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

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Keywords

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

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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 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 (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, 1989a,b; Meats 1989a,b; Drew & Romig, 2000) and as part of modelling exercises (Yonow & Sutherland, 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 (1922a, b, c, 1923, 1924, 1925a, b, c, 1926a, 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 disinfection 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 management 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; McKeechnie, 1972, 1975; Bellas & Fletcher, 1979; Neale, 1989; An et al., 2002; 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 & 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 (1967a, 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. (2003a) (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. melas*.

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**

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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; 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 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 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 CO₂

Elevated atmospheric CO₂ 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 CO2 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 CO2. Further, elevated CO2 leads to production of more and larger fruit (Downton 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 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 qualitative and quantitative 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 & Trumble, 1999; Stiling & 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; 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, 1925b, 1931; Gurney, 1925; Perkins & Hines, 1933; Caldwell & May, 1943) 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 fenithion 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-butanoic acid) 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) (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 (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

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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, 1986; Drew, 1987a), 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 bait, 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 km²’. 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 emerged 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 if 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, 1961a,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). Dominika (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., 2009b).

**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 *Ceratitis 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, 1983b). 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’ (1983b) 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, 2000b). 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 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 (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; Courtie & 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; Courtie & 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 Ceratitis 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 (peach) 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 CO₂ 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, 2001a,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 (Lalé 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 (≤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, 2000b). Further characterisation of the complex mixture of headspace volatiles of host fruit for *B. tryoni*, using olfactometers and field 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 chemotactic 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, α-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, 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 researched 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 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, 1963a,b, 1964a,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, 1983a, 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, 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 opine braconids (Hymenoptera: Braconidae: Opiinae). Opines 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 opines were liberated into Australia for *B. tryoni* control during the 1930s (Gurney, 1936; Allman, 1939) and then again in the 1950s (Snowball et al., 1962a,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 ophiilus* 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 opine 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, *Opisthogaster froggatti* (Fullaway), *Psyllaustia 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 orientated 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 preupal/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 deterreants 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, *Dipterophaga 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 lfenuron, 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 pheromones 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 pheromones 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 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 and would like to acknowledge the support of the Macquarie University Vice Chancellor’s Innovation Centres Program. P.W.T. acknowledges the support of the Australian Government’s Cooperative Research project 40088 and would like to acknowledge the support of 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 and would like to acknowledge the support of the Macquarie University Vice Chancellor’s Innovation Centres Program. P.W.T. acknowledges the support of the Australian Government’s Cooperative Research project 40088 and would like to acknowledge the support of this review through CRC for National Plant Biosecurity project 40088 and would like to acknowledge the support of the Australian Government’s Cooperative Research Centre 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.

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