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The ecology of *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae): what do we know to assist pest management?

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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* s.s., *B. neohumeralis*, *B. melas* and *B. aquilonis*. The species status of *B. melas* and *B. aquilonis* are 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 CO₂, 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 which is covered in a companion paper). We conclude that there are major gaps in the knowledge required to implement most non-insecticide 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 Australia's worst horticultural pest insect, attacking most fruit and many vegetable crops. 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). 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 \$28.5mill/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 mill in the years 2003-2008 (PHA 2008).

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. Drew and Romig 2000; Fletcher 1989a; b; Meats 1989a; b) and as part of modelling exercises (Yonow and 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 [(Allman 1938; Allman 1939; Allman 1941; Allman and Friend 1948)] and Jarvis [(Jarvis 1922a; b; c; 1923; 1924; 1925a; b; c; 1926a; b; 1931)] are notable exceptions). However, paradoxically, most of this 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 post-harvest 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 practise. 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 post-harvest 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), non-commercial host plants and non-crop habitats (manipulated through habitat management). To make these alternatives viable replacements for chemical treatments, or to maintain their use (eg 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 don't 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 don't 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 identify and justify priority issues for further research. This review does not touch on post-harvest 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 Sterile Insect Technique which is dealt with in a companion paper.

***Bactrocera tryoni* complex**

Accurate species identification is a central tenant of successful pest management (Paterson 1991; Walter 2003). While this may appear a simple and self-evident statement, defining the 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 systematic 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 done on *B. tryoni sensu stricto* (Gilchrist *et al.* 2006; Gilchrist and 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* s.s.. 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 been done on understanding the relationship between *B. tryoni* and *B. neohumeralis* (An *et al.* 2002; Bellas and Fletcher 1979; Birch 1961; Gee 1966; 1969; Gibbs 1967; McKechnie 1972; 1975; Neale 1989; Vogt 1970; Wang *et al.* 2003). The two species can be separated from each on one clear behavioural difference; *B. tryoni* mates at dusk and *B. neohumeralis* in the middle of the day (Lewontin and Birch 1966; Pike and 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 hybridization (Birch 1961; Pike 2004), more recent genetic analysis (Gilchrist and Ling 2006) confirms the earlier work of Wolda (Wolda 1967a; b) that variation in the colour of the humeral calli is a genetic trait of the parent and not a reflection of hybridization. Until recently, genetic tests could not readily discriminate between *B. tryoni* and *B. neohumeralis* (An *et al.* 2002; Armstrong *et al.* 1997; Green and Frommer 2001; Morrow *et al.* 2000), but microsatellite techniques have now proved useful in discriminating between the species (Gilchrist and 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 and Meats (2002) and Meats *et al.* (2003a) (for time of mating); Pike (2004) and Gilchrist and Ling (2006) (for variation in the humeral calli); and Wang *et al.* (2003) and Gilchrist and 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 (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 also regarded as endemic to Papua New Guinea (Drew 1989). Having a much more restricted host range than Australian populations, and with essentially non-existent host 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 (Drew and Lambert 1986; Morrow *et al.* 2000) supported the validity of this species, 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 1980's when this previously non-pest 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.* (in press) 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 supports 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 and 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 inter-specific 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 and 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 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* need to be confirmed as a matter of urgency to determine if they are valid species, or are both junior synonyms of *B. tryoni*. Results either way 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 probably 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 (Maelzer 1990a; b; Maelzer *et al.* 2004a; b; May 1963; Meats *et al.* 2006), and a single outbreak was detected and successfully eradicated from Perth, Western Australia (Ayling 1989; Fisher 1996). However, these parts of Australia usually remain free of *B. tryoni* due to isolation from the permanent distribution range of *the fly* by intervening regions with unsuitable conditions (Meats 1981; Yonow and 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 and 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, determines the southern extent of the distribution of *B. tryoni* (Meats 1981; O'Loughlin *et al.* 1984; Yonow and Sutherst 1998). 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 and 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 *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 and Fay 1976; 1977; O'Loughlin *et al.* 1984). In addition to plasticity in their ability to tolerate cool temperatures, *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).

Dry stress is considered a key factor restricting the distribution and abundance of Queensland fruit fly (Yonow and Sutherst 1998), 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 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.

Distribution under climate change

Atmospheric CO₂ 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 CO₂ concentrations, as well as other greenhouse gases including methane and nitrous oxide, has been linked to rapid increases in global temperature (Pachauri and 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 and 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 0.4-1.8°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 modeled 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 rate 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 25mm 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 CO₂

Elevated atmospheric CO₂ has a “fertilization effect” on plant growth through higher rates of photosynthesis that leads to increased production of above- and below-ground biomass. Growth effects of elevated CO₂ may be dramatic in urban and horticultural systems where soil water and nutrients are not limiting (Idso and 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 CO₂. Further, elevated CO₂ 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 CO₂ (Kimball *et al.* 2007).

The quantitative and qualitative changes in fruit produced by plants grown at elevated CO₂ 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 and Trumble 1999; Stiling and Cornelissen 2007). There has so far been no research on the consequences of elevated CO₂ 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; Kaspri *et al.* 2002; Nestel *et al.* 2004)

Ecology Relevant to Control Techniques

Lure and kill techniques / trapping

Introduction

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, 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), non-volatile 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; Petacchi *et al.* 2003; Suckling 2000).

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 and Voller 1899). While Benson and Voller were unsuccessful in finding a lure¹, lures remained a focal point for early fruit fly workers (Caldwell and May 1943; Gurney 1925; Jarvis 1923; 1925b; 1931; Perkins and Hines 1933) and were recommended as control options (Jarvis 1926b), although with limited initial success (Jarvis 1925b). 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. This section reviews the science underpinning lure and kill approaches for *B. tryoni* and, while focusing on MAT and PBS, also discusses the potential for female chemical and physical lures.

Protein Bait Spray and Bacteria

Both male and female *B. tryoni* need protein in order to sexually mature (Meats and Leighton 2004; Perez-Staples *et al.* 2008; Perez-Staples *et al.* 2007). In nature, *B. tryoni* is presumed to get the majority of its protein through feeding on leaf surface bacteria (Courtice and Drew 1984; Drew and Lloyd 1987; 1989; 1991; Lloyd 1991; Lloyd *et al.* 1986). 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; Vijayasegaran *et al.* 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 coevolved system (Drew and Lloyd 1987; Prokopy *et al.* 1991), or happens incidentally as part of routine foraging (Raghu *et al.* 2002). A study conducted by Fitt and 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 the *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

¹ They were successful in finding repellents, one of which was reported as: "A mixture made as follows:- Boil 2 lb. of sulphur and 1 lb. of 98 per cent. caustic soda in 2 gallons of water till the sulphur is dissolved, and a mixture known as sulphide of soda is formed. Add 6 lb. of whale-oil soap, 80 per cent.; and boil for half an hour, adding boiling water to make 5 gallons of mixture; then add 40 fl. oz. of black leaf tobacco extract. Next add water to make 40 gallons, and it is ready to use."

(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 and 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; Lloyd *et al.* 2003), with few formal publications on the use of the technique in the field (Hargreaves *et al.* 1986; Jones and Skepper 1965; Lloyd *et al.* in press; Smith and Nannan 1988).

The extensive literature on *B. tryoni* - bacteria interactions adds only a little to the science underpinning protein bait spray technology. Bateman and Morton (1981) showed that ammonia was the volatile attracting flies to protein, but this was considered unlikely by Drew and 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 and 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. A valuable contribution of this latter paper is the recording 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, i.e. flies already on a fruit host plant for other purposes may detect the protein volatiles from short distances away, but may have little ability to detect the protein volatiles when in other locations. If targeting gravid females then this is particularly likely to be the case, as 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/non-sterile) influences attractiveness and effectiveness of baits (Barry *et al.* 2003; Yee 2006 ; Yee and Chapman 2005); determining where flies forage for baits and how this might be used in management (e.g. with respect to border applications) (McQuate and Vargas 2007 ; Prokopy *et al.* 2004); and determining how protein bait sprays interact with other components of AWM (Lloyd *et al.* in press; Pinero *et al.* 2009; Stark *et al.* 2004; Vargas *et al.* 2002). 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.

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 (i.e. raspberry ketone) (Metcalf 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* (Bateman and Arretz 1973; Dominiak *et al.* 2003a; Monro and Richardson 1969). 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 and 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 done on the functional role (if any) 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 and Hartland 1999), while the presence of cue-lure in the local environment increases *B. tryoni* flight activity (Dalby-Ball and 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 12m), but in the open canopy environments of a eucalypt forest and citrus orchard no effect was evident in the height ranges of 0.1-12m and 0.1-3.6m, respectively (Hooper and Drew 1979). As for other *Bactrocera* species, female *B. tryoni* are traditionally regarded as being non-lure responsive (Drew 1987a; Hill 1986), 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 is associated with the mating system, 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 and 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 Q-fly 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 80m apart in a grid, or 400m apart in line, states that “pairs of cue-lure traps spaced 0.4km apart along a trap line in sclerophyll bushland caught approximately 8% of the males per week in the surrounding area of 0.16 km²”. Similarly, Monro and 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 400m 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 400m. Meats (Meats 1998a; b) collates data from a number of different trapping programmes and, applying several modelling approaches, concludes that a 1000m trapping grid is significantly less effective (approximately 1/6th) than a 400m 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), it is not clear how much of this variation may be due to variation in trap efficiency (i.e. the same number of flies are present, but traps vary in their ability to catch flies) and how much is due to differences in absolute population numbers (i.e. lower trap catches are because there are fewer flies in the area, and *vice versa*). Cue-lure traps are strongly influenced by weather conditions (MacFarlane *et al.* 1987; Monro and Richardson 1969) and this influences their efficiency.

Female Lures

Sexually mature and mated female *B. tryoni* do not respond to cue-lure (Drew 1987) and there are no effective lures for female *B. tryoni* currently available (although this is an area of active research). Caldwell and 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; 1961a; b; 1963; May and 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 non-target 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 (Gonzalez *et al.* 2006; Malo *et al.* 2005; Rasgado *et al.* 2009b).

Colour traps & 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 and Prokopy 1992; Duan and Prokopy 1993; 1995; Reynolds and Prokopy 1997). Fruit mimics have also been developed or researched for other pest tephritids, including *Neoceratitis cyanescens* (Brévault and Quilici 2007) and *Ceratitis capitata* (Katsoyannos and 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 1983b). When exposed on flat sticky traps, colours most closely associated with the wavelength of green foliage colour (550nm) (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 and 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 and 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 50mm diameter spheres proving more attractive than clusters of 15mm 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 addition of fruit odours to fruit mimicking coloured spheres has been trialled only once for *B. tryoni* (Dalby-Ball and Meats 2000b). The results are ambiguous with respect to development of fruit mimics, however, because the focus of the study was on *B. tryoni* flight activity, not development of attractants. The data showed increased alighting of flies on fruit mimics when a chemical odour was associated with the mimic. Weldon and Meats (2007) added protein autolysate to hollow black or yellow sticky spheres, but their study was concerned with the protein attraction, not the sphere *per se*. Semiochemicals associated with *B. tryoni* host location and oviposition are covered later in this review, but in general are poorly studied. Hill and Hooper (1984) found that when cue-lure was added to flat sticky traps, the lure response dominated over colour influences. Based on research done 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 done.

Area-wide Management and Areas of Low Pest Prevalence

Area-wide Management (AWM) involves the suppression of a pest population over an entire agricultural district (including its towns). 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.* (in press) detail a specific case of *B. tryoni* AWM in the Central Burnett district of SE Queensland. The knowledge required to operate an effective AWM program 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).

It is anticipated that ALPP-FFs will become more common in Australia, especially as the currently fruit fly free areas become increasingly difficult to maintain due to operational and economic constraints. In this section we cover those areas of the ecology of *B. tryoni* pertinent to both ALPP-FF and AWM.

Habitat use

“Habitat” is a fundamental concept in ecology, however, it is recognized 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, eg “*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 and Walter 1999; Mitchell and Powell 2003; Walter 2003; Walter and 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). While this may have been the case, *B. tryoni* is now rare in rainforests compared to other habitat types. In a study in the Cooloola 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 (Dominiak *et al.* 2006; Fletcher 1974b; Mavi and Dominiak 2001; Mavi and Dominiak 1999), but its rarity in its supposedly endemic forest habitat is less commonly noted.

At the landscape level, *B. tryoni* is known to be collected more frequently around water courses than in less sheltered or open areas (Courtice and Drew 1984; Fletcher 1974a; 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) and this may partially explain why they are found less in open areas. 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 (Courtice and Drew 1984; Drew 1987a; Drew *et al.* 1983; Drew and Lloyd 1987; 1989; 1991; Drew and Romig 2000; Drew and Yuval 2000; Prokopy *et al.* 1991) has 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 behaviors 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 & Movement

Dispersal distance

Dispersal is considered an important characteristic of *B. tryoni*, with both immigration and emigration playing a role in local population dynamics (Bateman and Sonleitner 1967; Fletcher 1973; Sonleitner and Bateman 1963). High rates of dispersion in this species are considered an evolved behaviour associated with finding suitable hosts in rainforest (Fletcher 1974a). Using mark/release/recapture techniques 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 94km 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 1977; Bateman and Sonleitner 1967; Dominiak *et al.* 2003b; Fletcher 1973; 1974a; MacFarlane *et al.* 1987; Meats *et al.* 2006; Weldon and Meats 2007; Weldon 2005; Weldon and Meats 2009). Modelled analysis of *B. tryoni* trap data similarly reflects relatively low dispersal distances, but also reinforces the problems of detecting low populations of flies (Meats 1998b; 2007; Meats and Edgerton 2008; Meats *et al.* 2006; Meats *et al.* 2003b).

Role of wind

Fletcher (1974a) and Dominak *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 and Meats 2003) and so it is possible that the sexes separate somewhat after emergence.

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 and Bateman 1963). When undertaking pre-winter 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 (Fletcher 1979). Irrespective of the immediate suitability of a location for breeding, post-teneral flies move away from their emergence sites (Fletcher 1973). However, Fletcher notes that these post-teneral flies re-enter breeding localities when they are sexually mature if fruits are available and the weather favorable. 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.* in press; Gilchrist *et al.* 2006; Yu *et al.* 2001; Yu *et al.* 2000), while in inland southern regions, where the fly is incursive, fly populations are best considered as meta-populations with reinvasion from source populations and regular local extinction (Gilchrist *et al.* 2006).

Host Use

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 35-45 ovarioles (Anderson and 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 pers comm..) eggs per female per day. Oviposition rate is likely to be influenced by host plant and environmental factors, particularly temperature (Yonow and Sutherst 1998). The eggs of *B. tryoni* are smaller than those of the closely related *B. jarvisi* and it 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 and Khoo 1976), thereby reducing the potential number of eggs available for oviposition.

Oviposition behaviour

The specific actions of *B. tryoni* oviposition behaviour were described 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 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*. They reported 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 also begin ovipositing than 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 (Hancock *et al.* 2000; May 1953; 1957; 1960); 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 and McCarthy (1993) reported that although cucurbits had previously not been a known host 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 and Elson-Harris 1992). *Bactrocera tryoni* may have a broader host range than is currently known and this requires further investigation, along with a comparative analysis of the relative susceptibility of its hosts and associated fruit traits.

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 and assist with potential breeding programs for resistance. Within host plant species, variation in susceptibility is likely to be quite broad, but very few studies have examined this. 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 due to both chemical and physical properties of the host (Balagawi *et al.* 2005).

Host location

Adult female tephritids possess olfactory, gustatory, hygro-, thermal-, photo-, mechano- and chemo-receptors (Rice 1989), although the structure and specific function of these receptors is poorly defined for *B. tryoni*. From studies using artificial fruit, olfactory and visual stimuli are known to attract *B. tryoni* to fruit prior to oviposition (Fowler 1977). Studies to identify the chemical attractants involved for specific host fruit 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 stimulates the effect of ethylene in ripening fruit, the influence of 2-chloroethanol on *B. tryoni* was examined in laboratory studies (Fletcher and Watson 1974). Ethylene was found to attract gravid females to fruit and to stimulate their oviposition response in apples at low concentrations (< or equal to 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 and Meats 2000b). Further characterisation of the complex mixture of headspace volatiles of host fruit for *B. tryoni*, using either conventional coupled electro-antennagram/gas chromatography (EAG/GC) or new generation 'electronic nose' (Lebrun *et al.* 2008), may enable the identification of compounds which either attract or deter gravid females from the host.

Fruit abundance is also important in location of suitable hosts. Using potted orange trees, Dalby-Ball and 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 been conducted in the presence of a mosaic of multiple host species, or with hosts other than citrus or pome fruit.

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* (Bateman 1972; Fletcher 1973; 1974b; 1987; Katsoyannos 1989; Prokopy 1968). 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 and 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 pers comm.; O. Reynolds, pers comm.; A. Jessup pers comm.). 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 and 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 effect 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 CO₂ from blemished fruit stimulated oviposition. Eisemann and 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 thin 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).

Fruit chemical properties

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 host plant location and oviposition response in *B. tryoni* cover a diverse range of compounds including 2-chloroethanol (Fletcher and Watson 1974), fructose (Eisemann and Rice 1985), 2-butanone, n-butyric acid, carbon sesquiterpene, α -farnesene (Eisemann and Rice 1992) and carbon dioxide (Stange 1999). Oviposition stimulants such as fructose have been shown to be effective at between 4-50mM concentration in stimulating oviposition into an artificial membrane, whilst the presence of calcium chloride appears to deter oviposition (Eisemann and Rice 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 and Fletcher 1985; Hull 1998; Hull and Cribb 1997) specific chemoreceptor functions have not yet been fully characterised. Using an electroantennogram, 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 and Cribb 2001a; 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 research overseas (Malo *et al.* 2005; Rasgado *et al.* 2009a).

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 mauritanum*, 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.

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 due to 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 four weeks feeding and developing in fruit. The external and internal morphology of *B. tryoni* immature stages have been well characterised (Anderson 1962; 1963a; b; 1964a; b; Elson-Harris 1988; Exley 1955). 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 reduce hatch and delayed larval maturity and development (Allman 1939; 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 (Bateman 1968; Meats 1983a; 1984; 1987; Meats and Fitt 1987; O'Loughlin 1964; O'Loughlin *et al.* 1984), larval density, fruit suitability and maturity, but less so on moisture as larvae are located in stable moist environments (Meats 1989b). 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 and Kvedaras in press).

Parasitoids

Despite having a native fruit fly parasitoid fauna in Australia (Carmichael *et al.* 2005), a fact recognised by the earliest fruit fly workers (French 1910; Gurney 1910; Tryon 1892), exotic opiines were liberated into Australia for *B. tryoni* control during the 1930s (Allman 1939; Gurney 1936) and then again in the 1950s (Snowball 1966; Snowball and Lukins 1964; Snowball *et al.* 1962a; Snowball *et al.* 1962b). A comprehensive review of classical biological control releases targeted against *B. tryoni* is provided by Waterhouse and Sands (2001). With the exception of post-release work carried out by Snowball (Snowball 1966; Snowball and 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.* (in press) 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 pers comm.; E. Hamacek pers comm.). Australian parasitoids have also been exported and data accumulated as part of offshore biological control programs (particularly for *D. kraussii* and *D. tryoni*), while a small number of postgraduate research programs have also been completed (Carmichael 2009; Ero 2009; Quimio 2000; Rungrojwanich 1994). 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*, this does not automatically make them suitable for all pre-harvest 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 (for example tomato but not zucchini), and appeared in an orchard only after adult fruit flies were present. The wasp did not orient to uninfested fruit, 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. As such inundative releases of the wasp could not be used successfully as a routine treatment to prevent damage as the wasps are likely to depart the area before damage occurred. In contrast, however, the wasp could be used as

part of an integrated, area-wide suppression program, so long as it oriented to the dominant crop types in the target region. Similar research with *F. arisanus* has highlighted that host utilisation strategies are not straightforward in that species either (Quimio and 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 1999; Duan & Messing 1997, 2000a, b; and others). 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 non-crop 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 90% or more 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 (Aluja *et al.* 2005; Bigler *et al.* 1986; 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 and 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 and 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 programs occur. In endemic areas where fly pressures are higher, very effective pesticides for pre-harvest management and post-harvest treatment have also meant that Queensland fruit fly has been highly manageable. This situation is, however, changing dramatically and rapidly. The operational and logistic issues associated with maintaining area freedom means that it is likely that some fruit fly free zones will disappear in the near future, to be replaced by areas of low pest prevalence. In addition, the anticipated loss of dimethoate as a post-harvest treatment for fruit with edible peel will dramatically affect growers in all regions, particularly in tropical and subtropical horticultural production areas.

With the loss of area freedom and 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.* in press; Lloyd *et al.* 2007; Lloyd *et al.* 2000) 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 to solving its insect pest problems through a coordinated research program that included the states, 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. 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; Navarro-Llopis *et al.* 2007) and, if applied to *B. tryoni*, potentially 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 non-crop hosts in regional population dynamics: essential for area-wide management programs.
- Development of a workable monitoring system which is not also used as a control device, so that monitoring is not confounded with control (as currently exists for cue-lure which is used both as a monitoring and management tool).
- 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 part of area wide management.
- Critical appraisal of the impact of new generation insecticides on *B. tryoni*, 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. chemosterilization).
- Resolution of the genuine flight distance of fruit flies. 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.

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