2006), but it is now more widely established in eastern Australia and has invaded some South Pacific island nations (Drew *et al.*, 1978). Outbreaks have also occurred and then been eradicated in other Australian states where the fly does not normally occur (e.g. South Australia (Maelzer, 1990a,b) and Western Australia (Ayling, 1989)). Adult flies lay their eggs into

fruit and the larvae, which feed within the fruit, cause direct fruit damage and induce decay and premature fruit drop. Economic losses, estimated at \$28.5 million/annum in 2000 (Sutherst *et al.*, 2000), result from direct yield losses, direct and indirect management costs and loss or limit to domestic and international markets. Expenditure on fruit fly activities in Australia (with the vast majority focused on *B. tryoni*) was estimated at \$128 million in the years 2003–2008 (PHA, 2008). This expenditure included direct control costs, postharvest treatments, on-going surveillance for area freedom and research.

The literature on *B. tryoni* began over 115 years ago (Tryon, 1889) and now includes over 450 refereed papers and book chapters, at least 40 research masters and PhD theses, and a large 'grey' literature. The entire literature

has never been reviewed, although components have been included in generic fruit fly reviews (Bateman, 1972; Fletcher, 1987), specialist book chapters (e.g. Fletcher, 1989*a,b*; Meats 1989*a,b*; Drew & Romig, 2000) and as part of modelling exercises (Yonow & Sutherst, 1998; Yonow *et al.*, 2004). With a literature this large it might be assumed that we know all we need to know about this pest, but as we will make clear in this review, while we have very detailed information about select aspects of the insect's biology, much knowledge of the organism's general biology and ecology, particularly that pertinent to developing sustainable pest management options, is largely lacking.

As a major pest species, *B. tryoni* has been the focus of several major research initiatives over the last 50 years (work before the 1950s was sparse, although the works of Allman (1938, 1939, 1941; Allman & Friend, 1948) and Jarvis (1922*a, b, c*, 1923, 1924, 1925*a, b, c*, 1926*a, b*, 1931) are notable exceptions). However, paradoxically, most research (at least the published research) has not focused on issues related to the control of the fly. Rather, major blocks of work have focused on very specific theoretical, physiological or ecological issues, including: the density dependence/independence debate; speciation and the timing of mating behaviour as an isolating mechanism; rapid physiological adaptation following movement of the organism into a previously unfavourable environment; bacteria as a fruit fly food source; and male pheromones. While there are some obvious exceptions, including the literature covering postharvest disinfestation treatments and a body of more recent work derived from activities associated with the southern fruit fly free zone and the sterile insect technique (SIT), most of the available *B. tryoni* literature cannot be used to directly support pest management research.

While stating that the majority of research work on *B. tryoni* is not generally applicable to pest management, we are not implying that every paper on the fly should address a specific management issue or practice. Rather, we believe that targeted behavioural, physiological and ecological research is needed to progress Queensland fruit fly control, a view which has been well argued for pest systems in general (Walter, 2003).

Why is targeted behavioural, physiological and ecological research pertinent to *B. tryoni* management and why is it important now? Management of *B. tryoni* is currently undergoing a crisis. Two chemicals, dimethoate and fenthion, long used for in-field control and postharvest commodity treatment, are expected to have substantially restricted use following current reviews by the Australian Pesticides and Veterinary Medicines Authority (PHA, 2008). In their absence, in-field management of the fly will need to rely on alternative control strategies.

For *B. tryoni*, these will include controls which manipulate the fly's use of resources. Such resources include protein food sources (manipulated through protein-bait sprays), male parapheromones (manipulated through male annihilation technique), mates (manipulated through SIT), noncommercial host plants and noncrop habitats (manipulated through habitat management). The better application of biological controls, largely ignored for the last 50 years, may also become important. To make these alternatives viable replacements for chemical treatments, or to maintain their use (e.g. in the case of area freedom), a new period of intensive research on *B. tryoni* is beginning (as illustrated by the recent release of the National Fruit Fly Strategy (PHA, 2008)). Our current review, summarising what we know and what we do not know about *B. tryoni* behaviour and ecology with reference to pest management, is part of this larger process.

This review focuses initially on the species status of *B. tryoni* and closely related taxa within the *B. tryoni* complex. It then presents a summary of the distribution of Queensland fruit fly, factors limiting that distribution and likely changes in distribution under climate change. The remainder of the review focuses on major control techniques, identifying what we know and do not know about the fly based on the information required for the techniques to be successfully implemented or improved. In this way we hope not only to cover existing information, but also to identify and justify priority issues for further research. This review does not touch on postharvest controls or regulatory controls (e.g. road blocks, Interstate Certification Assurances, community awareness programmes) and also excludes, because of space constraints, the very large literature pertinent to the SIT which is dealt with in a companion paper.

### ***Bactrocera tryoni* complex**

Accurate species identification is a central tenet of successful pest management (Paterson, 1991; Walter, 2003). While this may appear a simple and self-evident statement, defining species is not always a straightforward task. Tephritid fruit flies, along with other groups (e.g. mosquitoes, Rona *et al.*, 2009; Weitzel *et al.*, 2009), often contain groups of biologically distinct, but morphologically similar or indistinguishable species (=sibling species, or species complexes). Sibling species can vary in important biological traits such as host use, pest status, geographic distribution and seasonal phenology (Barik, 2009; Clarke *et al.*, 2001; Garros *et al.*, 2006). Within the economic fruit flies, the best-known species complexes include the *Anastrepha fraterculus* complex (Cáeres *et al.*, 2009), the *Ceratitis rosa* complex (Virgilio *et al.*, 2008), the *Bactrocera dorsalis* complex

(Clarke *et al.*, 2005), the *B. tau* complex (Jamnongluk *et al.*, 2003) and the *B. tryoni* complex.

*Bactrocera tryoni* is recognised by Drew (1989) as belonging to a species complex with three other species; *B. neohumeralis* (Hardy) (=lesser Queensland fruit fly), *B. aquilonis* (May) and *B. melas* (Perkins & May). All of these species are sympatric with each other for all or part of their geographic ranges with the exception of *B. aquilonis*, which occurs allopatrically from the others in northwestern Australia (Drew *et al.*, 1978). There is yet to be a comprehensive phylogenetic analysis of the complex, so the sisterhood relationships of species within the complex are unknown. It is also not known if the complex is monophyletic, or if additional species currently not placed within the complex belong there.

Despite its critical importance to management and trade, the species status of flies within the *B. tryoni* complex is not well understood. Significant population genetic work has been performed on *B. tryoni sensu stricto* (Gilchrist *et al.*, 2006; Gilchrist & Ling, 2006; Morrow *et al.*, 2000; Shearman *et al.*, 2006; Wang *et al.*, 2003) and there is no evidence of unrecognised, cryptic species within *B. tryoni* ssp. While separation of *B. tryoni* from *B. neohumeralis* is based on variation in mating behaviour, the species status of the two other species in the complex (*B. aquilonis* and *B. melas*) is less clear.

#### *Bactrocera tryoni* and *B. neohumeralis*

Most work within the complex has involved understanding the relationship between *B. tryoni* and *B. neohumeralis* (Birch, 1961; Gee, 1966, 1969; Gibbs, 1967; Vogt, 1970; McKechnie, 1972, 1975; Bellas & Fletcher, 1979; Neale, 1989; An *et al.*, 2002; Wang *et al.*, 2003). The two species can be separated from each other on one clear behavioural difference; *B. tryoni* mates at dusk and *B. neohumeralis* in the middle of the day (Lewontin & Birch, 1966; Pike & Meats, 2002). Other traits that have been investigated to discriminate these species, however, are ambiguous. The one morphological feature once thought to separate the species, the colour of the humeral calli (it is typically yellow in *B. tryoni* and brown in *B. neohumeralis*) has since proven to be a poor character, showing continuous variation between the two extremes. While intermediate colour states in the humeral calli have been inferred as support for field hybridisation (Birch, 1961; Pike, 2004), more recent genetic analysis (Gilchrist & Ling, 2006) confirms the earlier work of Wolda (1967*a, b*) that variation in the colour of the humeral calli is a genetic trait of the parent and not a reflection of hybridisation. Until recently, genetic tests could not readily discriminate between *B. tryoni* and *B. neohumeralis* (Armstrong *et al.*, 1997; Morrow *et al.*, 2000; Green & Frommer,

2001; An *et al.*, 2002), but microsatellite techniques have now proved useful in discriminating between the species (Gilchrist & Ling, 2006; Wang *et al.*, 2003). For a more comprehensive background on the large literature pertaining to the *B. tryoni*/*B. neohumeralis* pair, see Pike & Meats (2002) and Meats *et al.* (2003*a*) (for time of mating); Pike (2004) and Gilchrist & Ling (2006) (for variation in the humeral calli); and Wang *et al.* (2003) and Gilchrist & Ling (2006) for genetic separation.

Despite their very close genetic similarity (Morrow *et al.*, 2000), *B. tryoni* and *B. neohumeralis* have very different pest status. Their recorded host lists are similar (Hancock *et al.*, 2000), but *B. tryoni* is the major pest fruit fly for all of eastern Australia, while *B. neohumeralis* is, at worst, a pest of the tropics and subtropics (Drew *et al.*, 1978). Why there is this difference in pest status of two such closely related species is almost entirely uninvestigated. Gibbs (1965, 1967) carried out comparative studies on the host use of the two species in Rockhampton and concluded that inter-species competition was not the answer, while Meats (2006) concluded that an inability to handle cold did not restrict the southern range of *B. neohumeralis*. No other direct comparative ecological studies have been carried out on the two species. Better understanding of why one species of this pair has become a major, invasive pest, and the other not, offers much for the study of fruit fly invasion biology.

*Bactrocera neohumeralis* is the only member of the Queensland fruit fly complex which naturally occurs outside of Australia, being regarded as endemic to Papua New Guinea (Drew, 1989). Having a much more restricted host range than Australian populations, and with an essentially nonexistent pest status, it is possible that the species currently recognised as *B. neohumeralis* in Papua New Guinea is an unrecognised additional species within the complex (Leblanc *et al.*, 2001).

#### *Bactrocera aquilonis*

*Bactrocera aquilonis*, the third member of the *B. tryoni* complex, was described by May (1965) based on material collected around Darwin in 1961. While morphologically very similar to *B. tryoni*, two subsequent papers supported the validity of this species (Drew & Lambert, 1986; Morrow *et al.*, 2000), although Wang *et al.* (2003) found no such support using microsatellite analysis. The uncertainty of *B. aquilonis*' species status became an issue in the late 1980s when this previously nonpest species expanded its known host range from four commercial crops (Drew, 1989) to 40 (Smith *et al.*, 1988). As reviewed by Cameron (2006), the reason for this expanded host range was thought to be one of the following: (i) pest flies may be an invasion of *B. tryoni* from the east coast;

(ii) they may be *B. aquilonis* which has expanded its host range; or (iii) the flies may be hybrids between *B. tryoni* and *B. aquilonis*.

Cameron (2006) and Cameron *et al.* (2010) have undertaken an extensive analysis of the *B. aquilonis* question, using trapping data, morphological data and a very extensive genetic analysis. Cameron's data strongly support the conclusion that *B. aquilonis* is simply a western, allopatric population of *B. tryoni* which has become increasingly pestiferous as more tropical crops are grown in the north. Cameron also presents evidence that the conclusions of Morrow *et al.* (2000), concerning *B. aquilonis*, are unreliable because of small sample size, and that the data from Drew & Lambert (1986) are of limited value because a known out-group was not included in the analysis, thus making it impossible to reliably estimate what might constitute intra versus interspecific variation.

Quoting directly from Chapter 7 of her thesis, Cameron (2006) states:

*'The current study [of B. aquilonis/B. tryoni] provides genetic evidence . . . that there is a single species present in the Northern Territory. No differentiation was found across the region studied, from Gove in the east to the Western Australian border in the west, using samples from rural, urban and native areas.*

*When Northern Territory samples were compared with samples from the East coast, there was very little genetic differentiation between the two groups. The level of differentiation was greater than that seen between East coast populations but smaller than between East coast B. tryoni and B. neohumeralis, suggesting that the species previously identified as B. aquilonis is actually an allopatric population of B tryoni'.*

### *Bactrocera melas*

Like *B. aquilonis*, the species status of the fourth member of the complex, *B. melas*, is unclear. *Bactrocera melas* was described by Perkins & May (1949) from material collected in southern Queensland, but Drew *et al.* (1978) subsequently discussed the likelihood that *B. melas* was simply a melanic form of *B. tryoni*. In a subsequent formal revision of the Australasian fruit flies, Drew (1989) referred to his earlier paper (Drew *et al.*, 1978) when discussing *B. melas*, but took the point no further. Rather, a full description of the species is presented, along with designations of a lectotype and two paralectotypes, which can only be interpreted by inference that the species stands as a recognised taxonomic entity. While

the absence of research on *B. melas* in any studies (except formal taxonomic ones) on the *B. tryoni* complex tends to reinforce the point that most Australian entomologists accept this species as a synonym of *B. tryoni*, this does not discount the fact it continues to hold the status of a valid taxonomic species. As such, *B. melas* remains on Australia's pest list where it is attracting increased interest from our international trading partners. The species status of both *B. aquilonis* and *B. melas* needs to be confirmed as a matter of urgency to determine if they are valid species, or are both junior synonyms of *B. tryoni*. Either result will have important implications for domestic and international trade.

## Geographic distribution

### Geographic distribution

Queensland fruit fly is widespread in eastern Australia, as well as being invasive in New Caledonia, French Polynesia, Pitcairn Islands and Cook Islands (<http://www.spc.int/Pacifly/>). Originally considered endemic to patches of tropical and subtropical rainforests extending along the east coast from Cape York to southern NSW (Meats, 1981), the development of commercial fruit production in Australia has promoted range expansion into more temperate and drier areas (May, 1961a). *Bactrocera tryoni* were first reported in the Sydney region in the late 1800s (May, 1961a) and now have a permanent range extending inland into central Queensland and New South Wales as well as in Alice Springs and Darwin (Osborne *et al.*, 1997), and possibly more widely throughout the Northern Territory and northern Western Australia depending on the species status of *B. aquilonis* (see discussion above). Sporadic outbreaks occur in Victoria and South Australia (May, 1963; Maelzer, 1990a,b; Maelzer *et al.*, 2004; Meats *et al.*, 2006), and a single outbreak was detected in 1989 and then successfully eradicated from Perth, Western Australia (Ayling, 1989; Fisher, 1996). However, these parts of Australia usually remain free of *B. tryoni* because of isolation from the permanent distribution range of the fly by intervening regions with unsuitable conditions (Meats, 1981; Yonow & Sutherst, 1998).

### Environmental factors influencing distribution

The three factors considered to determine the suitability of a region for *B. tryoni* survival and reproduction are temperature, moisture and availability of suitable larval host fruits (May, 1963; Meats, 1981; Yonow & Sutherst, 1998). The influence of temperature on the survival and reproduction of Queensland fruit fly has been extensively



studied and is reviewed elsewhere (Meats, 1989a). Tolerance of high temperatures varies with life stage but is modulated by the pattern of exposure; larvae do not suffer mortality to the same extent as eggs and pupae under cyclical temperature regimes with daily maxima of 38°C and 40°C (Meats, 1984). Tolerance of extreme low temperatures, the minimum temperature required for mating and development rate in cool temperatures determine the southern extent of the distribution of *B. tryoni* (Meats, 1981; O'Loughlin *et al.*, 1984; Yonow & Sutherst, 1998). Adult winter survival is poor in areas with an average yearly minimum temperature lower than 2.6°C (Meats, 1976b, 1981). Breeding can occur where daily maximum temperatures exceed 20°C (Meats & Fay, 2000), and areas where temperatures permit fewer than three generations per year are unlikely to ever have high populations (Meats, 1981). Detailed studies have demonstrated the capacity of adult *B. tryoni* to rapidly acclimate to low temperatures experienced at the southern extent of their range and high altitude regions (Meats, 1976a, b, c, 1987; Meats & Fay, 1976, 1977; O'Loughlin *et al.*, 1984). In addition to plasticity in their ability to tolerate cool temperatures, adult *B. tryoni* populations may also exhibit adaptation to their local thermal environment. Populations along the east coast of Australia are known to exhibit differences in survival and reproductive capacity over a range of constant temperatures that relate to differences in local climate conditions (Bateman, 1967). Little is known about the ability of *B. tryoni* to survive winter in the pupal form, although it is generally considered that they do not (Jarvis, 1924, 1925b; Fletcher, 1975, 1986).

Dry stress is considered a key factor restricting the distribution and abundance of Queensland fruit fly (Yonow & Sutherst, 1998; Dominiak *et al.*, 2006), suggesting that they are susceptible to water loss and desiccation. It has been noted that *B. tryoni* populations near Sydney, NSW, reach their highest numbers in wet years and decline during periods of drought (Bateman, 1968). However, with the exception of one unpublished PhD from the early 1960s (Besly, 1962), there have been no major studies of *B. tryoni* water relations or its potential impact on their distribution. Bateman (1968) suggested that the observed relationship between rainfall and *B. tryoni* abundance could result from lower female fecundity in dry years. Citing Besly, Bateman also posited that mortality during conditions of low humidity could result from increased levels of water loss as a consequence of cuticular damage caused by emergence through dry soil. Hulthen & Clarke (2006) showed nearly complete pupal mortality in soils with zero percent soil moisture, but increasing soil moisture to only 10% resulted in nearly 100% pupal survival.

### Distribution under climate change

Atmospheric CO<sub>2</sub> has increased rapidly from 280 ppm to current levels of 380 ppm since the late 18th century, and is expected to rise to above 550 ppm by 2050. This rise in atmospheric CO<sub>2</sub> concentration, as well as other greenhouse gases including methane and nitrous oxide, has been linked to rapid increases in global temperature (Pachauri & Reisinger, 2007). Observed climate anomalies during the 20th century and the predicted influence of greenhouse gas emission scenarios on the Australian climate are published (CSIRO & BoM, 2007) and have recently been reviewed (Garneau, 2008). In summary, under current climate change scenarios and without mitigation, temperature is predicted to increase between 0.4 and 1.8°C above 1990 levels by 2030. Median annual average rainfall is expected to decline across Australia. While average rainfall may not change in some areas, there is an expected increase in the intensity of rainfall events and an increase in the number of days without rainfall.

The consequences of a changing climate for the distribution of Queensland fruit fly have been modelled by Sutherst *et al.* (2000) using CLIMEX. The model produced an ecoclimatic index for the suitability of regions in Australia for *B. tryoni* survival, development and reproduction given a mean temperature increase of 0.5°C, 1°C and 2°C. These simulations clearly indicated that increased average temperature will result in the southerly spread of *B. tryoni*, primarily as a consequence of longer seasons, increased development and, consequently, an increase in the number of generations per year. The model also indicated a marked decline in the suitability of areas in northern and central Queensland as temperatures increase, which reflects temperature regimes exceeding the thermal tolerance maximum of *B. tryoni*. This predicted phenomenon is supported by recent evidence from a range of tropical insects (Deutsch *et al.*, 2008).

The simulations of Sutherst *et al.* (2000) incorporate the effect of increasing temperatures on evaporation and humidity, while also assuming a top-up of weekly rainfall with irrigation to equate to 25 mm per week. However, uncertainty about the effects of climate change on rainfall patterns presents challenges to the accurate prediction of the distribution of *B. tryoni* under climate change conditions. This is further complicated by the relative paucity of data on desiccation resistance and water balance of Queensland fruit fly and the demonstrated capacity for *B. tryoni* to adapt to local environmental conditions (Bateman, 1967).

### Indirect effects of elevated atmospheric CO<sub>2</sub>

Elevated atmospheric CO<sub>2</sub> has a 'fertilisation effect' on plant growth through higher rates of photosynthesis that

leads to increased production of above and below-ground biomass. Growth effects of elevated CO<sub>2</sub> may be dramatic in urban and horticultural systems where soil water and nutrients are not limiting (Idso & Kimball, 1997). For example, biomass production of cherry (Centritto *et al.*, 1999), sour orange (Kimball *et al.*, 2007), Valencia orange (Downton *et al.*, 1987), peach (Centritto *et al.*, 2002) and tomato (Islam *et al.*, 1996) is substantially increased by elevated CO<sub>2</sub>. Further, elevated CO<sub>2</sub> leads to production of more and larger fruit (Downton *et al.*, 1987; Islam *et al.*, 1996; Jablonski *et al.*, 2002; Reinert *et al.*, 1997), sometimes associated with elevated sugar concentration and quantitative changes in acid content (Idso *et al.*, 2002; Islam *et al.*, 1996). Importantly, higher nutrient availability in urban and horticultural settings means that tissue carbon to nitrogen ratios may be preserved at elevated CO<sub>2</sub> (Kimball *et al.*, 2007). The ratio of carbon to nitrogen in plant material influences many insect herbivores (Bernays & Chapman, 1994) and any changes in this ratio may influence host plant selection and utilisation.

The quantitative and qualitative changes in fruit produced by plants grown at elevated CO<sub>2</sub> may have important implications for frugivorous insects. *Bactrocera tryoni* spends its larval phase developing in fruit, but all previous studies on the consequences of climate change for insect–plant interactions have focused on chewing and sucking insect larvae (Coviella & Trumble, 1999; Stiling & Cornelissen, 2007). There has so far been no research on the consequences of elevated CO<sub>2</sub> on the development, longevity and reproduction of frugivorous insects. This is an important oversight in relation to tephritid flies in view of the unambiguous demonstration that larval host environment has a significant influence on larval, pupal and adult quality (Dukas *et al.*, 2001; Kaspi *et al.*, 2002; Nestel *et al.*, 2004).

## Ecology relevant to control techniques

### Lure and kill techniques/trapping

Lure and kill techniques operate on the principle of using a lure to attract a pest organism to a point (the source of the lure) where it can be killed (El-Sayed *et al.*, 2009). For insects the killing device is generally an insecticide mixed with, or placed adjacent to, the lure, but alternatives include liquid traps where the pest enters and drowns, or sticky traps which hold the insect until it dies. The lure itself can be a semiochemical (including pheromones, kairomones and food-based volatiles), nonvolatile food attractants, colour attractants and host mimics, or a combination of these. Lure and kill approaches used at low densities can be effective monitoring tools, or

if applied at high densities can be effective controls (De Souza *et al.*, 1992; Suckling, 2000; Petacchi *et al.*, 2003).

There has been a long history of using lures against *B. tryoni*, for both monitoring and control. The first experimental (cf. survey or taxonomic) paper on fruit fly in Australia dealt with attractants and repellents for 'fruit fly' (*B. tryoni* is not mentioned by name) (Benson & Voller, 1899). While Benson and Voller were unsuccessful in finding a lure, lures remained a focal point for early fruit fly workers (Jarvis, 1923, 1925*b*, 1931; Gurney, 1925; Perkins & Hines, 1933; Caldwell & May, 1943) and were recommended as control options (Jarvis, 1926*b*), although with limited initial success (Jarvis, 1925*b*). Since those early investigations, lure and kill techniques have become a standard part of the monitoring and pest management toolkit for *B. tryoni*. Two lure and kill approaches, male annihilation technique (MAT) and protein-bait spray (PBS), are particularly important and are likely to become more so as dimethoate and fenthion use is restricted.

### Protein-bait spray and bacteria

Both male and female *B. tryoni* need protein in order to sexually mature (Meats & Leighton, 2004; Perez-Staples *et al.*, 2007, 2008). In nature, *B. tryoni* is presumed to obtain the majority of its protein through feeding on leaf surface bacteria (Courtice & Drew, 1984; Lloyd *et al.*, 1986; Drew & Lloyd, 1987, 1989, 1991, Lloyd, 1991). The presence of unidentified bacteria in the diet of *B. tryoni* has been shown to enhance survival, sexual maturity and egg maturation (Drew *et al.*, 1983), while leaf surface bacteria may provide adult *B. tryoni* with at least one primary source of food (Vijayasegaran *et al.*, 1997, 2002). In contrast, however, Meats *et al.* (2009) found no nutritional benefit to *B. tryoni* of a diet including live cultures of nitrogen-fixing bacteria.

There is evidence that bacteria are spread by the flies, but it is not clear if this is part of a co-evolved system (Drew & Lloyd, 1987; Prokopy *et al.*, 1991), or happens incidentally as part of routine foraging (Raghu *et al.*, 2002). A study conducted by Fitt & O'Brien (1985) aimed to identify any symbiotic association. Bacterial isolates were collected from egg, pupal and adult stages from both wild and laboratory colonies of *B. tryoni*, but there was no consistency in bacterial genera present. In a morphological study examining the ultrastructure of *B. tryoni*'s digestive system, no evidence of intracellular symbionts was observed (Murphy, 1990; Murphy *et al.*, 1994). Whilst the wide host range of *B. tryoni* may account for some of this lack of consistency, available data do suggest that no single bacterial species is involved in a primary symbiotic relationship with the

fly, and exploitation of any symbiosis is unlikely to assist management of this pest.

With respect to more general lure and kill techniques, however, information on the fly's protein needs and foraging behaviour is relevant because artificial protein sources (generally in the form of a protein hydrolysate) are attractive to foraging flies. When mixed with an insecticide, protein can be applied as strip or spot sprays to lure and kill adult flies of both sexes (Bateman, 1972; Bateman & Arretz, 1973; McQuate, 2009). For Queensland fruit fly most information on protein-bait spray application is contained in final project reports (Lloyd *et al.*, 2000, 2003), with few formal publications on the use of the technique in the field (Jones & Skepper, 1965; Hargreaves *et al.*, 1986; Smith & Nannan, 1988; Lloyd *et al.*, 2010).

The extensive literature on *B. tryoni*-bacteria interactions adds only a little to the science underpinning protein-bait spray technology. Bateman & Morton (1981) showed that ammonia was the volatile attracting flies to protein, but this was considered unlikely by Drew & Fay (1988), who found that volatiles produced by bacteria breeding within the protein, rather than ammonia, were the likely source of attraction to flies. Within this framework they then discussed the possibility that flies were most responsive to protein when sprayed on fruiting host plants because such plants already had high bacterial loads, which 'inoculated' the protein and made it more attractive. The findings of Drew and Fay support a second paper by Morton & Bateman (1981), which clarifies their first paper by recognising that ammonia on its own is not highly attractive to flies, but is when exposed in a synergistic fashion with various amino acids and other components of protein hydrolysate.

Morton & Bateman (1981) document that most volatile chemicals from commercial protein hydrolysates are of very high molecular weight and hence very low volatility. This may be another, or alternative, reason why protein-bait sprays are most effective when sprayed on a fruiting host plant, that is flies already on a fruit host plant for other purposes, for example ovipositing or sheltering, may detect the protein volatiles from short distances away, but may have little ability to detect the protein volatiles when in other locations. Note here that detection is not synonymous with attractiveness. A chemical may have high detectability, but low attractiveness, and *vice versa*. Attractiveness of protein to female flies does vary with physiological status: protein-fed, gravid females are less active in protein foraging than immature, protein-hungry females (Prokopy *et al.*, 1991).

As a likely core tool of *B. tryoni* area-wide management (AWM), there are very significant gaps in biological knowledge underpinning the use of protein-bait

technology. With examples from international studies, these include: identifying the most attractive protein mixtures (Barry *et al.*, 2006; Yee, 2007); identifying how the physiology of the fly (e.g. prior feeding history, reproductive status, sterile/nonsterile) influences attractiveness and effectiveness of baits (Barry *et al.*, 2003; Yee & Chapman, 2005; Yee, 2006); determining where flies forage for baits and how this might be used in management (e.g. with respect to border applications) (Prokopy *et al.*, 2004; McQuate & Vargas, 2007); and determining how protein-bait sprays interact with other components of AWM (Vargas *et al.*, 2002; Stark *et al.*, 2004; Pinero *et al.*, 2009; Lloyd *et al.*, 2010). Additional to these areas which focus predominantly on the biology of the fly, the mode of actions and integration of new generation insecticides (e.g. spinosad, fipronil) into protein-bait technology for *B. tryoni* are also areas needing urgent research (see Mahat, 2009 for recent work in this area).

### Male Annihilation Technique (MAT)

#### *Cue-lure*

Males of *B. tryoni* respond to cue-lure (Drew, 1989), making *B. tryoni* one of approximately 60% of *Bactrocera* species in which the males respond strongly and positively to either cue-lure (4-(4-acetoxyphenyl)-2-butanone) or methyl-eugenol (4-allyl-1,2-dimethoxybenzene) (Drew, 1974). While methyl-eugenol occurs widely in nature, cue-lure does not, although it is chemically related to naturally occurring compounds (e.g. raspberry ketone) (Metcalfe, 1990). The possible processes associated with the evolution of fruit fly response to lures are reviewed by Raghu (2004). When mixed with an appropriate insecticide, cue-lure is an extremely effective lure and kill tool for monitoring and managing *B. tryoni* (Monro & Richardson, 1969; Bateman & Arretz, 1973; Dominiak *et al.*, 2003a). Raspberry ketone is the hydroxy equivalent of cue-lure (i.e. 4-(p-hydroxyphenyl) butan-2-one) and was discovered as attractive to *B. tryoni* by Willison in 1959 (Bateman *et al.*, 1966a): it subsequently became known in the *B. tryoni* literature as Willison's lure. The discovery that *Bactrocera* species are attracted to these chemicals is considered to have occurred independently with the discovery of Willison's lure and cue-lure in 1960 (Beroza *et al.*, 1960). Monro & Richardson (1969) subsequently confirmed cue-lure to be more attractive to *B. tryoni*. There are no publications testing the attractiveness of the formate form of cue-lure, 'Melolure™', against *B. tryoni*, although this form of cue-lure is 1.5–2 times more attractive to *B. cucurbitae* than is traditional cue-lure (Casana Giner *et al.*, 2003).

Very little work has been carried out on the functional role of cue-lure for *B. tryoni*. For other *Bactrocera* species

the male lures can enhance male mating competitiveness, act as mate rendezvous sites and afford protection from predators (see a review by Raghu, 2004). Only some of these issues have been researched for *B. tryoni*. Male *B. tryoni* forage most strongly for cue-lure in the morning (Weldon *et al.*, 2008), but peaks of foraging activity may depend on local ambient temperature (Brieze-Stegeman *et al.*, 1978). Foraging is related to sexual maturity, with sexually mature males being most responsive (Weldon *et al.*, 2008). Attraction to cue-lure by *B. tryoni* is through up-wind anemotaxis (Meats & Hartland, 1999), while the presence of cue-lure in the local environment increases *B. tryoni* flight activity (Dalby-Ball & Meats, 2000b). In a closed rainforest environment, trap catches of *B. tryoni* in cue-lure baited traps increased with increasing height (from 0.1 to 12 m), but in the open canopy environments of a eucalypt forest and citrus orchard no effect was evident in the height ranges of 0.1–12 m and 0.1–3.6 m, respectively (Hooper & Drew, 1979). As for other *Bactrocera* species, female *B. tryoni* are traditionally regarded as being nonlure responsive (Hill, 1986; Drew, 1987a), but this view is changing slightly as more data are gathered. Sexually mature, but virgin *B. tryoni* have been demonstrated to respond to cue-lure in field cages (Weldon *et al.*, 2008), leading the authors of that study to suggest that cue-lure may be associated with the mating system (acting as a mate rendezvous signal or male pheromone precursor), as has been suggested or confirmed for other cue-lure and ME responsive species (Raghu, 2004). Drew (1987a) also reported that sexually immature females of *B. tryoni* were responsive to cue-lure and he considered 2-butanone to be the chemically active component of cue-lure with respect to possible mating activities.

#### MAT

While widely used, there is little literature available on the use of cue-lure, mixed with an insecticide, as a control technology for *B. tryoni*. Bateman and colleagues have carried out the only published work in this field and demonstrated that traps baited with Willison's lure (Bateman *et al.*, 1966a) and cue-lure (Bateman *et al.*, 1966b) could adequately suppress *B. tryoni* populations in isolated towns, although the impact was better early in the season, if used in conjunction with a protein bait, and applied over more than one year. Bateman & Arretz (1973) also applied cue-lure blocking, along with protein-bait sprays, in the successful eradication of *B. tryoni* from Easter Island, but the relative effectiveness of the different control approaches was not reported.

While commercially available MAT devices are now available for *B. tryoni* population suppression, there is

a substantial shortfall in fundamental knowledge if the technique is to be routinely incorporated into on-farm or area-wide management systems. No formal studies have been undertaken on the linear distance of attraction of cue-lure to *B. tryoni*, but some sampling efficiency estimates are available. Fletcher (1974b), using mark-recapture data and traps placed either 80 m apart in a grid, or 400 m apart in line, states that 'pairs of cue-lure traps spaced 0.4 km apart along a trap line in sclerophyll bushland caught approximately 8% of the males per week in the surrounding area of 0.16 km<sup>2</sup>'. Similarly, Monro & Richardson (1969) report that 'Funnel traps baited with cue lure and malathion and spaced 0.4 km apart in a square grid pattern caught 4.1% of newly emergent flies and 9% of mature flies (2–3 weeks old) released in the centre of the grid.' There is no inherent justification in these papers why 400 m was chosen as a distance for analysis but, what is valuable about these papers, is that the capture rate for mature flies (8% and 9%) is remarkably similar and at least provides an experimental basis for the trapping efficiency for a cue-lure grid of 400 m. Meats (1998a,b) collates data from a number of different trapping programmes and, applying several modelling approaches, concludes that a 1000-m trapping grid is significantly less effective (approximately one-sixth) than a 400 m grid, although this is highly dependent on the size of the fly population and the source of the flies with respect to individual traps within the grid.

A critical, un-researched issue is that of variation in trap efficiency. While it is documented that different numbers of flies can be caught in different areas of a local environment (see section below on foraging), or at different times of the year (Fletcher 1973, 1974a, b, 1975), it is not clear how much of this variation may be because of variation in trap efficiency versus differences in absolute fly numbers. Where trap efficiency varies spatially or temporally, differences in trap catch may reflect true change in the population size, an error associated with the trap's ability to catch flies, or some combination of the two. Cue-lure traps are strongly influenced by weather conditions (Monro & Richardson 1969; MacFarlane *et al.*, 1987) and this influences their efficiency, but how this variation impacts on our ability to accurately measure local fly populations over space and time is unknown.

#### Female lures

Sexually mature and mated female *B. tryoni* do not respond to cue-lure (Drew, 1987a) and there are no effective lures for female *B. tryoni* currently commercially available. Caldwell & May (1943) developed a liquid lure, based on orange and ammonia, which attracted both



female and male *B. tryoni* and this was used extensively by May in later work (May, 1958, 1961*a,b*, 1963; May & Caldwell, 1944): the lure is commonly known as May's orange-ammonia lure. Unfortunately, while valuable in select experimental situations, the lure is weakly attractive and has a short life-span, and traps using the lure need to be cleared at least weekly (preferably sooner) as flies rapidly decay. Liquid protein used in traps has similar problems, as well as attracting nontarget species, although current research overseas is targeting more specific protein attractants (Heath *et al.*, 2009). Dominiak (2006) reviews the use of liquid protein traps, and to a lesser extent liquid ammonia-based lures, for *B. tryoni* monitoring. No researchers have yet published on the potential for fruit-based, chemical attractants for female *B. tryoni*, an approach that is being pursued internationally for other pest tephritids (Malo *et al.*, 2005; Gonzalez *et al.*, 2006; Rasgado *et al.*, 2009*b*).

### Colour traps and fruit mimics

For the tephritids, fruit mimics offer a potentially useful lure and kill approach for monitoring and population reduction (Economopoulos, 1989; Katsoyannos, 1989). Perhaps the best-known example of this is for apple maggot fly, *Rhagoletis pomonella* (Walsh), where fruit-mimicking red spheres, often combined with artificial, plant-derived semiochemicals, are used commercially for pest management (Duan & Prokopy, 1992, 1993, 1995; Reynolds & Prokopy, 1997). Fruit mimics have also been developed or researched for other pest tephritids, including *Neoceratitis cyanescens* Bezzi (Brévault & Quilici, 2007) and *Ceratitidis capitata* (Wiedmann) (Katsoyannos & Hendrichs, 1995).

The potential for fruit mimics to be used in *B. tryoni* monitoring or control has received scant attention. The fly does show distinct colour preferences, but these vary depending on the way they are offered, with contrast, grain size and silhouette all influencing response (Meats, 1983*b*). When exposed on flat sticky traps, colours most closely associated with the wavelength of green foliage colour (550 nm) (daylight fluorescent (DF) Saturn Yellow, and then Lime, Blaze Orange and Emerald) were most attractive to *B. tryoni* and caught more males than females (Hill & Hooper, 1984). The same study found that the shape of the flat surface also influenced capture, with circular and square traps capturing more flies than triangular, rectangular and diamond shaped traps. Further, Hill and Hooper reported that *B. tryoni* response to colour was quite different if exposed on a sphere: more flies were caught on black spheres than yellow or green spheres. Drew *et al.* (2003), working exclusively with spheres, reported both sexes of *B. tryoni* as most

responsive to blue or white spheres over red, orange, yellow, green or black spheres. Weldon & Meats (2007) found no difference in the effectiveness of yellow versus black spheres. Sphere size was also found important by Drew *et al.* (2003), with 50-mm-diameter spheres proving more attractive than clusters of 15-mm-diameter spheres. Further, colours became more attractive to flies when the ultraviolet-reflectance level was enhanced, which Drew *et al.* interpreted as mimicking the effects of an ultraviolet-reflecting waxy bloom found on some native *B. tryoni* hosts. The reasons for the discrepancies between results of some of the above papers are not easy to explain. The research itself is relatively straightforward to do and so experimental error is unlikely. Rather, the mix of results probably reflects Meats' (1983*b*) finding that colour response is variable and dependant on an array of factors influencing how the colour is exposed to the fly.

The addition of fruit odours to fruit-mimicking coloured spheres has been trialled only once for *B. tryoni* (Dalby-Ball & Meats, 2000*b*). The data showed increased alighting of flies on fruit mimics when a chemical odour was associated with the mimic. Semiochemicals associated with *B. tryoni* host location and oviposition are covered later in this review, but in general are poorly studied. Hill & Hooper (1984) found that when cue-lure was added to flat sticky traps, the lure response dominated over colour influences. Based on research on other flies, fruit mimics offer potential as, at least, a monitoring device for *B. tryoni* which may be independent of male cue-lure traps. As a research field, however, nearly everything remains to be performed.

### Area-wide management and areas of low pest prevalence

Area-wide Management (AWM) involves the suppression of a pest population over large geographical areas (greater than individual farms or fields), with the size of the management area ideally defined by criteria based on the biology of the pest (e.g. dispersal distance, sequential host use, etc.) (Faust, 2008). In addition to knowing the biology of the fly within an orchard or commercial crop, and direct pest management tools, it also requires knowledge of how a pest moves within a district and between districts, what hosts support the pest outside of commercial cropping systems, and when and where the fly occurs when not in those cropping system. Hendrichs *et al.* (2007) provide an excellent recent review of the concept of AWM in entomology, while Jessup *et al.* (2007) discuss the generalities of AWM of fruit flies in Australia and Lloyd *et al.* (2010) detail a specific case of *B. tryoni* AWM in the Central Burnett district of SE Queensland. The knowledge required to operate an effective AWM programme

is very similar to that required to establish a Fruit Fly Free Zone or an Area of Low Pest Prevalence for fruit fly (ALPP-FF) (as defined by ISPM No. 30 (IPPC, 2008)). In addition to certain technical requirements, biological elements that need to be considered when establishing an ALPP-FF include: 'the number of [fly] generations per year, host range, temperature thresholds, behaviour, reproduction and dispersion capacity... host diversity and abundance, host preference and host sequence' (IPPC, 2008).

### Habitat use

'Habitat' is a fundamental concept in ecology, however, it is recognised that the term is used in at least two ways. Habitat can be used in a generic sense to describe the type of environment in which we might go to look for something, for example 'this bird lives in a rainforest habitat'. Alternatively, habitat may be used much more specifically to describe the environmental requirements of individuals within a species, eg 'the habitat requirements of species X are...' (Hengeveld & Walter, 1999; Mitchell & Powell, 2003; Walter, 2003; Walter & Hengeveld, 2000).

In the generic use of the term habitat, *B. tryoni* is traditionally considered an endemic insect of the tropical and subtropical east coast rainforests, where many of its native hosts are found (Drew, 1989). *Bactrocera tryoni* is now, however, rare in rainforests compared to other habitat types. In a study in the Cooloolo coastal forest of south-east Queensland, *B. tryoni* was, on average, more than twice as abundant in peripheral sites than in the rainforest (Zalucki *et al.*, 1984). In a simultaneous sampling of rainforest, eucalypt forest and suburbia, Raghu *et al.* (2000) and Ero (2009) found the fly to be rare in rainforest, but highly abundant in suburban sites. That *B. tryoni* is highly abundant in urban areas has been documented or suspected by other authors because of large numbers of host plants and high local humidity (Fletcher, 1974b; Mavi & Dominiak, 1999; Mavi & Dominiak, 2001; Dominiak *et al.*, 2006), but its rarity in its supposedly endemic forest habitat is less commonly noted.

At the landscape level, *B. tryoni* collected more frequently around water courses than in less sheltered or open areas (Fletcher, 1974a; Courtice & Drew, 1984; MacFarlane *et al.*, 1987) and it has been postulated that watercourses direct movement of flies across the landscape (Fletcher, 1989b), but the evidence for this is circumstantial. Fly foraging in the landscape may be linked to tree shapes or silhouettes as there is some evidence they will actively orientate to tree silhouettes (Meats, 1983b). At the microhabitat level, only Worsley *et al.* (2008) have attempted to correlate trap catch levels

with local site attributes. While their data set is too small to provide firm outputs, their GIS-based approach should be pursued using larger datasets.

The habitat specific requirements of *B. tryoni* include water, food (especially proteins and sugars), shelter, mates and oviposition sites (Bateman, 1972; Fletcher, 1987). Little is known about how *B. tryoni* forages in the environment for these resources and how this translates to local dispersion patterns of the fly. Using *B. tryoni* largely as his model system, Drew and colleagues (Drew *et al.*, 1983; Courtice & Drew, 1984; Drew, 1987a; Drew & Lloyd, 1987, 1989, 1991; Prokopy *et al.*, 1991; Drew & Romig, 2000; Drew & Yuval, 2000) have argued strongly that the larval host plant is the 'centre of activity' for fruit flies, with all activities (maturation, feeding, mating, oviposition and larval development) occurring there. While oviposition must occur at the larval host plant, the evidence for other behaviours being entirely restricted to the host plant is largely circumstantial and may reflect inadequate sampling elsewhere. Even if most behaviours are restricted to the host plant, how flies disperse between plants, choose between one plant and another, and behave when no host plants are fruiting, are still critical questions for AWM and ALPP-FF. These issues are developed further below.

### Dispersal and movement

#### *Dispersal distance*

Dispersal is considered an important characteristic of *B. tryoni*, with both immigration and emigration playing a role in local population dynamics (Sonleitner & Bateman, 1963; Bateman & Sonleitner, 1967; Fletcher, 1973). High rates of dispersion in this species are considered an evolved behaviour associated with finding suitable hosts in rainforest (Fletcher, 1974a). Using the mark/release/recapture technique, considerable effort has been made into determining how far *B. tryoni* can disperse. Dispersal distance has implications for the setting of quarantine restrictions. While a single *B. tryoni* was recorded at 94 km from a release point by MacFarlane *et al.* (1987), this is considered highly unusual (Dominiak *et al.*, 2003b), with most reported dispersal being over much shorter distances of only a few hundred meters to a few kilometres (Bateman & Sonleitner, 1967; Fletcher, 1973, 1974a; Bateman, 1977; MacFarlane *et al.*, 1987; Dominiak *et al.*, 2003b; Weldon, 2005; Meats *et al.*, 2006; Weldon & Meats, 2007; Weldon & Meats, 2009). Modelled analysis of *B. tryoni* trap data similarly not only reflects relatively low dispersal distances, but also reinforces the problems of detecting low populations of flies (Meats, 1998b, 2007; Meats *et al.*, 2003b, 2006; Meats & Edgerton, 2008).

### Role of wind

Fletcher (1974a) and Dominiak *et al.* (2003b) found no relation between prevailing wind and recaptures of marked flies, while in contrast MacFarlane *et al.* (1987) found that strong south westerly winds preceded long-distance recoveries in areas north-east of the release point. MacFarlane *et al.*, however, also detected long-distance travel in the absence of strong winds, indicating multiple means of such dispersal. Male *B. tryoni* have a greater tendency to move upwind than do either mated or virgin females (Pike & Meats, 2003) and so it is possible that the sexes separate somewhat after emergence, although why this should be case, or further detail, is unknown.

### Host availability

Availability of hosts influences the flight distance and long-distance flights are more likely if there is low fruit abundance in the surrounding area (Fletcher, 1974a). Dispersive flights, in which *B. tryoni* travels between habitats, are likely to depend on the timing of local fruit availability. However, the relationship between timing of fruit availability and movement is not clearly defined. It has been reported that flies from distant habitats enter a fruit rich locality (e.g. an orchard) sometime after fruit is first available and the length of time the flies remain at the site is principally determined by the amount of fruit suitable for oviposition (Fletcher, 1973, 1974a). On the other hand, mature adult flies may move away from a previously suitable habitat under conditions of lower fruit availability, low temperatures and dryness, or if they are seeking over-wintering sites (e.g. eucalypt forest) (Fletcher, 1973, 1974a; Sonleitner & Bateman, 1963). When undertaking prewinter dispersal, male *B. tryoni* are more likely to leave previously occupied habitats than females and this may be because the females are attracted by local fruit trees which are going to have ripe fruit available in the coming spring, that is females may be more influenced by future suitability of a site for oviposition than shelter (Fletcher, 1979). Irrespective of the immediate suitability of a location for breeding, postteneral flies move away from their emergence sites (Fletcher, 1973). However, Fletcher notes that these postteneral flies re-enter breeding localities when they are sexually mature if fruits are available and the weather favourable. Regular dispersal from breeding sites is one reason why there appears to be very little or no genetic structuring of *B. tryoni* in its endemic tropical range (Cameron *et al.*, 2010; Yu *et al.*, 2000; Yu *et al.*, 2001; Gilchrist *et al.*, 2006), while in inland southern regions, where the fly is incursive, fly populations are best considered as source-sink with reinvasion from

source populations and regular local extinction (Gilchrist *et al.*, 2006).

### Host use

While fruit flies use fruiting host plants primarily for oviposition, they also use them for other purposes including sites for adult resting, shelter, feeding and mating (Drew, 1987a; Drew & Lloyd, 1987). While nearly all research on how fruit flies find and utilise hosts is related to fruit selection for oviposition, some work has been performed on other aspects of host use by fruit flies. For example, plant architectural traits are known to influence the selection of plants for resting in *Bactrocera cacuminata* (Hering) (Raghu *et al.*, 2004) and for mating in *Ceratitidis capitata* (Shelly & Whittier, 1995; Kaspi & Yuval, 1999). With the exception of Drew and colleagues' work with bacteria/fly interactions (discussed in preceding sections), such work is lacking in *B. tryoni* and so the following section of this paper focuses solely on *B. tryoni*'s host use with respect to oviposition. This does not, however, negate the importance, or need, for research on other aspects of host use by *B. tryoni*.

### Adult fecundity

Adults adjust the number of eggs they lay depending on the ovariole status, fruit size, environmental conditions and time of day (Fletcher, 1987). *Bactrocera tryoni* has two ovaries, each with between 35 and 45 ovarioles (Anderson & Lyford, 1965; Fitt, 1990a), making it a more prolific egg producer than many other tephritids (Fitt, 1990b; Fletcher, 1987). Egg production per female per day is variable, with upper limits ranging from 80 (Yonow *et al.*, 2004) to 100–120 (maximum 160) (A. Jessup, personal communication) eggs per female per day. Oviposition rate is likely to be influenced by host plant and environmental factors, particularly temperature (Yonow & Sutherst, 1998). The eggs of *B. tryoni* are smaller than those of the closely related *B. jarvisi* and *B. tryoni* lays them in smaller batch numbers, giving it a competitive advantage in locating and exploiting patches of fruit under field conditions (Fitt, 1990a). Cool winter temperatures trigger resorption of the contents of developing follicles (Fletcher, 1975, 1986; Meats & Khoo, 1976), thereby reducing the potential number of eggs available for oviposition.

### Oviposition behaviour

The specific actions of *B. tryoni* oviposition behaviour were recorded in detail by Pritchard (1969), who described the movements of the head and ovipositor of the mature

female on the surface of both natural and artificial fruits. The process, which occurs in the daytime, involves the adult female dabbing its labella on the fruit surface and piercing the fruit cuticle with the ovipositor once a suitable oviposition site has been detected. Eggs are laid in batches of 4–20 through an oviposition tube, the ovipositor is then withdrawn and the process repeated at another suitable site. On selecting an oviposition site, gravid females also exhibit aggressive protective behaviour and drive away other females, in turn reducing population pressure. In contrast, Prokopy *et al.* (1999) reported facilitation in oviposition behaviour of gravid female *B. tryoni*. The authors showed that if a female arrives at an oviposition site and another female is in the act of oviposition, the new female is more likely to begin ovipositing than she would in the absence of another ovipositing female.

#### Host range

*Bactrocera tryoni* has a very broad host range of both commercial and wild fruit and vegetables (Hancock *et al.*, 2000), making it one of the most polyphagous of all the tephritids. The fly has been recorded on 117 hosts, including commercial crops such as citrus, nuts, stone and pome fruit, tomato, banana and coffee (May, 1953, 1957, 1960; Hancock *et al.*, 2000); the relative suitability of these hosts has rarely been compared in a systematic way. Bateman (1991) lists fruits in different levels of preference for fruit flies, but the scientific quantification behind this listing is unavailable. Drew (1976) and Drew *et al.* (1978) report that pineapple and strawberry are the only two commercial fruit crops of any significance which are not hosts, however, it is now recognised that strawberry is a host (PIRSA, 2006). Jessup & McCarthy (1993) reported that although cucurbits were not previously recognised as hosts of *B. tryoni* (O'Loughlin, 1975), females could oviposit and larvae subsequently develop under laboratory conditions in those plants. Grapes have also been previously listed as a poor host for *B. tryoni*, yet in the laboratory table grapes can support the insect through to the adult stage (Jessup *et al.*, 1998) and recent outbreaks in the Hunter Valley of New South Wales have seen high levels of damage to wine grapes (Loch, 2008). *Bactrocera tryoni* has also been recorded on 60 wild hosts from 25 plant families (Drew, 1989; White & Elson-Harris, 1992).

Although *B. tryoni* has a diverse host range, most fundamental studies on the insect's host–plant interactions have focused on a relatively small group of economically important fruit crops and, even within this group, very little research has compared varietal differences to determine relative susceptibility to the pest to assist with potential breeding programmes for resistance. In a laboratory study comparing *B. tryoni* oviposition

preference to three tomato cultivars, host plant variety influenced peak oviposition period, ovipositional preference and offspring performance and this may have been because of both chemical and physical properties of the host (Balagawi *et al.*, 2005).

Host range may potentially be influenced by abundance of fruit in the environment. Using potted orange trees, Dalby-Ball & Meats (2000a) showed that by increasing the abundance of trees in a given area wild female flies visited more trees and increased their duration on each plant. No studies of this type have, however, been conducted in the presence of a mosaic of multiple host species, or with hosts other than citrus or pome fruit, so it is not clear how abundance of different fruit types might influence host searching and selection.

#### Host selection

Olfactory, tactile and visual characteristics of fruit, including chemical, nutritional and physical properties, as well as size, colour and shape, influence oviposition site selection by female *B. tryoni* (Prokopy, 1968; Bateman, 1972; Fletcher, 1973, 1974b, 1987; Katsoyannos, 1989). Most tephritid fruit flies oviposit in ripe or overripe fruit and *B. tryoni* is thought to be no exception. *Bactrocera tryoni* will rarely oviposit into unripe fruit, although this assumption is based on testing of only a limited host range (Eisemann & Rice, 1985). Direct observation, however, suggests that *B. tryoni* will oviposit into unripe fruit in the field, a behaviour perhaps dependent on fruit type, pest pressure and existing fruit damage (H. Fay, O. Reynolds, A. Jessup, personal communication). Other *Bactrocera* species, such as *B. dorsalis*, can oviposit into unripe fruit (Rattanapun *et al.*, 2009) and this ability needs to be investigated more rigorously for *B. tryoni*. Acceptance of a particular host plant fruit as an oviposition site may also depend on prior experience of the gravid adult female. Prokopy & Fletcher (1987) provided evidence that prior exposure to one fruit type (pear) led to a greater propensity for *B. tryoni* to oviposit in that fruit compared to other fruit types (tomato and grape).

#### Fruit physical properties

Little information has been published on the physical properties of fruit skin and how this may affect the detection and successful penetration of a suitable oviposition site. Early studies involved mechanical puncturing of apple fruit which resulted in rapid oviposition (Allman, 1939). The puncture lesion may allow release of volatiles which aid location, but what volatiles are involved and how this may vary with fruit type or variety has received very little attention.



Stange (1999) found that releases of CO<sub>2</sub> from blemished fruit stimulated oviposition. Eisemann & Rice (1989), in controlled laboratory studies using an artificial 'fruit' layer in the form of Parafilm, determined that the female's ovipositor sensilla are stimulated to oviposit by either a thick (2 mm) surface layer, or a thinner surface layer (<0.5 mm) with underlying moisture. In real systems, however, there is a paucity of data on the impact of fruit pericarp thickness and texture on *B. tryoni*'s host use for oviposition across its wide host range.

*Bactrocera tryoni* prefer to oviposit in fruit that is soft enough to allow oviposition punctures, or in existing lesions in the fruit skin (Allman, 1939; Pritchard, 1969). That pericarp toughness is important is suggested in a study where cherry tomatoes, with a tougher pericarp, were not used for oviposition in contrast to larger tomato fruit varieties with relatively soft pericarps (Balagawi *et al.*, 2005). Modifying the physical properties of fruit could potentially be used in breeding programmes for the development of fruit fly resistant cultivars. Another potential management option which could also be exploited is use of spray applications which deter females from ovipositing. Studies using mineral oil applications on tomatoes, for example, have shown a marked reduction in oviposition probing (Liu *et al.*, 2002; Nguyen *et al.*, 2007) and research in this area is ongoing.

#### *Fruit chemical properties*

Adult female tephritids possess olfactory, gustatory, hygro, thermal, photo, mechano and chemo-receptors (Rice, 1989), with the structure and specific function of at least some of these receptors elucidated (Hull, 1998; Hull & Cribb, 1997, 2001*a,b*). From studies using artificial fruit, olfactory stimuli are known to attract *B. tryoni* to fruit prior to oviposition (Fowler, 1977).

Studies to identify the long to medium range chemical attractants involved with *B. tryoni* host location are relatively limited and have primarily focused on single volatile components of selected fruit hosts, despite the fact that fruit commonly produce complex volatile mixtures that may include over 150 compounds (Lalel *et al.*, 2003). Ethylene is a common hormonal constituent in ripening fruit. As 2-chloroethanol simulates the effect of ethylene in ripening fruit, the influence of 2-chloroethanol on *B. tryoni* was examined in laboratory studies (Fletcher & Watson, 1974). Ethylene was found to attract gravid females to fruit and to stimulate their oviposition response in apples at low concentrations ( $\leq 1\%$  concentration) and to deter oviposition at higher concentrations. Isoamyl acetate and guava fruit pulp have also been shown to attract adult females (Dalby-Ball & Meats, 2000*b*). Further characterisation of the complex

mixture of headspace volatiles of host fruit for *B. tryoni*, using olfactometers and fielding testing, coupled electro-antennogram/gas chromatography (EAG/GC), or new generation 'electronic nose' (Lebrun *et al.*, 2008), should enable the identification of compounds which either attract or deter gravid females from the host.

Short-range chemotactile cues are reported to be involved in the oviposition process, yet again surprisingly little data exist on the chemicals that trigger *B. tryoni* oviposition. Pritchard (1969), using a range of fruit juices, showed that greater numbers of eggs were oviposited in cucumber juice, which is a very poor host, compared to apple juice which is considered a more suitable host. Studies conducted to determine chemical cues that may influence oviposition response in *B. tryoni* cover a diverse range of compounds including 2-chloroethanol (Fletcher & Watson, 1974), fructose (Eisemann, 1985), 2-butanone, n-butyric acid, carbon sesquiterpene,  $\alpha$ -farnesene (Eisemann & Rice, 1992) and carbon dioxide (Stange, 1999). Oviposition stimulants such as fructose have been shown to be effective at between 4 and 50 mM concentration in stimulating oviposition into an artificial membrane, whilst the presence of calcium chloride appears to deter oviposition (Eisemann, 1985).

The antennal response to volatile cues is important in host plant location. Although the morphology of antennal sensilla of adult *B. tryoni* has been described (Giannakakis & Fletcher, 1985; Hull, 1998; Hull & Cribb, 1997) specific chemoreceptor functions have not yet been fully characterised. Using an electro-antennogram, olfactory neuron receptor types have been identified in gravid females that respond to methyl butyrate, 2-butanone, farnesene, carbon dioxide, ethanol, n-butyric acid and ammonia (Hull & Cribb, 2001*a,b*).

Most chemoecology studies conducted to date have focused on specific fruit hosts or single volatiles under laboratory conditions and do not consider the host plant nutritional status, variety or whether a complex mix of attractants are involved. Studies on volatile and chemical composition of a broader range of host plants, and their varieties under different environmental and management conditions, could potentially enable identification of the fundamental volatile and gustatory cues involved in both host plant selection and oviposition response by gravid females. Such information may be a key to development of resistant crops or new attractants and is being actively researched overseas (Malo *et al.*, 2005; Rasgado *et al.*, 2009*a*).

#### *Oviposition deterrence*

While there are limited published trials on *B. tryoni* host plant preference, one conducted by Fitt (1986) indicates

that some fruit may have deterrent characteristics. When comparing *B. tryoni* oviposition preference on seven fruit types, females avoided oviposition in *Solanum mauritianum*, despite it being recorded as a suitable host for larval survival, suggesting that this fruit is protected by an oviposition deterrent. Further comparative studies on other host plant types may give further insights into possible deterrent traits, which in other herbivores may include secondary plant chemicals and morphological traits (Bernays & Chapman, 1994).

*Bactrocera tryoni* prefer to oviposit in fruit in which larvae are not already present (Fitt, 1984). Although not assessed, Fitt hypothesised the discriminatory ability of the female may be because of chemical changes in the fruit as a result of larval presence, causing a short-range olfactory response. Identification of such volatile compounds could potentially lead to the development of oviposition inhibitory chemicals. The presence of other fruit fly species and the potential for competition between species for oviposition sites in the same habitat has rarely been considered. Gibbs (1967) compared *B. neohumeralis* with *B. tryoni* and found that even though the two share the same preference for some host plants, competition for oviposition sites appeared unimportant in deterring one species or the other from using a host. This type of study, however, would need to be conducted under a range of population pressures and with different species interactions to draw firm conclusions.

#### Larval development

Following oviposition, the larvae can spend up to 4 weeks feeding and developing in fruit. The external and internal morphology of *B. tryoni* immature stages have been well characterised (Exley, 1955; Anderson, 1962, 1963*a,b*, 1964*a,b*; Elson-Harris, 1988). Larval development rate and success varies between fruit species and is affected by fruit maturity, but this has only been tested on a limited range of host fruits. Eggs deposited in apples exhibit reduced hatch and delayed larval maturity and development compared to pears (Bateman, 1968). In a study comparing six apple varieties at different states of fruit maturity, late season varieties showed greater larval mortality (Bower, 1977). Larval mortality and development rates also depend on temperature (O'Loughlin, 1964; Bateman, 1968; Meats, 1983*a*, 1984, 1987; O'Loughlin *et al.*, 1984; Meats & Fitt, 1987), larval density, fruit suitability and maturity, but less so on moisture as larvae are located in stable moist environments (Meats, 1989*b*). In one study, Bower (1977) found that larval mortality was significantly lower in picked fruit over unpicked fruit, but this work has never been pursued, despite its obvious implications for host status testing. The quality of the

larval environment not only impacts on the larvae, but in other tephritids has been shown to directly impact on the emergent adult flies (Dukas *et al.*, 2001; Kaspi *et al.*, 2002; Nestel *et al.*, 2004). This has not been studied in *B. tryoni* and warrants investigation.

#### Natural enemies

Natural enemies have rarely been used in the active management of *B. tryoni* and very little is known about them. The best-known natural enemies of *Bactrocera* species are opiine braconids (Hymenoptera: Braconidae: Opiinae). Opiines have been used extensively as classical biological control agents (Sime *et al.*, 2008), but more recently they have also been used in augmentative and inundative releases (Montoya *et al.*, 2000), sometimes in conjunction with other techniques such as SIT (Rendon *et al.*, 2006). It is considered that their use in conjunction with other techniques is the most promising way forward for fruit fly parasitoids (Gurr & Kvedaras, 2010).

#### Parasitoids

Despite having a native fruit fly parasitoid fauna in Australia (Carmichael *et al.*, 2005), a fact recognised by the earliest fruit fly workers (Tryon, 1892; French, 1910; Gurney, 1910), exotic opiines were liberated into Australia for *B. tryoni* control during the 1930s (Gurney, 1936; Allman, 1939) and then again in the 1950s (Snowball *et al.*, 1962*a,b*; Snowball & Lukins, 1964; Snowball, 1966). A comprehensive review of classical biological control releases targeted against *B. tryoni* is provided by Waterhouse & Sands (2001). With the exception of postrelease work carried out by Snowball (Snowball, 1966; Snowball & Lukins, 1964), there has been no comprehensive published data on the influence of braconid parasitism, either native or introduced, on *B. tryoni* populations. Snowball (1966) concluded that while *Fopius arisanus* (Sonan) (introduced as *Opius oophilus* Fullaway) was well established after liberation, it was exerting no noticeable control on *B. tryoni*. He made similar conclusions for other native and introduced parasitoids, as did Bateman (1968) when summarising the Wilton orchard study. If judged by the subsequent lack of published research, this lack of support appears to have put a damper on fruit fly parasitoid research in Australia for nearly 40 years. Snowball's interpretations of his own data do, when relooking at the figures, seem a little surprising, as parasitism of some samples were as high as 78%, although most were much lower at 20% or less. Lloyd *et al.* (2010) record 7.4% pupal parasitism of *B. tryoni* in backyard fruit in the Central Burnett, which supports Snowball's and

Bateman's conclusions. Nevertheless, *B. tryoni* parasitism rates of greater than 50% have been recorded by other authors, including French (1910), Gurney (1910) and Gibbs (1967). Eight opiine braconids, either native, or exotic and permanently established, are now known from *B. tryoni* in Australia. These are: *Diachasmimorpha kraussii* (Fullaway), *D. longicaudata* (Ashmead), *D. tryoni* (Cameron), *Fopius arisanus*, *F. schlingeri* Wharton, *Opius froggatti* (Fullaway), *Psytallia fijiensis* (Fullaway) and *Utetes perkinsi* (Fullaway) (Carmichael *et al.*, 2005).

Only in the last decade has there been renewed interest in the fruit fly parasitoids. State Department researchers have cultured wasps and some small experimental inundative releases have been made (A. Jessup, E. Hamacek, personal communication) and one major initiative in parasitoids is underway in New South Wales (O. Reynolds, personal communication). Australian parasitoids have also been exported and data accumulated as part of off-shore biological control programmes (particularly for *D. kraussii* and *D. tryoni*), while a number of postgraduate research programmes have also been completed (Rungrojwanich, 1994; Quimio, 2000; Carmichael, 2009; Ero, 2009; Harris, 2009; Pratt, 2009). This research shows that while species such as the native *D. kraussii* and the introduced *F. arisanus* can be successfully reared and will parasitise *B. tryoni*, including irradiated *B. tryoni* (Harris, 2009; Pratt, 2009), this does not automatically make them suitable for all preharvest control uses. For example, after studying the host location mechanisms of *D. kraussii*, Ero (2009) concluded that inundative releases of this parasitoid would only be suitable for use in 'mopping-up' fruit fly populations after commercial harvest had finished, and probably only in selected crops. This was because the wasp orientated only to infested fruit of some fruit species (e.g. tomato but not zucchini), and appeared in an orchard only after adult fruit flies were present. The wasp did not orient to uninfested fruit (Ero *et al.*, in press a), it did not routinely orientate to adult flies, and it did not orientate equally to all fruit types offered, even when infested by the same maggot species. In contrast, however, the wasp could be used as part of an integrated, area-wide suppression programme, so long as it oriented to the dominant crop types in the target region (Ero *et al.*, in press b). The wasp could also be used to suppress *B. tryoni* populations breeding in noncommercial fruit sources (if that was commercially viable). Similar research with *F. arisanus* has highlighted that host utilisation strategies are not straightforward in that species either (Quimio & Walter, 2001). In addition to basic host location and utilisation data, biological data for the majority of Australian fruit fly parasitoids is almost entirely lacking (but see Rungrojwanich & Walter, 2000a,b; and off-shore work by Messing & Ramadan (2000); Duan &

Messing (1997, 2000a,b); and others). Basic biological data on host range, wasp longevity, reproductive strategies, food and shelter requirements, etc. will be needed if wasps are to be used for conservation, augmentative or inundative biological control (Bellows & Fischer, 1999). At a population level, with the exception of limited work reported by Snowball (references above), we also have no detailed knowledge of the current distribution of Australian fruit fly parasitoids, or their changing spatial and temporal abundance within their distributions.

#### *Other natural enemies*

Parasitoids are not the only natural enemies of *B. tryoni*. Drew (1987b) has argued strongly that in natural systems vertebrate frugivores play a large role in the reduction of fruit fly numbers, a theory which was directly tested and subsequently supported by Wilson (2008). While Drew's original work was on fruit flies other than *B. tryoni*, and in rainforest ecosystems, the role of vertebrate frugivores in controlling *B. tryoni* in noncrop plants and feral crop plants deserves further research. Calls to remove feral crop plants in a cropping district as part of area-wide management may be premature if 60–80% or more (Drew, 1987b; Wilson, 2008) of the fruit (and hence any resident maggots) are consumed by birds or small mammals. Additional to vertebrate predation, Bateman (1968) refers to 10% *B. tryoni* pupal mortality being caused by ants in the Wilton orchard, but no experimental data are provided to support this claim. Ants are known to be important prepupal/pupal mortality agents in other fruit fly systems (Bigler *et al.*, 1986; Aluja *et al.*, 2005; Urbaneja *et al.*, 2006) and more research needs to be conducted on them in Australia, including their potential use as deterrents or mortality agents of adult flies (Peng & Christian, 2006; Van Mele *et al.*, 2009).

Two other groups of natural enemies are also reported from *B. tryoni*, these being a strepsid parasite, *Dipterophagus daci* Drew & Allwood (Strepsiptera: Dipterophagidae) (Drew & Allwood, 1985) and a mortality causing cytoplasmic inclusion virus (Moussa, 1978). What impact, if any, these organisms have on *B. tryoni* individuals in nature is unknown.

#### Conclusions

Queensland fruit fly management has, over the last several decades, been in the enviable position of having a number of highly effective control strategies. In the southern states the large area-free zone has provided market access opportunities for growers in the zone, as well as providing significant additional support for growers in the adjoining buffer regions, where suppression

programmes occur. In endemic areas where fly pressures are higher, very effective pesticides for preharvest management and postharvest treatment have also meant that Queensland fruit fly has been highly manageable. This situation is, however, changing dramatically and rapidly. The anticipated loss of dimethoate and fenthion, as pre and postharvest treatments for fruit with edible peel, will dramatically affect growers in all regions, particularly in tropical and subtropical horticultural production areas.

With the loss of easily applied chemicals, significantly more effort will need to be applied to developing true integrated pest management approaches for this insect. While the well-known Central Burnett citrus example (Lloyd *et al.*, 2000, 2007, 2010) demonstrates that flies can be managed using an integrated approach, the flip side of this example is that it was built upon nearly a decade's work in one tightly defined production area for a commodity of relatively low host status. The issue thus becomes how practical is it to develop similar management packages for all fruit fly affected production areas and the answer is, with our current state of knowledge, very challenging.

Australian horticultural producers are currently facing a crisis very similar to that faced by Australian cotton growers in the mid-1980s. At that time the cotton industry was similarly faced with dominant key pests (i.e. *Helicoverpa* spp.) which were highly mobile, highly polyphagous on both crop and native plants, endemic and widely distributed (Zalucki *et al.*, 1986); substantial restrictions on insecticide usage had to be substantially curtailed (because of resistance management and environmental issues); and production areas ranging from tropical to temperate – all situations which are highly analogous to the current Queensland fruit fly problem.

The cotton industry made substantial progress toward solving its insect pest problems through a coordinated research programme that included the State government research agencies, CSIRO and the universities and focused not just on issues of direct pest management, but also developed in-depth understanding of *Helicoverpa* spp biology, host–plant interactions, ecology outside the cropping system, etc. (Zalucki, 1991). This allowed the development of fundamental knowledge that could then be applied across different cropping regions and crops, plus more sophisticated control approaches: *B. tryoni* researchers need to do the same.

What do fruit fly pest managers have to work from? There are positives. The availability of spinosad-based protein-bait sprays and parapheromones provides organic, as well as conventional growers with control options for *B. tryoni* which are not available for many other pests. SIT, particularly if fully supported in operations and research, should continue to play an

important role. Having these options, even with the loss of cover sprays, is fortuitous and provides a sound base from which to develop more effective fruit fly management. The use of attractants such as protein and parapheromones for delivering chemosterilants, biopesticides or translocatable pesticides is an area that is now being considered for other tephritids (Navarro-Llopis *et al.*, 2004, 2007) and, if applied to *B. tryoni*, potentially could deliver results similar to those achieved through SIT (even if slower) and overcome the cost of rearing flies and quality/competitiveness issues.

Based on where *B. tryoni* management is likely to go (i.e. greater reliance on areas of low pest prevalence, systems approaches and the use of lure and kill management techniques), and our current level of knowledge as presented in this review, we recommend the following areas as priority for research.

- The systematics of the *B. tryoni* complex needs to be resolved as a matter of urgency. Both trade and research are heavily impacted by uncertainty as to the biological status of different taxonomic species.
- Understanding spatial and temporal foraging patterns for resources (including protein, cue-lure, mates and oviposition sites). Outcomes will allow better targeting of protein-bait spray, MAT and SIT.
- Detailed studies of host–plant interactions, including host use ranking, varietal differences, ripening effects and sequential host use in the field. Outcomes allow better quantification of crop risk at different population levels, opens up potential for resistance breeding, allows better quantification of field population dynamics.
- Greater emphasis placed on understanding the role of noncrop hosts in regional population dynamics: essential for area-wide management programmes.
- Significantly greater effort put into developing food- and fruit-odour-based baits tailored for *B. tryoni*.
- Refined assessment of the role of natural enemies and their potential to be used as an integrated part of *B. tryoni* management programmes.
- Critical appraisal of the impact of new generation insecticides on *B. tryoni* (larvae, adults and pupae), particularly where those chemicals which are being used for the control of other horticultural pests in IPM systems and the investigation of other innovative techniques which manipulate flies resources (e.g. chemosterilisation).
- Resolution of the genuine flight distance of *B. tryoni*. This will immediately impact on quarantine distances. Given the geometric expansion of areas to be treated unnecessarily by each kilometre



of quarantine radius, this is a fundamental matter to resolve, for trade, quarantine, the minimisation of pesticides in the environment and for SIT.

## Acknowledgements

The following colleagues made valuable comments and additions to the manuscript: Harry Fay, Hainan Gu, Andrew Jessup, Edward Hamacek, Bernie Dominiak, Olivia Reynolds and Peter Leach. Bernie Dominiak, particularly, made many pertinent comments, unfortunately only a few of which could we incorporate because of the scope of the paper. A.R.C. received funding for this review through CRC for National Plant Biosecurity project 40088 and would like to acknowledge the support of the Australian Government's Cooperative Research Centres Program. P.W.T. acknowledges the support of the Macquarie University Vice Chancellor's Innovation Fellowship. C.W.W. was supported by Horticulture Australia Limited (HAL) in partnership with Australian Citrus Growers and was funded by the Citrus levy (project codes: CT05002 and CT07036). The Australian Commonwealth Government provides matched funding for all HAL R&D activities.

## References

- Allman S.L. (1938) Breeding experiments with the Queensland fruit-fly (*Strumeta tryoni* Frogg.). *Journal of the Australian Institute of Agricultural Science*, **4**, 204–205.
- Allman S.L. (1939) The Queensland fruit fly. Observations on breeding and development. *New South Wales Agricultural Gazette*, **50**, 499–501.
- Allman S.L. (1941) Observations on various species of fruit flies. *Journal of the Australian Institute of Agricultural Science*, **7**, 155–156.
- Allman S.L., Friend A.H. (1948) New insecticides and fruit fly control. *Agricultural Gazette of New South Wales*, **59**, 531–533.
- Aluja M., Sivinski J., Rull J., Hodgson P.J. (2005) Behavior and predation of fruit fly larvae (*Anastrepha* spp.) (Diptera: Tephritidae) after exiting fruit in four types of habitats in tropical Veracruz, Mexico. *Environmental Entomology*, **34**, 1507–1516.
- An X., Wilkes K., Bastian Y., Morrow J.L., Frommer M., Raphael K.A. (2002) The period gene in two species of tephritid fruit fly differentiated by mating behaviour. *Insect Molecular Biology*, **11**, 419–430.
- Anderson D.T. (1962) The embryology of *Dacus tryoni* (Frogg.) [(Diptera, Trypetidae (=Tephritidae)], the Queensland fruit-fly. *Journal of Embryology and Experimental Morphology*, **10**, 248–292.
- Anderson D.T. (1963a) The embryology of *Dacus tryoni* 2. Development of imaginal discs in the embryo. *Journal of Embryology and Experimental Morphology*, **11**, 339–351.
- Anderson D.T. (1963b) The larval development of *Dacus tryoni* (Frogg.) (Diptera: Trypetidae) I. Larval Instars, imaginal discs, and haemocytes. *Australian Journal of Zoology*, **11**, 202–218.
- Anderson D.T. (1964a) The embryology of *Dacus tryoni* (Diptera) 3. Origins of imaginal rudiments other than the principal discs. *Journal of Embryology and Experimental Morphology*, **12**, 65–75.
- Anderson D.T. (1964b) The larval development of *Dacus tryoni* (Frogg.) (Diptera: Trypetidae) II. Development of imaginal rudiments other than the principal discs. *Australian Journal of Zoology*, **12**, 1–8.
- Anderson D.T., Lyford G.C. (1965) Oogenesis in *Dacus tryoni* (Frogg.) (Diptera: Trypetidae). *Australian Journal of Zoology*, **13**, 423–435.
- Armstrong K.F., Cameron C.M., Frampton E.R. (1997) Fruit fly (Diptera: Tephritidae) species identification: a rapid molecular diagnostic technique for quarantine application. *Bulletin of Entomological Research*, **87**, 111–118.
- Ayling G. (1989) The Queensland fruit fly eradication campaign. *Western Australia Journal of Agriculture*, **30**, 159–162.
- Balagawi S., Vijayasegaran S., Drew R.A.I., Raghu S. (2005) Influence of fruit traits on oviposition preference and offspring performance of *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) on three tomato (*Lycopersicon lycopersicum*) cultivars. *Australian Journal of Entomology*, **44**, 97–103.
- Barik T.K. (2009) A review on *Anopheles culicifacies*: from bionomics to control with special reference to Indian subcontinent. *Acta Tropica*, **109**, 87–97.
- Barry J.D., Vargas R.I., Miller N.W., Morse J.G. (2003) Feeding and foraging of wild and sterile Mediterranean fruit flies (Diptera: Tephritidae) in the presence of spinosad bait. *Journal of Economic Entomology*, **96**, 1405–1411.
- Barry J.D., Miller N.W., Pinero J.C., Tuttle A., Mau R.F.L., Vargas R.I. (2006) Effectiveness of protein baits on melon fly and oriental fruit fly (Diptera: Tephritidae): attraction and feeding. *Journal of Economic Entomology*, **99**, 1161–1167.
- Bateman M.A. (1967) Adaptations to temperature in geographic races of the Queensland fruit fly, *Dacus (Strumeta) tryoni*. *Australian Journal of Zoology*, **15**, 1141–1161.
- Bateman M.A. (1968) Determinants of abundance in a population of the Queensland fruit fly. *Symposium of the Royal Entomological Society of London*, **4**, 119–131.
- Bateman M.A. (1972) The ecology of fruit flies. *Annual Review of Entomology*, **17**, 493–518.
- Bateman M.A. (1977) Dispersal and species interaction as factors in the establishment and success of tropical fruit

- flies in new areas. *Proceedings of the Ecological Society of Australia*, **10**, 106–112.
- Bateman M.A. (1991) *The Impact of Fruit Flies on Australian Horticulture*. 81. pp. Horticultural Policy Council Report No. 3. Canberra: Department of Primary Industries.
- Bateman M.A., Arretz P. (1973) The eradication of Queensland fruit fly from Easter Island. *FAO Plant Protection Bulletin*, **21**, 114.
- Bateman M.A., Friend A.H., Hampshire F. (1966a) Population suppression in the Queensland fruit fly, *Dacus (Strumeta) tryoni* I. The effects of male depletion in a semi-isolated population. *Australian Journal of Agricultural Research*, **17**, 687–697.
- Bateman M.A., Friend A.H., Hampshire F. (1966b) Population suppression in the Queensland Fruit fly, *Dacus (Strumeta) tryoni*. II. Experiments on isolated populations in Western New South Wales. *Australian Journal of Agricultural Research*, **17**, 699–718.
- Bateman M.A., Morton T.C. (1981) The importance of ammonia in proteinaceous attractants for fruit flies (Family: Tephritidae). *Australian Journal of Agricultural Research*, **32**, 883–903.
- Bateman M.A., Sonleitner F.J. (1967) The ecology of a natural population of the Queensland fruit fly, *Dacus tryoni* I. The parameters of the pupal and adult populations during a single season. *Australian Journal of Zoology*, **15**, 303–335.
- Bellas T., Fletcher B.S. (1979) Identification of the major components in the secretion from the rectal pheromone glands of the Queensland fruit flies, *Dacus tryoni* and *Dacus neohumeralis* (Diptera: Tephritidae). *Journal of Chemical Ecology*, **5**, 795–803.
- Bellows T.S., Fischer T.W. (Eds) (1999) *Handbook of Biological Control*. San Diego, CA, USA: Academic Press.
- Benson A.H., Voller S. (1899) Fruit fly experiments. *Queensland Agricultural Journal*, **4**, 1–4.
- Bernays E.A., Chapman R.F. (1994) *Host-plant Selection by Phytophagous Insects*. New York, USA: Chapman & Hall.
- Beroza M., Alexander B.H., Steiner L.F., Mitchell W.C., Miyashita D.H. (1960) New synthetic lures for the male melon fly. *Science*, **131**, 1044–1045.
- Besly M.A. (1962) The effect of dryness upon loss of water and length of life in the Queensland fruit fly, *Dacus tryoni*. Ph.D. Thesis, University of Sydney.
- Bigler F., Neunschwander P., Delucchi V., Michelakis S. (1986) Natural enemies of preimaginal stages of *Dacus oleae* Gmel. (Diptera: Tephritidae) in western Crete, Greece. II. Impact on Olive fly populations. *Bollettino del Laboratorio di Entomologia Agraria Filippo Silvestri*, **43**, 79–96.
- Birch L.C. (1961) Natural selection between two species of tephritid fruit flies of the genus *Dacus*. *Evolution*, **15**, 360–374.
- Bower C.C. (1977) Inhibition of larval growth of the Queensland fruit fly, *Dacus tryoni* (Diptera: Tephritidae) in apples. *Annals of the Entomological Society of America*, **70**, 97–100.
- Brévault T., Quilici S. (2007) Visual response of the tomato fruit fly, *Neoceratitis cyanescens*, to colored fruit models. *Entomologia Experimentalis et Applicata*, **125**, 45–54.
- Brieze-Stegeman R., Rice M.J., Hooper G.H.S. (1978) Daily periodicity in attraction of male tephritid fruit flies to synthetic chemical lures. *Journal of the Australian Entomological Society*, **17**, 341–346.
- Cáeres C., Segura D.F., Vera M.T., Wornoayporn V., Cladera J.L., Teal P., Sapountzis P., Bourtzis K., Zacharopoulou A., Robinson A.S. (2009) Incipient speciation revealed in *Anastrepha fraterculus* (Diptera: Tephritidae) by studies on mating compatibility, sex pheromones, hybridization, and cytology. *Biological Journal of the Linnean Society*, **97**, 152–165.
- Caldwell N.E.H., May A.W.S. (1943) Fruit fly luring investigations. *Queensland Agricultural Journal*, **57**, 166–168.
- Cameron E. (2006) Fruit fly pests of Northwestern Australia. Ph.D. Thesis, University of Sydney.
- Cameron E.C., Sved J.A., Gilchrist A.S. (2010) Pest fruit fly (Diptera: Tephritidae) in northwestern Australia: one species or two? *Bulletin of Entomological Research*, **100**, 197–206.
- Carmichael A.E. (2009) Taxonomy and diagnostics of fruit fly infesting opiine braconids in Australia and the South Pacific. M. Appl. Sc. Thesis, Queensland University of Technology.
- Carmichael A.E., Wharton R.A., Clarke A.R. (2005) Opiine (Hymenoptera: Braconidae: Opiinae) parasitoids of tropical fruit flies (Diptera: Tephritidae: Dacinae) of the Australian and South Pacific region. *Bulletin of Entomological Research*, **85**, 545–569.
- Casana Giner V., Oliver J.E., Jang E.B., Carvalho L.A., Khirmian A., Demilo A.B., Mcquate G.T. (2003) Raspberry ketone formate as an attractant for the melon fly, (Diptera: Tephritidae). *Journal of Entomological Science*, **38**, 120–126.
- Centritto M., Lee H.S., Jarvis P.G. (1999) Interactive effects of elevated CO<sub>2</sub> and drought on cherry (*Prunus avium*) seedlings. I. Growth, whole-plant water use efficiency and water loss. *New Phytologist*, **141**, 129–140.
- Centritto M., Lucas M.E., Jarvis P.G. (2002) Gas exchange, biomass, whole-plant water-use efficiency and water uptake of peach (*Prunus persica*) seedlings in response to elevated carbon dioxide concentration and water availability. *Tree Physiology*, **22**, 699–706.
- Clarke A.R., Allwood A., Chinajariyawong A., Drew R.A.I., Hengsawad C., Jirasurat M., Kong Krong C., Kritsaneepaiboon S., Vijaysegaran S. (2001) Seasonal abundance and host use patterns of seven *Bactrocera* Macquart species (Diptera: Tephritidae) in Thailand and Peninsular Malaysia. *Raffles Bulletin of Zoology*, **49**, 207–220.

- Clarke A.R., Armstrong K.F., Carmichael A.E., Milne J.R., Raghu S., Roderick G.K., Yeates D.K. (2005) Invasive phytophagous pests arising through a recent tropical evolutionary radiation: the *Bactrocera dorsalis* complex of fruit flies. *Annual Review of Entomology*, **50**, 293–319.
- Courtice A.C., Drew R.A.I. (1984) Bacterial regulation of abundance in tropical fruit flies (Diptera: Tephritidae). *Australian Zoologist*, **21**, 251–268.
- Coviella C.E., Trumble J.T. (1999) Effects of elevated atmospheric carbon dioxide on insect–plant interactions. *Conservation Biology*, **13**, 700–712.
- CSIRO & BoM (2007) *Climate Change in Australia: Technical Report 2007*. Melbourne, Australia: CSIRO.
- Dalby-Ball G., Meats A. (2000a) Effects of fruit abundance within a tree canopy on the behaviour of wild and cultured Queensland fruit flies, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). *Australian Journal of Entomology*, **39**, 201–207.
- Dalby-Ball G., Meats A. (2000b) Influence of the odour of fruit, yeast and cue-lure on the flight activity of the Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). *Australian Journal of Entomology*, **39**, 195–200.
- De Souza K.R., McVeigh L.J., Wright D.J. (1992) Selection of insecticides for lure and kill studies against *Spodoptera littoralis* (Lepidoptera: Noctuidae). *Journal of Economic Entomology*, **85**, 2100–2106.
- Deutsch C.A., Tewksbury J.J., Huey R.B., Sheldon K.S., Ghalambor C.K., Haak D.C., Martin P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6668–6672.
- Dominiak B. (2006) Review of the use of protein food based lures in McPhail traps for monitoring Queensland fruit fly *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). *General and Applied Entomology*, **35**, 7–12.
- Dominiak B.C., Gilmour A.R., Kerruish B., Whitehead D. (2003a) Detecting low populations of Queensland fruit fly, *Bactrocera tryoni* (Froggatt) with McPhail and Lynfield traps. *General and Applied Entomology*, **32**, 49–53.
- Dominiak B.C., Westcott A.E., Barchia I.M. (2003b) Release of sterile Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae), at Sydney, Australia. *Australian Journal of Experimental Agriculture*, **43**, 519–528.
- Dominiak B.C., Mavi H.S., Nicol H.I. (2006) Effect of town microclimate on the Queensland fruit fly *Bactrocera tryoni*. *Australian Journal of Experimental Agriculture*, **46**, 1239–1249.
- Downton W.J.S., Grant W.J.R., Loveys B.R. (1987) Carbon dioxide enrichment increases yield of Valencia orange. *Australian Journal of Plant Physiology*, **14**, 493–501.
- Drew R.A.I. (1974) The responses of fruit fly species (Diptera: Tephritidae) in the South Pacific area to male attractants. *Journal of the Australian Entomology Society*, **13**, 267–270.
- Drew R.A.I. (1976) Important pests of Agricultural crops in Queensland. Part 10. The Queensland Fruit fly. *Entomological Society of Queensland News Bulletin*, **3**, 171–173.
- Drew R.A.I. (1987a) Behavioural strategies of fruit flies of the genus *Dacus* (Diptera: Tephritidae) significant in mating and host–plant relationships. *Bulletin of Entomological Research*, **77**, 73–81.
- Drew R.A.I. (1987b) Reduction in fruit fly (Tephritidae: Dacinae) populations in their endemic rainforest habitat by frugivorous vertebrates. *Australian Journal of Zoology*, **35**, 283–288.
- Drew R.A.I. (1989) The tropical fruit flies (Diptera: Tephritidae: Dacinae) of the Australasian and Oceanian regions. *Memoirs of the Queensland Museum*, **26**, 1–521.
- Drew R.A.I., Allwood A.J. (1985) A new family of Strepsiptera parasitizing fruit flies (Tephritidae) in Australia. *Systematic Entomology*, **10**, 129–134.
- Drew R.A.I., Fay H.A.C. (1988) Comparison of the roles of ammonia and bacteria in the attraction of *Dacus tryoni* (Froggatt) (Queensland fruit fly) to proteinaceous suspensions. *Journal of Plant Protection in the Tropics*, **5**, 127–130.
- Drew R.A.I., Lambert D.M. (1986) On the specific status of *Dacus (Bactrocera) aquilonis* and *D. (Bactrocera) tryoni* (Diptera: Tephritidae). *Annals of the Entomological Society of America*, **79**, 870–878.
- Drew R.A.I., Lloyd A.C. (1987) Relationship of fruit flies (Diptera: Tephritidae) and their bacteria to their host plants. *Annals of the Entomological Society of America*, **80**, 629–636.
- Drew R.A.I., Lloyd A.C. (1989) Bacteria associated with fruit flies and their host plants. In *Fruit Flies, their Biology, Natural Enemies and Control*, pp. 131–140. Eds A.S. Robinson and G. Hooper. Amsterdam: Elsevier Science Publishers.
- Drew R.A.I., Lloyd A.C. (1991) Bacteria in the lifecycle of tephritid fruit flies. In *Microbial Mediation of Plant–Herbivore Interactions*, pp. 441–465. Eds P. Barbosa, V.A. Krischik and C.G. Jones. New York: John Wiley and Sons.
- Drew R.A.I., Romig M.C. (2000) The biology and behavior of flies in the Tribe Dacini (Dacinae). In *Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior*, pp. 535–546. Eds M. Aluja and A.L. Norrbomm. Boca Raton, FL, USA: CRC Press.
- Drew R.A.I., Yuval B. (2000) The evolution of fruit fly feeding behavior. In *Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior*, pp. 731–749. Eds M. Aluja and A.L. Norrbom. New York: CRC Press.
- Drew R.A.I., Hooper G.H.S., Bateman M.A. (1978) *Economic Fruit Flies of the South Pacific Region*. Brisbane, Australia: Queensland Department of Primary Industries.
- Drew R.A.I., Courtice A.C., Teakle D.S. (1983) Bacteria as a natural source of food for adult fruit flies (Diptera: Tephritidae). *Oecologia*, **60**, 279–284.

- Drew R.A.I., Prokopy R.J., Romig M.C. (2003) Attraction of fruit flies of the genus *Bactrocera* to colored mimics of host fruit. *Entomologia Experimentalis et Applicata*, **107**, 39–45.
- Duan J.J., Messing, R.H. (1997) Effects of two opiine parasitoids (Hymenoptera: Braconidae) introduced for fruit fly control on a non-target native Hawaiian tephritid, *Trupanea dubautiae* (Diptera: Tephritidae). *Biological Control*, **8**, 177–184.
- Duan J.J., Messing, R.H. (2000) Host specificity tests of *Diachasmimorpha kraussii* (Hymenoptera: Braconidae), a newly introduced opiine fruit fly parasitoid with four non-target tephritids in Hawaii. *Biological Control*, **19**, 28–34.
- Duan J.J., Messing R.H. (2000) Effects of host substrate and vibration cues on ovipositor-probing behavior in two larval parasitoids of tephritid fruit flies. *Journal of Insect Behavior*, **13**, 175–186.
- Duan J.J., Prokopy R.J. (1992) Visual and odour stimuli influencing effectiveness of sticky spheres for trapping apple maggot flies. *Journal of Applied Entomology*, **113**, 271–279.
- Duan J.J., Prokopy R.J. (1993) Toward developing pesticide treated spheres for controlling apple maggot flies: carbohydrates and amino acids as feeding stimulants. *Journal of Applied Entomology*, **115**, 176–184.
- Duan J.J., Prokopy R.J. (1995) Control of apple maggot flies with pesticide-treated red spheres. *Journal of Economic Entomology*, **88**, 700–707.
- Dukas R., Prokopy R.J., Duan J.J. (2001) Effects of larval competition on survival and growth in Mediterranean fruit flies. *Ecological Entomology*, **26**, 587–593.
- Economopoulos A.P. (1989) Use of traps based on color and/or shape. In *World Crop Pests. Fruit Flies, Their Biology, Natural Enemies and Control*, pp. 315–327. Eds A.S. Robinson and G. Hooper. Amsterdam, The Netherlands: The Elsevier Science Publishers.
- Eisemann C.H., Rice M.J. (1985) Oviposition behaviour of *Dacus tryoni*: the effects of some sugars and salts. *Entomologia Experimentalis et Applicata*, **39**, 61–71.
- Eisemann C.H., Rice M.J. (1989) Behavioural evidence for hygro- and mechanoreception by ovipositor sensilla of *Dacus tryoni* (Diptera: Tephritidae). *Physiological Entomology*, **14**, 273–277.
- Eisemann C.H., Rice M.J. (1992) Attractants for the gravid Queensland fruit fly *Dacus tryoni*. *Entomologia Experimentalis et Applicata*, **62**, 125–130.
- El-Sayed A.M., Suckling D.M., Byers J.A., Jang E.B., Wearing C.H. (2009) Potential of 'lure and kill' for long-term pest management and eradication of invasive species. *Journal of Economic Entomology*, **102**, 815–835.
- Elson-Harris M.M. (1988) Morphology of the immature stages of *Dacus tryoni* (Froggatt) (Diptera: Tephritidae). *Journal of the Australian Entomological Society*, **27**, 91–98.
- Ero M.M. (2009) Host searching behaviour of *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera: Braconidae: Opiinae), a polyphagous parasitoid of Dacinae fruit flies (Diptera: Tephritidae). Ph.D. Thesis, Queensland University of Technology.
- Ero M.M., Hamacek E., Peek T., Clarke A.R., (2010) Preference among four *Bactrocera* species (Diptera: Tephritidae) by *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera: Braconidae). *Australian Journal of Entomology*, (in press).
- Ero M.M., Neale C.J., Hamacek E., Peek T., Clarke A.R., (2010). Preference and performance of *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera: Braconidae) on five commercial fruit species. *Journal of Applied Entomology*. doi: 10.1111/j.1439-0418.2010.01556.x.
- Exley E.M. (1955) Comparative morphological studies of the larvae of some Queensland Dacinae (Trypetidae, Diptera). *Queensland Journal of Agricultural Science*, **12**, 119–150.
- Faust R.M. (2008) General introduction to areawide pest management. In *Areawide Pest Management: Theory and Application, Chapter 1*, pp. 1–4. Eds O. Koul. G.W. Cupers and N. Elliott. Wallingford, UK: CAB International.
- Fisher K. (1996) Queensland fruit fly (*Bactrocera tryoni*): eradication from Western Australia. *Fruit Fly Pests a World Assessment of Their Biology and Management*, pp. 535–541. Delray Beach, Florida, USA: St Lucie Press.
- Fitt G.P. (1984) Oviposition behaviour of two tephritid fruit flies, *Dacus tryoni* and *Dacus jarvisi*, as influenced by the presence of larvae in the host fruit. *Oecologia*, **62**, 37–46.
- Fitt G.P. (1986) The roles of adult and larval specialisations in limiting the occurrence of five species of *Dacus* (Diptera: Tephritidae) in cultivated fruits. *Oecologia*, **69**, 101–109.
- Fitt G.P. (1990a) Comparative fecundity, clutch size, ovariolo number and egg size of *Dacus tryoni* and *D. jarvisi*, and their relationship to body size. *Entomologia Experimentalis et Applicata*, **55**, 11–21.
- Fitt G.P. (1990b) Variation in ovariolo number and egg size of species of *Dacus* (Diptera: Tephritidae) and their relation to host specialization. *Ecological Entomology*, **15**, 255–264.
- Fitt G.P., O' Brien R.W. (1985) Bacteria associated with four species of *Dacus* (Diptera: Tephritidae) and their role in the nutrition of the larvae. *Oecologia*, **67**, 447–454.
- Fletcher B.S. (1973) The ecology of a natural population of the Queensland fruit fly, *Dacus tryoni* IV. The immigration and emigration of adults. *Australian Journal of Zoology*, **21**, 541–565.
- Fletcher B.S. (1974a) The ecology of a natural population of the Queensland fruit fly, *Dacus tryoni* V. The dispersal of adults. *Australian Journal of Zoology*, **22**, 189–202.
- Fletcher B.S. (1974b) The ecology of a natural population of the Queensland fruit fly, *Dacus tryoni* VI. Seasonal changes in fruit fly numbers in the areas surrounding the orchard. *Australian Journal of Zoology*, **22**, 353–363.



- Fletcher B.S. (1975) Temperature-regulated changes in the ovaries of overwintering females of the Queensland fruit fly, *Dacus tryoni*. *Australian Journal of Zoology*, **23**, 91–102.
- Fletcher B.S. (1979) The overwintering survival of adults of the Queensland fruit fly, *Dacus tryoni*, under natural conditions. *Australian Journal of Zoology*, **27**, 403–411.
- Fletcher B.S. (1986) The overwintering strategy of the Queensland fruit fly, *Dacus tryoni*. In *Fruit Flies: Proceedings of the second international symposium, Colymbari, Crete, Greece*, pp. 375–382. Eds A.P. Economopoulos. Amsterdam, the Netherlands: Elsevier Science Publications.
- Fletcher B.S. (1987) The biology of Dacine fruit flies. *Annual Review of Entomology*, **32**, 115–144.
- Fletcher B.S. (1989a) Life history strategies of tephritid fruit flies. In *Fruit Flies Their Biology, Natural Enemies and Control*, pp. 195–208. Eds A.S. Robinson and G. Hooper. Amsterdam, the Netherlands: Elsevier.
- Fletcher B.S. (1989b) Movements of tephritid fruit flies. In *Fruit flies their Biology, Natural Enemies and Control*, pp. 209–219. Eds A.S. Robinson and G. Hooper. Amsterdam, the Netherlands: Elsevier.
- Fletcher B.S., Watson C.A. (1974) The ovipositional response of the tephritid fruit fly, *Dacus tryoni*, to 2-Chloro-Ethanol in laboratory bioassays. *Annals of the Entomological Society of America*, **67**, 21–23.
- Fowler A.J. (1977) Host selection by wild and laboratory cultured *Dacus tryoni*. Ph.D. Thesis, University of Sydney.
- French C. (1910) Notes on fruit flies (Trypetidae). *Proceedings of the Linnaean Society of New South Wales*, **35**, 886.
- Garneau R. (2008) *The Garneau Climate Change Report*. Melbourne, Australia: Cambridge University Press.
- Garros C., Van Bortel W., Trung H.D., Coosemans M., Manguin S. (2006) Review of the *minimus* complex of *Anopheles*, main malaria vector in Southeast Asia: from taxonomic issues to vector control strategies. *Tropical Medicine & International Health*, **11**, 102–114.
- Gee J.H. (1966) Selective differences between the tephritid fruit flies, *Dacus tryoni* and *D. neohumeralis*. Ph.D. Thesis, University of Sydney.
- Gee J.H. (1969) An analysis of natural selection in laboratory populations of *Dacus* (Diptera: Tephritidae). *Evolution*, **23**, 212–224.
- Giannakakis A., Fletcher B.S. (1985) Morphology and distribution of antennal sensilla of *Dacus tryoni* (Froggatt) (Diptera: Tephritidae). *Journal of the Australian Entomological Society*, **24**, 31–35.
- Gibbs G.W. (1965) Comparative ecology and sexual isolation of two species of *Dacus* (Tephritidae: Diptera). Ph.D. Thesis, University of Sydney.
- Gibbs G.W. (1967) The comparative ecology of two closely related, sympatric species of *Dacus* (Diptera) in Queensland. *Australian Journal of Zoology*, **15**, 1123–1139.
- Gilchrist A.S., Ling A.E. (2006) DNA microsatellite analysis of naturally occurring colour intermediates between *Bactrocera tryoni* (Froggatt) and *Bactrocera neohumeralis* (Hardy) (Diptera: Tephritidae). *Australian Journal of Entomology*, **45**, 157–162.
- Gilchrist A.S., Dominiak B., Gillespie P.S., Sved J.A. (2006) Variation in population structure across the ecological range of the Queensland fruit fly, *Bactrocera tryoni*. *Australian Journal of Zoology*, **54**, 87–95.
- Gonzalez R., Toledo J., Cruz-Lopez L., Virgen A., Santiesteban A., Malo E.A. (2006) A new blend of white sapote fruit volatiles as potential attractant to *Anastrepha ludens* (Diptera: Tephritidae). *Journal of Economic Entomology*, **99**, 1994–2001.
- Green C.L., Frommer M. (2001) The genome of the Queensland fruit fly *Bactrocera tryoni* contains multiple representatives of the mariner family of transposable elements. *Insect Molecular Biology*, **10**, 371–386.
- Gurney W.B. (1910) Fruit flies and other insects attacking cultivated and wild fruit in New South Wales. Part I. *Agricultural Gazette of New South Wales*, **21**, 423–433.
- Gurney W.B. (1925) The control of fruit fly. *The Agricultural Gazette of New South Wales*, **36**, 879.
- Gurney W.B. (1936) In search of fruit fly parasites in India – A summary of investigations made in 1935. *The Agricultural Gazette*, **47**, 374–378.
- Gurr G.M., Kvedaras O.L. (2010) Synergizing biological control: scope for sterile insect technique, induced plant defences and cultural techniques to enhance natural enemy impact? *Biological Control*, **52**, 198–207.
- Hancock D.L., Hamacek E.L., Lloyd A.C., Elson-Harris M.M. (2000) *The Distribution and Host Plants of Fruit Flies (Diptera: Tephritidae) in Australia*. Brisbane, Australia: DPI Publications.
- Hargreaves J.R., Murray D.A.H., Cooper L.P. (1986) Studies on the stinging of passionfruit by Queensland Fruit fly, *Dacus tryoni* and its control by bait and cover sprays. *Queensland Journal of Agriculture and Animal Sciences*, **43**, 33–40.
- Harris A. (2009) Can the Queensland fruit fly larval parasitoid *Diachasmimorpha kraussii* (Hymenoptera: Braconidae) be reared on irradiated larval hosts? M.Sc. Thesis. Imperial College, London.
- Heath R.R., Vazquez A., Schnell E.Q., Villareal J., Kendra P.E., Epsky N.D. (2009) Dynamics of pH modification of an acidic protein bait used for tropical fruit flies (Diptera: Tephritidae). *Journal of Economic Entomology*, **102**, 2371–2376.
- Hendrichs J., Kenmore P., Robinson A.S., Vreysen M.J.B. (2007) Area-wide integrated pest management (AW-IPM): principles, practice and prospects. In *Area-Wide Control of Insect Pests: From Research to Field Implementation*, pp. 3–33. Eds M.J.B. Vreysen, A.S. Robinson and J. Hendrichs. Dordrecht, the Netherlands: Springer.

- Hengeveld R., Walter G.H. (1999) The two coexisting ecological paradigms. *Acta Biotheoretica*, **47**, 141–170.
- Hill A.R. (1986) Reduction in trap captures of female fruit flies (Diptera: Tephritidae) when synthetic male lures are added. *Journal of the Australian Entomological Society*, **25**, 211–214.
- Hill A.R., Hooper G.H.S. (1984) Attractiveness of various colours to Australian tephritid fruit flies in the field. *Entomologia Experimentalis et Applicata*, **35**, 119–128.
- Hooper G.H.S., Drew R.A.I. (1979) Effect of height of trap on capture of Tephritid fruit flies with cuelure and methyl eugenol in different environments. *Environmental Entomology*, **8**, 786–788.
- Hull C.D. (1998) The olfactory physiology of the Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae): structure and function of the olfactory apparatus. Ph.D. Thesis, The University of Queensland.
- Hull C.D., Cribb B.W. (1997) Ultrastructure of the antennal sensilla of Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera, Tephritidae). *International Journal of Insect Morphology and Embryology*, **26**, 27–34.
- Hull C.D., Cribb B.W. (2001a) Olfaction in the Queensland fruit fly, *Bactrocera tryoni*. I: Identification of olfactory receptor neuron types responding to environmental odors. *Journal of Chemical Ecology*, **27**, 871–888.
- Hull C.D., Cribb B.W. (2001b) Olfaction in the Queensland fruit fly, *Bactrocera tryoni*. II: response spectra and temporal encoding characteristics of the carbon dioxide receptors. *Journal of Chemical Ecology*, **27**, 889–906.
- Hulthen A.D., Clarke A.R. (2006) The influence of soil type and moisture on pupal survival of *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). *Australian Journal of Entomology*, **45**, 16–19.
- Idso S.B., Kimball B.A. (1997) Effects of long-term atmospheric CO<sub>2</sub> enrichment on the growth and fruit production of sour orange trees. *Global Change Biology*, **3**, 89–96.
- Idso S.B., Kimball B.A., Shaw P.E., Widmer W., Vanderslice J.T., Higgs D.J., Montanari A., Clark W.D. (2002) The effect of elevated atmospheric CO<sub>2</sub> on the vitamin C concentration of (sour) orange juice. *Agriculture, Ecosystems and Environment*, **90**, 1–7.
- IPPC. (2008) *International Standards for Phytosanitary Measures ISPM No. 30, Establishment of Areas of Low Pest Prevalence for Fruit Flies (Tephritidae)*. Rome: IPPC Secretariat, FAO.
- Islam M.S., Matsui T., Yoshida Y. (1996) Effect of carbon dioxide enrichment on physico-chemical and enzymatic changes in tomato fruits at various stages of maturity. *Scientia Horticulturae*, **65**, 137–149.
- Jablonski L.M., Wang X., Curtis P.S. (2002) Plant reproduction under elevated CO<sub>2</sub> conditions: a meta-analysis of reports on 79 crop and wild species. *New Phytologist*, **156**, 9–26.
- Jamnongluk W., Baimai V., Kittayapong P. (2003) Molecular phylogeny of tephritid fruit flies in the *Bactrocera tau* complex using the mitochondrial COI sequences. *Genome*, **46**, 112–118.
- Jarvis H. (1922a) Fruit fly investigations [First progress report]. *Queensland Agricultural Journal*, **17**, 246–247.
- Jarvis H. (1922b) Fruit fly investigations [Fourth progress report]. *Queensland Agricultural Journal*, **18**, 131–133, 344–345.
- Jarvis H. (1922c) Fruit fly investigations [Second progress report]. *Queensland Agricultural Journal*, **17**, 309–312.
- Jarvis H. (1923) Fruit fly investigations. *Queensland Agricultural Journal*, **19**, 1–4, 194–197, 369–370.
- Jarvis H. (1924) Report of the entomologist (Stanthorpe District) Mr. H. Jarvis, for September and October 1924. *Queensland Agricultural Journal*, **22**, 435–440.
- Jarvis H. (1925a) Fruit fly investigations. Entomologist's report (April–May). *Queensland Agricultural Journal*, **24**, 60–61.
- Jarvis H. (1925b) The fruit fly. Report on measures of possible control, 1924–25. *Queensland Agricultural Journal*, **24**, 48–52.
- Jarvis H. (1925c) Report of the entomologist, Stanthorpe District, Mr. H. Jarvis, April–May 1925. *Queensland Agricultural Journal*, **24**, 60–62.
- Jarvis H. (1926a) Fruit fly in the Stanthorpe district. *Queensland Agricultural Journal*, **25**, 367–370.
- Jarvis H. (1926b) The Queensland fruit fly (*Chaetodacus tryoni* Froggatt). *Queensland Agricultural Journal*, **26**, 101–104.
- Jarvis H. (1931) Experiments with a new fruit fly lure. *Queensland Agricultural Journal*, **36**, 485–491.
- Jessup A.J., McCarthy D. (1993) Host status of some Australian-grown cucurbits to *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) under laboratory conditions. *Journal of the Australian Entomological Society*, **32**, 97–98.
- Jessup A.J., Dalton S.P., Slogget R.F. (1998) Determination of host status of table grapes to Queensland fruit fly (*Bactrocera tryoni* (Froggatt)) (Diptera: Tephritidae), for export to New Zealand. *Journal of the Entomological Society of New South Wales*, **28**, 73–75.
- Jessup A.J., Dominiak B., Woods B., De Lima C.P.F., Tomkins A., Smallridge C.J. (2007) Area-wide management of fruit flies in Australia. In *Area-wide Control of Insect Pests. From Research to Field Implementation*, pp. 685–697. Eds M.J.B. Vreysen, A.S. Robinson and J. Hendrichs. The Netherlands: Springer.
- Jones E.L., Skepper A.H. (1965) Suppression of Queensland fruit fly, *Dacus (Strumeta) tryoni* (Frogg.), Trypetidae (Dipt.), in Narrandera, New South Wales. *Agricultural Gazette of New South Wales*, **76**, 501–503.
- Kaspi R., Yuval B. (1999) Lek site selection by male Mediterranean fruit flies. *Journal of Insect Behavior*, **12**, 267–276.

- Kaspi R., Mossinson S., Drezner T., Kamensky B., Yuval B. (2002) Effects of larval diet on development rates and reproductive maturation of male and female Mediterranean fruit flies. *Physiological Entomology*, **27**, 29–38.
- Katsoyannos B.I. (1989) Response to shape, size and color. In *World Crop Pests. Fruit Flies, Their Biology, Natural Enemies and Control*, pp. 307–324. Eds A. Robinson and G. Hooper. Amsterdam, The Netherlands: Elsevier.
- Katsoyannos B.I., Hendrichs J. (1995) Food bait enhancement of fruit mimics to attract Mediterranean fruit fly females. *Journal of Applied Entomology*, **119**, 211–213.
- Kimball B.A., Idso S.B., Johnson S., Rillig M.C. (2007) Seventeen years of carbon dioxide enrichment of sour orange trees: final results. *Global Change Biology*, **13**, 2171–2183.
- Lalel H.J., Singh Z., Tan S.C. (2003) Distribution of aroma volatile compounds in different parts of mango fruit. *Journal of Horticultural Science and Biotechnology*, **78**, 131–138.
- Leblanc L., Balagawi S., Mararuai A., Putulan D., Clarke A.R. (2001) *Fruit Flies in Papua New Guinea. Pest Advisory Leaflet No. 37*. Suva, Fiji: Secretariat of the Pacific Community-Plant Protection Service.
- Lebrun M.A., Plotto K., Goodner M.-N., Ducamp N., Baldwin E. (2008) Discrimination of mango fruit maturity by volatiles using the electronic nose and gas chromatography. *Postharvest Biology and Technology*, **48**, 122–131.
- Lewontin R.C., Birch L.C. (1966) Hybridization as a source of variation for adaptation to new environments. *Evolution*, **20**, 315–336.
- Liu Z.M., Beattie G.A.C., Johnson D., Spooner-Hart R. (2002) Influence of deposits of a horticultural mineral oil and selected fractions of paraffinic and naphthenic petroleum-derived oils on oviposition by Queensland fruit fly on tomato fruit. In *Spray Oils Beyond 2000*, pp. 142–146. Eds G.A.C. Beattie, D.M. Watson, M.L. Stevens, D.J. Rae and R.N. Spooner-Hart. NSW, Australia: University of Western Sydney.
- Lloyd A.C. (1991) Bacteria associated with *Bactrocera* species of fruit flies (Diptera: Tephritidae) and their host tress in Queensland. Ph.D. Thesis. The University of Queensland.
- Lloyd A.C., Drew R.A.I., Teakle D.S., Hayward A.C. (1986) Bacteria associated with some *Dacus* species (Diptera: Tephritidae) and their host fruit in Queensland. *Australian Journal of Biological Sciences*, **39**, 361–368.
- Lloyd A.C., Hamacek E.L., Smith D., Kopittke R.A. (2000) *Evaluation of Protein Bait Spraying and Inspection on the Packing Line as Quarantine Treatments for Fruit Fly in Citrus*. Horticulture Australia Project CT97036 Final Report. Sydney, Australia: Horticulture Australia Ltd.
- Lloyd A.C., Smith D., Hamacek E.L., Neale C.J., Kopittke R.A., Jessup A.J., De Lima C.P.F., Broughton S. (2003) *Improved Protein Bait Formulations for Fruit Fly Controls*. Horticulture Australia Project AH00012 Final Report. Sydney, Australia: Horticulture Australia Ltd.
- Lloyd A.C., Hamacek E.L., Peek T., Kopittke R.A., Wyatt P., Neale C.J., Eelkema M. (2007) *Area Wide Management of Fruit Flies Central Burnett*. Horticulture Australia Project Number AH03002 Final Report. Sydney, Australia: Horticulture Australia Ltd.
- Lloyd A.C., Hamacek E.L., Kopittke R.A., Peek T., Wyatt P.M., Neale C.J., Eelkema M., Gu H. (2010) Area-wide management of fruit flies (Diptera: Tephritidae) in the Central Burnett district of Queensland, Australia. *Crop Protection*, **29**, 462–469.
- Loch A. (2008) Queensland Fruit fly: an emerging insect pest of wine grapes. *Australian Viticulture*, **12**, 65–67.
- MacFarlane J.R., East R.W., Drew R.A.I., Belinski G.A. (1987) Dispersal of irradiated Queensland fruit flies, *Dacus tryoni* (Froggatt) (Diptera: Tephritidae), in South-eastern Australia. *Australian Journal of Zoology*, **35**, 275–281.
- Maelzer D.A. (1990a) Fruit fly outbreaks in Adelaide, S.A., from 1948–49 to 1986–1987. I. Demarcation, frequency and temporal patterns of outbreaks. *Australian Journal of Zoology*, **38**, 439–452.
- Maelzer D.A. (1990b) Fruit fly outbreaks in Adelaide, S.A., from 1948–49 to 1986–1987. II. The phenology of both pestilent species. *Australian Journal of Zoology*, **38**, 555–572.
- Maelzer D.A., Bailey P.T., Perepelicia N. (2004) Factors supporting the non-persistence of fruit fly populations in South Australia. *Australian Journal of Experimental Agriculture*, **44**, 109–126.
- Mahat K. (2009) Effects on attraction, feeding and mortality of *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) and beneficial organisms with protein bait-insecticide mixture. M.Phil. Thesis. Griffith University.
- Malo E.A., Cruz-Lopez L., Toledo J., Del Mazo A., Virgen A., Rojas J.C. (2005) Behavioral and electrophysiological responses of the Mexican fruit fly (Diptera: Tephritidae) to guava volatiles. *Florida Entomologist*, **88**, 364–371.
- Mavi H.S., Dominiak B. (2001) The role of urban landscape irrigation in inland New South Wales in changing the growth potential of Queensland fruit fly. Geospatial Information and Agriculture Conference, 5th Annual Symposium, pp. 224–235. Sydney.
- Mavi H.S., Dominiak B.C. (1999) Influence of urban climate and hydrology on the growth potential of Queensland fruit fly in south-eastern New South Wales, Australia. In *Proceedings of the 15th International Congress of Biometeorology and International Conference on Urban Climatology*. Eds R.J. de Dear and J.C. Potter. Sydney: Macquarie University.



- May A.W.S. (1953) Queensland host records for the Dacinae (fam. Trypetidae). *Queensland Journal of Agricultural Science*, **10**, 36–79.
- May A.W.S. (1957) Queensland host records for the Dacinae (Fam. Trypetidae). First supplementary lists. *Queensland Journal of Agricultural Science*, **14**, 29–39.
- May A.W.S. (1958) Fruit fly problem in Southern and Central Queensland. *Queensland Department of Agriculture and Stock, Division of Plant Industry Advisory leaflet No. 492*. Brisbane, Australia: Government Printer.
- May A.W.S. (1960) Queensland host records for the Dacinae (Fam. Trypetidae). Second supplementary lists. *Queensland Journal of Agricultural Science*, **17**, 195–200.
- May A.W.S. (1961a) The fruit fly problem in eastern Australia. *Journal of the Australian Entomological Society*, **1**, 1–4.
- May A.W.S. (1961b) A taxonomic and ecological study of the Dacinae (Family: Trypetidae) in Queensland. Ph.D. Thesis, University of Queensland.
- May A.W.S. (1963) An investigation of fruit flies (Trypetidae: Diptera) in Queensland. 1. Introduction, species, pest status and distribution. *Queensland Journal of Agricultural Science*, **20**, 1–82.
- May A.W.S. (1965) New species and records of Dacinae (Diptera: Trypetidae) from northern Australia. *Journal of the Entomological Society of Queensland*, **4**, 58–66.
- May A.W.S., Caldwell N.E.H. (1944) Fruit fly control. *Queensland Agricultural Journal*, **58**, 224–229.
- McKechnie S.W. (1972) Differences in specific proteins within populations of the *Dacus tryoni*-*neohumeralis* complex. Ph.D. Thesis, University of Sydney.
- McKechnie S.W. (1975) Enzyme polymorphism and species discrimination in fruit flies of the genus *Dacus* (Tephritidae). *Australian Journal of Biological Sciences*, **28**, 405–411.
- McQuate G.T. (2009) Effectiveness of GF-120NF Fruit Fly Bait as a suppression tool for *Bactrocera latifrons* (Diptera: Tephritidae). *Journal of Applied Entomology*, **133**, 444–448.
- McQuate G.T., Vargas R.I. (2007) Assessment of attractiveness of plants as roosting sites for the melon fly, *Bactrocera cucurbitae*, and oriental fruit fly, *Bactrocera dorsalis*. *Journal of Insect Science*, **7**, 57.
- Meats A. (1976a) Developmental and long term acclimation to cold by the Queensland fruit fly (*Dacus tryoni*) at constant and fluctuating temperatures. *Journal of Insect Physiology*, **22**, 1013–1019.
- Meats A. (1976b) Seasonal trends in acclimatization to cold in the Queensland fruit fly (*Dacus tryoni*, Diptera) and their prediction by means of a physiological model fed with climatological data. *Oecologia*, **26**, 73–87.
- Meats A. (1976c) Thresholds for cold-torpor and cold-survival in the Queensland fruit fly, and predictability of rates of change in survival threshold. *Journal of Insect Physiology*, **22**, 1505–1509.
- Meats A. (1981) The bioclimatic potential of the Queensland fruit fly, *Dacus tryoni*, in Australia. *Proceedings of the Ecological Society of Australia*, **11**, 151–161.
- Meats A. (1983a) Critical periods for developmental acclimation in the Queensland fruit fly, *Dacus tryoni*. *Journal of Insect Physiology*, **29**, 943–946.
- Meats A. (1983b) The response of Queensland fruit fly, *Dacus tryoni* to tree models. In *Fruit Flies of Economic Importance*, pp. 285–289. Eds R. Cavalloro. Rotterdam, the Netherlands: A.A. Balkema.
- Meats A. (1984) Thermal constraints to successful development of the Queensland fruit fly in regimes of constant and fluctuating temperature. *Entomologia Experimentalis et Applicata*, **36**, 55–59.
- Meats A. (1987) Survival of step and ramp changes of temperature by the Queensland fruit fly, *Dacus tryoni*. *Physiological Entomology*, **12**, 165–170.
- Meats A. (1989a) Abiotic mortality factors: temperature. In *Fruit Flies: Biology, natural enemies and control*. pp. 231–234. Eds A.S. Robinson and G.H.S. Hooper. Amsterdam, the Netherlands: Elsevier.
- Meats A. (1989b) Water relations of Tephritidae. In *Fruit Flies: Biology, Natural Enemies and Control*, pp. 241–246. Eds A.S. Robinson and G.H.S. Hooper. Amsterdam, the Netherlands: Elsevier.
- Meats A. (1998a) The power of trapping grids for detecting and estimating the size of invading propagules of the Queensland fruit fly and risks of subsequent infestation. *General and Applied Entomology*, **28**, 47–55.
- Meats A. (1998b) Predicting or interpreting trap catches resulting from natural propagules or releases of sterile fruit flies. An actuarial and dispersal model tested with data on *Bactrocera tryoni*. *General and Applied Entomology*, **28**, 29–38.
- Meats A. (2006) Attributes pertinent to overwintering potential do not explain why *Bactrocera neohumeralis* (Hardy) (Diptera: Tephritidae) does not spread further south within the geographical range of *B. tryoni* (Froggatt). *Australian Journal of Entomology*, **45**, 20–25.
- Meats A. (2007) Dispersion of fruit flies (Diptera: Tephritidae) at high and low densities and consequences of mismatching dispersions of wild and sterile flies. *Florida Entomologist*, **90**, 136–146.
- Meats A., Edgerton J.E. (2008) Short- and long-range dispersal of the Queensland fruit fly, *Bactrocera tryoni* and its relevance to invasive potential, sterile insect technique and surveillance trapping. *Australian Journal of Experimental Agriculture*, **48**, 1237–1245.
- Meats A., Fay H.A.C. (1976) The effect of acclimation on mating frequency and mating competitiveness in the Queensland fruit fly, *Dacus tryoni*, in optimal and cool mating regimes. *Physiological Entomology*, **1**, 207–212.
- Meats A., Fay H.A.C. (1977) Relative importance of temperature-acclimation and stage in the release of sterile flies for population suppression in Spring: a pilot, caged



- experiment with *Dacus tryoni*. *Journal of Economic Entomology*, **70**, 681–684.
- Meats A., Fay H.A.C. (2000) Distribution of mating frequency among males of the Queensland fruit fly, *Bactrocera tryoni*, in relation to temperature, acclimation and chance. *General and Applied Entomology*, **29**, 27–30.
- Meats A., Fitt G.P. (1987) Survival of repeated frosts by the Queensland fruit fly, *Dacus tryoni*: experiments in laboratory simulated climates with either step or ramp fluctuations in temperature. *Entomologia Experimentalis et Applicata*, **45**, 9–16.
- Meats A., Hartland C.L. (1999) Upwind anemotaxis in response to cue-lure by the Queensland fruit fly, *Bactrocera tryoni*. *Physiological Entomology*, **24**, 90–97.
- Meats A., Khoo K.C. (1976) The dynamics of ovarian maturation and oocyte resorption in the Queensland fruit fly, *Dacus tryoni*, in daily rhythmic and constant temperature regimes. *Physiological Entomology*, **1**, 213–221.
- Meats A., Leighton S.M. (2004) Protein consumption by mated, unmated, sterile and fertile adults of the Queensland fruit fly, *Bactrocera tryoni* and its relation to egg production. *Physiological Entomology*, **29**, 176–182.
- Meats A., Pike N., An X., Raphael K., Wang W.Y.S. (2003a) The effects of selection for early (day) and late (dusk) mating lines of hybrids of *Bactrocera tryoni* and *Bactrocera neohumeralis*. *Genetica*, **119**, 283–293.
- Meats A.W., Clift A.D., Robson M.K. (2003b) Incipient founder populations of Mediterranean and Queensland fruit flies in Australia: the relation of trap catch to infestation radius and models for quarantine radius. *Australian Journal of Experimental Agriculture*, **43**, 397–406.
- Meats A., Smallridge C.J., Dominiak B.C. (2006) Dispersion theory and the sterile insect technique: application to two species of fruit fly. *Entomologia Experimentalis et Applicata*, **119**, 247–254.
- Meats A., Streamer K., Gilchrist A.S. (2009) Bacteria as food had no effect on fecundity during domestication of the fruit fly, *Bactrocera tryoni*. *Journal of Applied Entomology*, **133**, 633–639.
- Messing R.H., Ramadan M.M. (2000) Host range and reproductive output of *Diachasmimorpha kraussii* (Hymenoptera: Braconidae), a parasitoid of tephritid fruit flies newly imported to Hawaii. In *Proceedings: Area-wide Control of Insect Pests, and the 5th International Symposium of Fruit Flies of Economic Importance*, 28 May - 5 June, Penang, Malaysia, pp. 713–718. Ed Tan H.-K. Penerbit Universti Sains Malaysia: Pulau Pinang, Malaysia.
- Metcalf R.L. (1990) Chemical ecology of dacine fruit flies (Diptera: Tephritidae). *Annals of the Entomological Society of America*, **83**, 1017–1030.
- Mitchell M.S., Powell R.A. (2003) Linking fitness landscapes with the behavior and distribution of animals. In *Landscape Ecology and Resource Management. Linking Theory with Practice*, pp. 93–124. Eds J.A. Bissonette and I. Storch. Washington, DC: Island Press.
- Monro J., Richardson N.L. (1969) Traps, male lures, and a warning system for Queensland fruit fly, *Dacus tryoni* (Frogg.) (Diptera: Tephritidae). *Australian Journal of Agricultural Research*, **20**, 325–328.
- Montoya P., Liedo P., Benrey B., Cancino J., Barrera J.F., Sivinski J., Aluja M. (2000) Biological control of *Anastrepha* spp. (Diptera: Tephritidae), in mango orchards through augmentative releases of *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). *Biological Control*, **18**, 216–224.
- Morrow J.L., Scott L., Congdon B., Yeates D., Frommer M., Sved J. (2000) Close genetic similarity between two sympatric species of tephritid fruit fly reproductively isolated by mating time. *Evolution*, **54**, 899–910.
- Morton T.C., Bateman M.A. (1981) Chemical studies on proteinaceous attractants for fruit flies, including the identification of volatile constituents, *Dacus tryoni*. *Australian Journal of Agricultural Research*, **32**, 905–916.
- Moussa A.Y. (1978) A new cytoplasmic inclusion virus from Diptera in the Queensland fruit fly, *Dacus tryoni* (Frogg.) (Diptera: Tephritidae). *Journal of Invertebrate Pathology*, **32**, 77–87.
- Murphy K. (1990) The association between Queensland fruit flies (*Dacus tryoni*) and their alimentary tract microflora, including dinitrogen-fixing bacteria. Ph.D. Thesis, University of Queensland.
- Murphy K.M., Teakle D.S., MacRae I.C. (1994) Kinetics of colonisation of adult Queensland fruit flies (*Bactrocera tryoni*) by dinitrogen-fixing alimentary tract bacteria. *Applied and Environmental Microbiology*, **60**, 2508–2517.
- Navarro-Llopis V., Sanchis-Cabanes J., Ayala I., Casaña-Giner V., Primo-Yúfera E. (2004) Efficacy of lufenuron as chemosterilant against *Ceratitidis capitata* in field trials. *Pest Management Science*, **60**, 914–920.
- Navarro-Llopis V., Sanchis J., Primo-Millo J., Primo-Yufer E. (2007) Chemosterilants as control agents of *Ceratitidis capitata* (Diptera: Tephritidae) in field trials. *Bulletin of Entomological Research*, **97**, 359–368.
- Neale C.J. (1989) Some aspects of the specific-mate recognition systems of *Dacus tryoni* and *Dacus neohumeralis*. M.Sc. Thesis, University of Queensland.
- Nestel D., Nemny-Lavy E., Chang C.L. (2004) Lipid and protein loads in pupating larvae and emerging adults as affected by the composition of Mediterranean fruit fly (*Ceratitidis capitata*) meridic larval diets. *Archives of Insect Biochemistry and Physiology*, **56**, 97–109.
- Nguyen V.L., Meats A., Beattie G.A.C., Spooner-Hart R., Liu Z.M., Jiang L. (2007) Behavioural responses of female Queensland fruit fly, *Bactrocera tryoni*, to mineral oil deposits. *Entomologia Experimentalis et Applicata*, **122**, 215–221.
- O'Loughlin G.T. (1964) The Queensland fruit fly in Victoria. *The Journal of Agriculture*, **62**, 391–402.

- O'Loughlin G.T. (1975) A new look at fruit fly in Victoria. *Journal of Agriculture (Victoria)*, **45**, 8–15.
- O'Loughlin G.T., East R.A., Meats A. (1984) Survival, development rates and generation times of the Queensland fruit fly, *Dacus tryoni*, in a marginally favourable climate: experiments in Victoria. *Australian Journal of Zoology*, **32**, 353–361.
- Osborne R., Meats A., Frommer M., Sved J.A., Drew R.A.I., Robson M.K. (1997) Australian distribution of 17 species of fruit flies (Diptera: Tephritidae) caught in cue lure traps in February 1994. *Australian Journal of Entomology*, **36**, 45–50.
- Pachauri R.K., Reisinger A. Eds (2007) *Climate Change 2007: Synthesis Report Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC.
- Paterson H.E.H. (1991) The recognition concept of cryptic species among economically important insects. In *Heliethis: Research Methods and Prospects*, pp. 1–10. Ed. M.P. Zalucki. New York: Springer-Verlag.
- Peng R.K., Christian K. (2006) Effective control of Jarvis's fruit fly, *Bactrocera jarvisi* (Diptera: Tephritidae), by the weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae), in mango orchards in the Northern Territory of Australia, **52**, 275–282.
- Perez-Staples D., Prabhu V., Taylor P.W. (2007) Post-teneral protein feeding enhances sexual performance of Queensland fruit flies. *Physiological Entomology*, **32**, 225–232.
- Perez-Staples D., Harmer A.M.T., Collins S.R., Taylor P.W. (2008) Potential for pre-release diet supplements to increase the sexual performance and longevity of male Queensland fruit flies. *Agricultural and Forest Entomology*, **10**, 255–262.
- Perkins F.A., Hines H.J.G. (1933) A note on some preliminary experiments with ammonia as a lure for the Queensland Fruit Fly (*Chaetodacus tryoni* Frogg.). *Proceedings of the Royal Society of Queensland*, **45**, 29.
- Perkins F.A., May A.W.S. (1949) Studies in Australian and Oriental Trypetidae. *Papers of the Department of Biology, University of Queensland*, **2**, 1–21.
- Petacchi R., Rizzi I., Guidotti D. (2003) The 'lure and kill' technique in *Bactrocera oleae* (Gmel.) control: effectiveness indices and suitability of the technique in area-wide experimental trials. *International Journal of Pest Management*, **49**, 305–311.
- PHA. (2008) *Draft National Fruit Fly Strategy: March 2008*. Canberra, Australia: Plant Health Australia.
- Pike N. (2004) Natural incidence of fruit flies with character states intermediate to those of the sibling species *Bactrocera tryoni* (Froggatt) and *B. neohumeralis* (Hardy) (Diptera: Tephritidae). *Australian Journal of Entomology*, **43**, 23–27.
- Pike N., Meats A. (2002) Potential for mating between *Bactrocera tryoni* (Froggatt) and *Bactrocera neohumeralis* (Hardy) (Diptera: Tephritidae). *Australian Journal of Entomology*, **41**, 70–74.
- Pike N., Meats A. (2003) Tendency for upwind movement in the sibling fruit fly species, *Bactrocera tryoni* and *B. neohumeralis* and their hybrids (Diptera: Tephritidae): influence of time of day, sex and airborne pheromone. *Bulletin of Entomological Research*, **93**, 173–178.
- Pinero J.C., Mau R.F.L., Vargas R.I. (2009) Managing Oriental fruit fly (Diptera: Tephritidae), with spinosad-based protein bait sprays and sanitation in papaya orchards in Hawaii. *Journal of Economic Entomology*, **102**, 1123–1132.
- PIRSA. (2006) Conditions of entry index – strawberry. Plant Quarantine Standard South Australia. Department of Primary Industries & Resources SA, Adelaide, South Australia.
- Pratt C. (2009) Can the Queensland fruit fly parasitoid *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera: Braconidae) be reared on hosts irradiated as eggs? M.Sc. Thesis, Imperial College, London.
- Pritchard G. (1969) The ecology of a natural population of Queensland fruit fly, *Dacus tryoni*. II The distribution of eggs and its relation to behaviour. *Australian Journal of Zoology*, **17**, 293–311.
- Prokopy R.J. (1968) Visual responses of apple maggot flies, *Rhagoletis pomonella* (Diptera: Tephritidae): Orchard studies. *Entomologia Experimentalis et Applicata*, **11**, 403–422.
- Prokopy R.J., Fletcher B.S. (1987) The role of adult learning in the acceptance of host fruit for egg laying by the Queensland Fruit fly, *Dacus tryoni*. *Entomologia Experimentalis et Applicata*, **45**, 259–263.
- Prokopy R.J., Drew R.A.I., Sabine B.N.E., Lloyd A.C., Hamacek E. (1991) Effect of physiological and experimental state of *Bactrocera tryoni* flies on intra-tree foraging behaviour for food (bacteria) and host fruit. *Oecologia*, **87**, 394–400.
- Prokopy R.J., Romig M.C., Drew R.A.I. (1999) Facilitation in ovipositional behavior of *Bactrocera tryoni* flies. *Journal of Insect Behavior*, **12**, 815–835.
- Prokopy R.J., Miller N.W., Pinero J.C., Oride L., Chaney N., Revis H., Vargas R.I. (2004) How effective is GF-120 Fruit Fly bait spray applied to border area sorghum plants for control of melon flies (Diptera: Tephritidae)? *Florida Entomologist*, **87**, 354–360.
- Quimio G.M. (2000) *Mating Behaviour and Host Relationships of the Fruit Fly Parasitoid Fopius Arisanus (Sonan) (Hymenoptera: Braconidae)*. Australia: The University of Queensland.
- Quimio G.M., Walter G.H. (2001) Host preference and host suitability in an egg-pupal fruit fly parasitoid, *Fopius arisanus* (Sonan) (Hym., Braconidae). *Journal of Applied Entomology*, **125**, 135–140.
- Raghu S. (2004) Functional significance of phytochemical lures to dacine fruit flies (Diptera: Tephritidae): an

- ecological and evolutionary synthesis. *Bulletin of Entomological Research*, **94**, 385–399.
- Raghu S., Clarke A.R., Drew R.A.I., Hulsman K. (2000) Impact of habitat modification on the distribution and abundance of fruit flies (Diptera: Tephritidae) in Southeast Queensland. *Population Ecology*, **42**, 153–160.
- Raghu S., Clarke A.R., Bradley J. (2002) Microbial mediation of fruit fly-host plant interactions: is the host plant the “centre of activity”? *Oikos*, **97**, 319–328.
- Raghu S., Drew R.A.I., Clarke A.R. (2004) Influence of host plant structure and microclimate on the abundance and behaviour of a tephritid fly. *Journal of Insect Behavior*, **17**, 179–190.
- Rasgado M.A., Malo E.A., Cruz-Lopez L., Rojas J.C., Toledo J. (2009a) Olfactory response of the Mexican fruit fly (Diptera: Tephritidae) to *Citrus aurantium* volatiles. *Journal of Economic Entomology*, **102**, 585–594.
- Rasgado M.A., Malo E.A., Cruz-Lopez L., Rojas J.C., Toledo J. (2009b) Olfactory response of the Mexican Fruit Fly (Diptera: Tephritidae) to *Citrus aurantium* volatiles. *Journal of Economic Entomology*, **102**, 585–594.
- Rattanapun W., Amornsak W., Clarke A.R. (2009) *Bactrocera dorsalis* preference for and performance on two mango varieties at three stages of ripeness. *Entomologia Experimentalis et Applicata*, **131**, 243–253.
- Reinert R.A., Eason G., Barton J. (1997) Growth and fruiting of tomato as influenced by elevated carbon dioxide and ozone. *New Phytologist*, **137**, 411–420.
- Rendon P., Sivinski J., Holler T., Bloem K., Lopez M., Martinez A., Aluja M. (2006) The effects of sterile males and two braconid parasitoids, *Fopius arisanus* (Sonan) and *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera), on caged populations of Mediterranean fruit flies, *Ceratitidis capitata* (Wied.) (Diptera: Tephritidae) at various sites in Guatemala. *Biological Control*, **36**, 224–231.
- Reynolds A.H., Prokopy R.J. (1997) Evaluation of odor lures for use with red sticky spheres to trap apple maggot (Diptera: Tephritidae). *Journal of Economic Entomology*, **90**, 1655–1660.
- Rice M.J. (1989) The sensory physiology of pest fruit flies: conspectus and prospectus. In *Fruit Flies – Their Biology, Natural Enemies and Control*. World Crop Pests 3A. Eds A.S. Robinson and G.H.S. Hooper. Amsterdam, the Netherlands: Elsevier.
- Rona L.P., Carvalho-Pinto C.J., Gentile C., Grisard E.C., Peixoto A.A. (2009) Assessing the molecular divergence between *Anopheles (Kerteszia) cruzii* populations from Brazil using the timeless gene: further evidence of a species complex. *Malaria Journal*, **8**, 60.
- Rungrojwanich K. (1994) *The Life Cycle, Mating Behaviour and Sexual Communication Signals of Diachasmimorpha Kraussii (Fullaway) (Hymenoptera: Braconidae), a Parasitoid of Dacine Fruit Flies (Diptera: Tephritidae)*. Ph.D. thesis. Brisbane, Australia: The University of Queensland.
- Rungrojwanich K., Walter G.H. (2000a) The Australian fruit fly parasitoid *Diachasmimorpha kraussii* (Fullaway): life history, ovipositional patterns, distribution and hosts (Hymenoptera: Braconidae: Opiinae). *Pan-Pacific Entomologist*, **76**, 1–11.
- Rungrojwanich K., Walter G.H. (2000b) The Australian fruit fly parasitoid *Diachasmimorpha kraussii* (Fullaway): mating behaviour, modes of sexual communication and crossing tests with *D. longicaudata* (Ashmead) (Hymenoptera: Braconidae: Opiinae). *Pan-Pacific Entomologist*, **76**, 12–23.
- Shearman D.C.A., Gilchrist A.S., Crisafulli D., Graham G., Lange C., Frommer M. (2006) Microsatellite markers for the pest fruit fly, *Bactrocera papayae* (Diptera: Tephritidae) and other *Bactrocera* species. *Molecular Ecology Notes*, **6**, 4–7.
- Shelly T.E., Whittier T.S. (1995) Lek distribution in the Mediterranean fruit fly: influence of tree size, foliage density and neighborhood. *Proceedings of the Hawaiian Entomological Society*, **32**, 32.
- Sime K.R., Daane K.M., Wang X.G., Johnson M.W., Messing R.H. (2008) Evaluation of *Fopius arisanus* (Hymenoptera: Braconidae) as a biological control agent for the olive fruit fly in California. *Agricultural and Forest Entomology*, **10**, 423–431.
- Smith D., Nannan L. (1988) Yeast autolysate bait sprays for control of Queensland fruit fly on passionfruit in Queensland. *Queensland Journal of Agricultural and Animal Sciences*, **45**, 169–177.
- Smith E.S.C., Chin D., Allwood A.J., Collins S.G. (1988) A revised host list of fruit flies (Diptera: Tephritidae) from the Northern Territory of Australia. *Queensland Journal of Agricultural and Animal Sciences*, **45**, 19–28.
- Snowball G.J. (1966) Status of introduced parasites of Queensland fruit fly *Dacus (Strumeta) Tryoni*, 1962–1965. *Australian Journal of Agricultural Research*, **17**, 719–739.
- Snowball G.J., Lukins R.G. (1964) Status of introduced parasites of Queensland fruit fly (*Strumeta tryoni*), 1960–1962. *Australian Journal of Agricultural Research*, **15**, 586–608.
- Snowball G.J., Wilson F., Campbell T.G., Lukins R.G. (1962a) The utilization of parasites of Oriental fruit fly (*Dacus dorsalis*) against Queensland fruit fly (*Strumeta tryoni*). *Australian Journal of Agricultural Research*, **13**, 443–460.
- Snowball G.J., Wilson F., Lukins R.G. (1962b) Culture and consignment techniques used for parasites introduced against Queensland fruit fly (*Strumeta tryoni* (Frogg.)). *Australian Journal of Agricultural Research*, **13**, 233–248.
- Sonleitner F.J., Bateman M.A. (1963) Mark recapture analysis of a population of Queensland fruit fly, *Dacus tryoni* (Frogg.) in an orchard. *Journal of Animal Ecology*, **32**, 259–269.



- Stange G. (1999) Carbon dioxide is a close-range oviposition attractant in the Queensland fruit fly, *Bactrocera tryoni*. *Naturwissenschaften*, **86**, 190–192.
- Stark J.D., Vargas R., Miller N. (2004) Toxicity of spinosad in protein bait to three economically important tephritid fruit fly species (Diptera: Tephritidae) and their parasitoids (Hymenoptera: Braconidae). *Journal of Economic Entomology*, **97**, 911–915.
- Stiling P., Cornelissen T. (2007) How does elevated carbon dioxide (CO<sub>2</sub>) affect plant-herbivore interactions? A field experiment and meta-analysis of CO<sub>2</sub>-mediated changes on plant chemistry and herbivore performance. *Global Change Biology*, **13**, 1823–1842.
- Suckling D.M. (2000) Issues affecting the use of pheromones and other semiochemicals in orchards. *Crop Protection*, **19**, 677–683.
- Sutherst R.W., Collyer B.S., Yonow T. (2000) The vulnerability of Australian horticulture to the Queensland fruit fly, *Bactrocera (Dacus) tryoni*, under climate change. *Australian Journal of Agricultural Research*, **51**, 467–480.
- Tryon H. (1889) Inquiry into diseases affecting the fruit trees and other economic plants in the Toowoomba district. Parliamentary Paper, Brisbane.
- Tryon H. (1892) The parasite of the fruit maggot. *Transactions of the Natural History Society of Queensland*, **1**, 8–9.
- Urbaneja A., Mari F.G., Tortosa D., Navarro C., Vanaclocha P., Bargues L., Castanera P. (2006) Influence of ground predators on the survival of the mediterranean fruit fly pupae, *Ceratitis capitata*, in Spanish citrus orchards. *Biocontrol*, **51**, 611–626.
- Van Mele P., Vayssieres J.F., Adandonon A., Sinzogan A. (2009) Ant cues affect the oviposition behaviour of fruit flies (Diptera: Tephritidae) in Africa. *Physiological Entomology*, **34**, 256–261.
- Vargas R.I., Miller N.W., Prokopy R.J. (2002) Attraction and feeding responses of Mediterranean fruit fly and a natural enemy to protein baits laced with two novel toxins, phloxine B and spinosad. *Entomologia Experimentalis et Applicata*, **102**, 273–282.
- Vijaysegaran S., Walter G.H., Drew R.A.I. (1997) Mouthpart structure, feeding mechanisms, and natural food sources of adult *Bactrocera* (Diptera: Tephritidae). *Annals of the Entomological Society of America*, **90**, 184–201.
- Vijaysegaran S., Walter G.H., Drew R.A.I. (2002) Influence of adult diet on the development of the reproductive system and mating ability of Queensland fruit fly *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). *Journal of Tropical Agriculture and Food Science*, **30**, 119–136.
- Virgilio M., Backeljau T., Barr N., Meyer M.D. (2008) Molecular evaluation of nominal species in the *Ceratitis fasciventris*, *C. anonae*, *C. rosa* complex (Diptera: Tephritidae). *Molecular Phylogenetics and Evolution*, **48**, 270–280.
- Vogt W.G. (1970) Identification of sexually isolated taxonomic clusters within the *Dacus tryoni*-*neohumeralis* complex. Ph.D. Thesis, University of Sydney.
- Walter G.H. (2003) *Insect Pest Management and Ecological Research*. Cambridge, UK: Cambridge University Press.
- Walter G.H., Hengeveld R. (2000) The structure of the two ecological paradigms. *Acta Biotheoretica*, **48**, 15–46.
- Wang Y., Yu H., Raphael K., Gilchrist A.S. (2003) Genetic delineation of sibling species of the pest fruit fly *Bactrocera* (Diptera: Tephritidae) using microsatellites. *Bulletin of Entomological Research*, **93**, 351–360.
- Waterhouse D.F., Sands D.P.A. (2001) *Bactrocera tryoni* (Froggatt) Diptera: Tephritidae Queensland fruit fly. *Classical Biological Control of Arthropods in Australia*, pp. 305–315. Canberra, Australia: ACIAR.
- Weitzel T., Collado A., Jöst A., Pietsch K., Storch V., Becker N. (2009) Genetic differentiation of populations within the *Culex pipiens* complex and phylogeny of related species. *Journal of the American Mosquito Control Association*, **25**, 6–17.
- Weldon C., Meats A. (2007) Short-range dispersal of recently emerged males and females of *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) monitored by sticky sphere traps baited with protein and Lynfield traps baited with cue-lure. *Australian Journal of Entomology*, **46**, 160–166.
- Weldon C.W. (2005) Dispersal and mating behaviour of Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae): implications for population establishment and control. Ph.D. Thesis, University of Sydney.
- Weldon C.W., Meats A. (2009) Dispersal of mass-reared sterile, laboratory domesticated and wild male Queensland fruit flies. *Journal of Applied Entomology*, **134**, 16–25.
- Weldon C.W., Perez-Staples D., Taylor P.W. (2008) Feeding on yeast hydrolysate enhances attraction to cue-lure in Queensland fruit flies (*Bactrocera tryoni*). *Entomologia Experimentalis et Applicata*, **129**, 200–209.
- White I.M., Elson-Harris M.M. (1992) *Fruit Flies of Economic Significance: Their Identification and Bionomics*. Canberra, Australia: ACIAR and Wallingford, UK: CAB International.
- Wilson A. (2008) Insect frugivore interactions: the potential for beneficial and neutral effects on host plants. Ph.D. Thesis, Queensland University of Technology.
- Wolda H. (1967a) Reproductive isolation between two closely related species of the Queensland Fruit Fly, *Dacus tryoni* (Frogg.) and *D. neohumeralis* Hardy (Diptera: Tephritidae): I variation in humeral callus pattern and the occurrence of intermediate colour forms in the wild. *Australian Journal of Zoology*, **15**, 501–513.
- Wolda H. (1967b) Reproductive isolation between two closely related species of the Queensland Fruit Fly, *Dacus tryoni* (Frogg.) and *D. neohumeralis* Hardy (Diptera: Tephritidae): II Genetic variation in humeral callus



- pattern in each species as compared with laboratory-bred hybrids. *Australian Journal of Zoology*, **15**, 515–539.
- Worsley P.M., Dominiak B.C., Gilmour A.R., James D.G. (2008) Pilot study at Cowra of intra-town dynamics of Queensland Fruit Fly (*Bactrocera tryoni* (Froggatt)) populations based on trap catch data. *Plant Protection Quarterly*, **23**, 86–89.
- Yee W.L. (2006) Feeding history effects on feeding responses of *Rhagoletis indifferens* (Dipt., Tephritidae) to GF-120 and Nulure. *Journal of Applied Entomology*, **130**, 538–550.
- Yee W.L. (2007) Attraction, feeding, and control of *Rhagoletis pomonella* (Diptera: Tephritidae) with GF-120 and added ammonia in Washington state. *Florida Entomologist*, **90**, 665–673.
- Yee W.L., Chapman P.S. (2005) Effects of GF-120 Fruit Fly Bait concentrations on attraction, feeding, mortality, and control of *Rhagoletis indifferens* (Diptera: Tephritidae). *Journal of Economic Entomology*, **98**, 1654–1663.
- Yonow T., Sutherst R.W. (1998) The geographical distribution of the Queensland fruit fly, *Bactrocera (Dacus) tryoni*, in relation to climate. *Australian Journal of Agricultural Research*, **49**, 935–953.
- Yonow T., Zalucki M.P., Sutherst R.W., Dominiak B.C., Maywald G.F., Maelzer D.A., Kriticos D.J. (2004) Modelling the population dynamics of the Queensland fruit fly, *Bactrocera (Dacus) tryoni*: a cohort-based approach incorporating the effects of weather. *Ecological Modelling*, **173**, 9–30.
- Yu H., Frommer M.K., Robson M.K., Sved J.A. (2000) A population analysis of the Queensland fruit fly *Bactrocera tryoni* using microsatellite markers. In *Area-Wide Control of Fruit Flies and Other Insect Pests*, pp. 497–508. Eds T. K-H. Pulau Pinang, Malaysia: Penerbit Universiti Sains Malaysia.
- Yu H., Frommer M., Robson M.K., Meats A.W., Shearman D.C.A., Sved J.A. (2001) Microsatellite analysis of the Queensland fruit fly *Bactrocera tryoni* (Diptera: Tephritidae) indicates spatial structuring: Implications for population control. *Bulletin of Entomological Research*, **91**, 139–147.
- Zalucki M.P. (Ed.) (1991) *Heliothis: Research Methods and Prospects*. Heidelberg, Germany: Springer-Verlag.
- Zalucki M.P., Drew R.A.I., Hooper G.H.S. (1984) Ecological studies of eastern Australian fruit flies (Diptera: Tephritidae) in their endemic habitat. II. The spatial pattern of abundance. *Oecologia*, **64**, 273–279.
- Zalucki M.P., Daghli G., Firempong S., Twine P. (1986) The biology and ecology of *Heliothis armigera* (Hubner) and *Heliothis punctigera* Wallengren (Lepidoptera, Noctuidae) in Australia – What do we know. *Australian Journal of Zoology*, **34**, 779–814.