Production levels and life history traits of mass reared Queensland fruit fly *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) during 1999/2002 in Australia

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Abstract
Quality control data for three years of production (1999–2002) at the Camden sterile insect facility was analyzed. Pupal weight was positively and significantly related to per cent emergence and flight ability. Lifespan was negatively related to pupal weight. Per cent emergence was positively and significantly related to flight ability. Increasing weekly production volumes adversely affected most variables but did not affect egg hatch. However egg hatch was significantly and negatively linked to pupal weight. Increasing pupal weight also adversely impacted on the proportion of males produced. The outside weather, assessed by CLIMEX also impacted on production, indicating that the facility climate control was not independent of the local weather conditions.

Introduction
The Sterile Insect Technique (SIT) is a pesticide free control strategy applicable to the control of many insects including fruit flies. It relies on flooding an area with sterile insects so that the few wild type insects present will mate with sterile flies and have no viable offspring. The technique has many advantages over traditional pesticide control strategies. SIT is socially more acceptable than pesticide use, and can impact the area surrounding the point/s of sterile insect release due to insect movement. It has some disadvantages in generally being more expensive and slower acting than chemicals. It also requires thorough research to be successful.

There are several factors to consider that ensure a successful SIT program for fruit flies. These include the production of high quality pupae, adequate pupal dying to discriminate wild from sterile flies during identification, effective sterilization by irradiation, efficient transport to release centres, scientifically supported release procedures and accurate monitoring and identifications services.

In New South Wales (NSW), Australia, the SIT has been used experimentally to suppress or eradicate Queensland fruit fly (Qfly), *Bactrocera tryoni* (Froggatt) since the early 1960s (Monro and Osborn 1967). The SIT has been used annually in and around the Fruit Fly Exclusion Zone (FFEZ) since 1996 (Horwood and Keenan 1994, Dominiak *et al.* 1998, 2003, Meats *et al.* 2003). Since 1990, SIT has been used in all mainland Australian states except Queensland.

High quality pupae are produced at the fruit fly mass rearing facility built at the Elizabeth Macarthur Agricultural Institute (EMAI), Camden, NSW that has been operational since 1996. The initial evaluation of production parameters were reported by Dominiak *et al.* (2002, 2007a). Factory processes and procedures are described in detail by Jiang *et al.* (2000, 2001). Following the establishment of standard procedures over the first two years of operation, this paper reports on quality parameters and their interaction, including with weekly production levels, for the 1999/2000, 2000/2001 and 2001/2002 years.

Materials and methods
Colony maintenance
An adult colony of *B. tryoni* was maintained on a diet of autolyzed brewers yeast, white sugar and water at the Queensland Fruit Fly Mass Rearing facility, EMAI (NSW Department of Primary Industries), Camden, NSW. Eggs were harvested from the adult colony and placed on media trays in the production facility. The resulting larvae were reared on a standard fruit fly media using Torula yeast, white sugar, lucerne chaff, water, citric acid and Niposet as a preservative. Approximately seven kilograms of media is placed in each tray, with 26 trays per tower. Mature larvae hop out of the media and are collected in moist vermiculite in a tray under each tower where they eventually pupate. The pupae are separated from the vermiculite by a rotary sorter, dyed with fluorescent marking dye for identification after recapture, and packed in plastic bags in two litre cartons with about 80,000 pupae per carton. Ten cartons are placed in a styrene foam box with about 0.8 million pupae per foam box. Plastic bags are sealed to reduce the amount of oxygen in bags to minimize irradiation burn. Irradiation occurs at the Australian Nuclear Science and Technology Organisation (ANSTO) at Lucas Heights in southern Sydney. A GATRI in-ground facility using a Cobalt-60 source was used to subject pupae at the two day pre-eclosion stage with 73 ± 2 Gy in normal air. Samples from each batch are returned to Camden for quality control evaluations.

Quality control rooms were maintained at 25 ± 1°C, 65 ± 5% RH and L12:D10 photoperiod with a 1 h dawn and dusk, and used to assess all variables. Weekly batch data from the years 1999/2000, 2000/2001 and 2001/2002 was compiled from standard quality control (QC) measurements taken from the colony and included percentage egg hatch, pupal weight (mg), percentage successful adult emergence, adult lifespan, fertility, percentage males produced, flight ability and the flight ability index. With the exception of egg hatch, all of these parameters were also recorded for irradiated flies. All data were linked to the weekly pupal yield. Pupal yield was the total weight (kg) of all pupae produced during the week and included pupae discarded or destroyed as excess to requirements. Each of the production variables described below were evaluated by sampling each week's batch of pupal production.

Pupal weight, emergence, percentage males produced
Each week, the average weight for pupae, both irradiated and non-irradiated, was determined by weighting three samples of 100 pupae, and dividing the weight by 100. Emergence of both irradiated and non irradiated pupae was assessed by taking three samples of 100 pupae from the respective weekly consignments. The samples of pupae were placed in plastic Petri dishes and allowed to emerge. No food or water was provided for flies and emergence counts (completely emerged adult flies) were made after all flies had died. For the percentage of males produced, three samples of 100 pupae were taken from each batch and allowed to emerge. Flies were allowed to die and the adults sexed.

Flight ability
The flight ability of *B. tryoni* was assessed using two replicates of 100 pupae for both irradiated and non-irradiated pupae. Pupae were placed in separate specially prepared 'flight ability' towers, 14 cm in diameter and 10 cm tall. The walls were lightly coated with talcum powder to prevent adult flies walking out of the towers.

Towers and flies were held inside netting cages. Food and water were placed in the further most point from the tower to encourage flies to fly out from the tower. Once emergence was completed the number of emerged adults, both inside and outside the tower, were counted. Flight ability (as a percentage) was calculated by dividing the number of flies which successfully flew out of the tower, by the total number of emerged flies. The flight ability index was calculated as the percentage sterile fliers divided by the percentage fertile fliers and is a measure of relative flight fitness after irradiation (FAO/IAEA/USDA 2003).

Egg hatch

Adult colony females laid eggs into egging cups and then the eggs were collected in water. Eggs from all cages were pooled each day and an estimate of per cent egg hatch was obtained from the pooled sample. Three samples of 100 eggs were placed on damp filter paper and percentage egg hatch scored on day four. To ensure that irradiation had been effective, irradiated (sterile) male flies were allowed to mate with non irradiated females from the facility colony. The hatch of the resultant eggs from the sterile/fertile mating was assessed, as above.

Adult lifespan

Adult lifespan was only recorded in 2001/2002. Life span (LS50) was recorded as the number of days after emergence until 50% of the population died. Tests were performed each week to ensure 50% of flies survived at least 45 days. Two groups of 100 both irradiated and non-irradiated flies (12–24 h old) were kept in mesh cages and supplied with food and water *ad lib*. The number of surviving flies per cage was counted daily until >50% of flies had died.

Climatic variables

As maximum production of *B. tryoni* usually occurred in mid summer, there was concern that external climatic factors (temperature and humidity) could cause additional production variations. About 25% of the facility air is drawn from the outside environment. Climatic data was sourced from SILO (Jeffrey *et al.* 2001) for Camden, and the software CLIMEX (Yonow and Sutherst 1998) was run to generate weekly averages and indices (Tmax = maximum temperature, Tmin = minimum temperature, RAIN = rainfall, EVAP = evaporation, DLNG = day length, DD = Day degrees, GI = growth index, TI = temperature index). These weekly figures were analyzed for relationships with the above production parameters.

Statistical analysis

A regression analysis was used to relate egg hatch, pupal yield, adult emergence, life span, percentage of males produced, and adult flight ability to pupal weight. Differences between sterile and fertile flies and their interaction with time (week of production) were examined by fitting a spline function. The parameter estimation followed the method described in Verbyla *et al.* (1999). A correlation analysis was used to relate production parameters to CLIMEX climatic variables.

Results

The relationship between the ten variables measuring quality of *B. tryoni* life stages are given in Table 1. The average and range for the variables is given in Table 2, and compared to two previous reports (Dominiak *et al.* 2002, 2007a). Table 3 presents the relationship between CLIMEX climate indices and seven quality parameters.

Egg hatch

Per cent egg hatch had a highly significant ($P < 0.01$) inverse relationship with pupal weight for both sterile and fertile flies and with emergence of fertile flies (Table 1). There were no significant relationships between egg hatch and the CLIMEX indices (Table 3).

Table 2. Life history variables of *Bactrocera tryoni* (Froggatt) in a laboratory culture evaluated (range in brackets) for the three year period 1999–2002, and a comparison with two earlier reports.

Variable	1999–2002 (This report)	1998–1999 (Dominiak *et al.* 2007)	1997–1998 (Dominiak *et al.* 2002)
Egg hatch (%)	75.6 (56.3–88.4)	62.6	*
Weekly Pupal yield (kg)	56.8 (0.32–156.8)	50.4 (17.1–78.9)	*
Pupal weight fertile (mg)	10.3 (8.5–11.5)	11.0 (10.0–12.3)	9.2
Pupal weight sterile (mg)	10.3 (8.3–11.7)	11.1 (10.0–12.0)	9.2
Emergence fertile (%)	83.5 (55.3–96.0)	88.7 (77.7–93.0)	77.9
Emergence sterile (%)	74.3 (46.0–92.3)	85.8 (80.0–97.0)	77.0
Flight ability fertile (%)	90.2 (73.5–97.8)	93.7 (86.7–100.0)	91.9
Flight ability sterile (%)	81.6 (49.7–98.2)	90.7 (74.3–96.4)	89.2
Flight ability index (%)	90.6 (60.0–110.8)	96.1 (82.6–101.8)	97.0
Life span fertile (days)	78.9 (56.0–106.0)	*	55.8
Life span sterile (days)	68.7 (44.5–113)	*	47.5
Male %	52.4 (33.8–68.8)	*	*

* = no data available.

Table 1. Regression coefficients between life history variables of *Bactrocera tryoni* (Froggatt) reared in a laboratory culture.

	Egg hatch	Pupal yield	Pupal weight fertile	Pupal weight sterile	Emergence fertile	Emergence sterile	Flight ability fertile	Flight ability sterile	Flight ability index	Male %
Egg hatch	1.000									
Pupal yield	0.160	1.000								
Pupal weight fertile	0.505**	0.322**	1.000							
Pupal weight sterile	0.508**	0.326**	0.937**	1.000						
Emergence fertile	0.262**	0.570**	0.642**	0.616**	1.000					
Emergence sterile	−0.011	0.537**	0.521**	0.504**	0.721**	1.000				
Flight ability Fertile	−0.178*	−0.162	0.288**	0.308**	0.250**	0.297**	1.000			
Flight ability Sterile	−0.062	0.298**	0.432**	0.419**	0.459**	0.591**	0.511**	1.000		
Flight ability index	−0.002	0.231**	0.345**	0.316**	0.386**	0.510**	0.030	0.863**	1.000	
Male %	−0.035	−0.072	−0.160	−0.174*	−0.089	−0.278**	−0.097	0.302**	0.305**	1.00

Note: * and ** denote significance at 5% and 1% levels respectively.

Table 3. Correlation coefficients between CLIMEX indices and Bactrocera tryoni (Froggatt) life history variables.

CLIMEX indices	Egg hatch %	Pupal yield	Pupal weight sterile	Pupal weight fertile	Emergence sterile	Emergence fertile	Flight ability sterile	Flight ability fertile	Flight ability index	Life span sterile	Life span fertile
Tmax	0.062	0.411**	0.363**	0.324**	0.150	0.057	0.335**	0.098	0.352**	0.396**	0.620**
Tmin	0.097	0.310**	0.470**	0.426**	0.270**	0.162	0.367**	0.080	0.397**	0.368**	0.615**
Rain	0.040	0.157	0.342**	0.307**	0.291**	0.129	0.223*	0.002	0.271**	0.253**	0.324**
Evaporation	0.041	0.271**	0.303**	0.272**	0.198*	0.060	0.393**	0.177*	0.368**	0.414**	0.601**
DLNG	0.049	0.273**	0.339**	0.323**	0.228**	0.082	0.435**	0.217*	0.389**	0.505**	0.687**
DD	0.087	0.373**	0.424**	0.374**	0.200*	0.097	0.312**	0.052	0.350**	0.377**	0.615**
GI	0.126	0.171	0.339**	0.320**	0.200*	0.188*	0.110	−0.030	0.145	−0.142	−0.202*
TI	0.086	0.373**	0.423**	0.373**	0.200*	0.096	0.314**	0.053	0.351**	−0.375	0.614**

Note: * and ** denote significant at 5% and 1% levels respectively.

Pupal yield
The weekly pupal yield had a negative relationship with all production parameters, except egg hatch. The relationships between weekly pupal yield and six parameters, including pupal weights and emergences from fertile and sterile pupae, were significant (P <0.01) (Table 1). However, these relationships are not linear with low weekly yields generally associated with higher quality. There was also a significantly positive relationship with six of the CLIMEX indices (Table 3).

Pupal weight
There were positive and significant relationships (P <0.01) between the pupal weights (fertile and sterile) and emergence of pupae (fertile and sterile) and the three flight parameters assessed. Both egg hatch and weekly pupal yield for both fertile and sterile pupal weights had a significant negative relationship (P <0.01) (Table 1). There was a significant relationship between pupal weight (sterile and fertile) with all CLIMEX indices (P <0.01) (Table 3).

Emergence
There was a significant positive relationship (P <0.01) between pupal emergence (sterile and fertile) and six parameters including pupal weight (sterile and fertile), and each of the three flight parameters (Table 1). There was a significant relationship between sterile emergence and seven of the CLIMEX indices however for fertile emergence only GI was significant (Table 3).

Flight ability and flight ability index
The flight ability (fertile and sterile) was positively and significantly (P <0.01) related to pupal weight (fertile and sterile) and emergence (fertile and sterile). The flight ability index was 90.6, indicating that the dying and irradiation process did reduce the ability of the insect to fly (Table 1). There was a significant relationship with seven of the CLIMEX parameters with sterile flight ability and the flight ability index but only two significant relationships with fertile flight ability (Table 3).

Percentage of males
There was a significant negative relationship with sterile pupal weight (P <0.05), sterile emergence (P <0.01), sterile flight ability (P <0.01) but no significant relationship with fertile pupal weight, fertile emergence or fertile flight ability (Table 1). There was a negative trend of percentage of males with all other parameters.

Lifespan
Lifespan (data not presented in tables) for fertile flies was positively and significantly (P <0.01) related to lifespan for sterile flies, and to percentage males (P <0.05) but negatively (P <0.01) related to pupal weight (fertile and sterile). Lifespan (fertile and sterile) was negatively and significantly (P <0.01) related to pupal yield. Lifespan was significantly (mostly P <0.01) and negatively related to all CLIMEX indices except the Growth Index.

CLIMEX indices
CLIMEX indices were significantly related (mostly P <0.01) with pupal weights (both sterile and fertile) and flight ability index, and negatively related (mostly P <0.01) to sterile and fertile life spans. Egg hatch, fertile emergence and flight ability were generally not significantly related or affected by the indices. Of the indices, GI had the fewest significant relationships (mostly P <0.05) with quality parameters being significantly linked to pupal weight and emergence. Nine of the eleven production parameters were significantly related (mostly P <0.01) to EVAP and DLNG, while eight were related to Tmin and DD.

Discussion

There seems to be a polarization of production variables with pupal weight, emergence and flight ability being antagonized by egg hatch, percentage males, life span and weekly production yields. The largely negative trends and relationships of weekly pupal yield to most other variables are disturbing. Factors which impact on pupal yield include the reliability of the controlled rooms, the quantity of eggs placed into the larval growth medium on the rearing trays, management of the temperature and moisture content of insect media, female fecundity, etc. Results reported in this paper suggest that at least some of these factors have a significant effect on weekly pupal yield. The effects of interactions between these factors are complex and some effects are discussed.

Pupal weight
Pupal weight seems to be a key factor impacting on most other variables. Pupal weight (fertile and sterile) was positively and significantly (P <0.01) related to pupal emergence and flight ability parameters. The maintenance of higher pupal weight in future production is likely to create a more robust sterile fly for release. The significant negative (P <0.01) relationship with weekly pupal yield is of most concern. There is increasing demand from SIT programs across Australia to provide higher numbers of sterile insects for release. As a result of this demand, attempting to meet these demands may have a negative impact on the quality of SIT programs. When comparing pupal weight, emergence and flight ability between two production years (Table 2), it is evident that these variables decline with increasing pupal yield. This would result in fewer sterile flies finding their way into monitoring traps, resulting in release staff asking for more flies. If production did increase, it would be reasonable to assume that even fewer sterile flies find their way into monitoring traps, resulting in release staff asking for even more flies. Acquiescence to these demands would only accelerate the demise of the SIT program. Dominiak *et al.* (2007b) reported that declining pupal weights resulted in declining emergence as a result of transport stress.

The positive response with many CLIMEX variables was unexpected. However, it may reflect the differences between the regulated climate inside the facility and the often extreme climatic conditions outside the facility at Camden. The climate

control at the facility does use a proportion (about 25%) of outside air. The results show that the climate control modifies the outside air and that climate control cannot be assumed to be independent of outside conditions. Yonow and Sutherst (1998) and Yonow *et al.* (2004) reviewed the impact of temperature and moisture on the life cycle of Qfly.

Emergence

Emergence was significantly positively related to the flight ability of both sterile and fertile flies. The maintenance of high emergence levels would ensure adequate flight ability of released sterile flies and their ability to fly to lek sites to compete for wild females. Unfortunately there is a significant ($P < 0.01$) negative impact on pupal emergence as production (weekly pupal yield) increases. The pursuance of high production levels would appear to be self defeating. The ideal production level is yet to be determined.

Dominiak *et al.* (2007a) found that emergence was not affected by pupal weights around 11 mg, however the lowest emergence levels occurred in late February. This was contrary to Dominiak *et al.* (2002) when a positive significant relationship between pupal weight (average 9.2 mg) and emergence was found. There appears to be no difference in emergence of pupae within the weight range of 10.3 to 11.0 mg. Dominiak *et al.* (2007b) found that emergence decline as a result of transport stress could be minimized by producing pupae with heavier weights (average 9.36 mg). Additional research is needed to clarify the situation.

Flight ability and flight ability index

The flight ability and flight ability index of irradiated and non-irradiated flies was significantly ($P < 0.01$) related to pupal weight and emergence. These results conflict with earlier reports. Dominiak *et al.* (2007a) found that only the flight ability of sterile flies was inversely and significantly correlated to pupal weight. Flight ability was related to the week of production, with the lowest level occurring in the second week of January. The earlier report (Dominiak *et al.* 2002) indicated that flight ability and flight ability index were not related to pupal weight. The two previous reports were based on smaller sample sizes and we assume that smaller sizes may have contributed to the lack of significance.

Egg hatch

Egg hatch was one of the few parameters that were not adversely linked to higher weekly pupal yields. Egg hatch however had a significant negative correlation with pupal weight. There was also a negative trend with most other parameters and with CLIMEX indices related to temperature and moisture. This suggests that Qfly has an increased egg hatch in drier and cooler conditions and this may be a survival mechanism to enhance survival under adverse conditions. If this is the case in wild populations, this factor may contribute to perceived difficulties in the eradication of autumn incursions into the FFEZ.

Percentage of males produced

There was a negative trend will all parameters assessed with an average of 52.4% of production being males. This is disappointing given that only sterile males are considered useful in SIT programs. There was a significant negative relationship with sterile pupal weight, sterile emergence and sterile flight ability, but not with the fertile equivalent parameters. Future research should examine procedures such as temperature control or alteration in the diet to alter the proportion of males produced.

Lifespan

Dominiak *et al*. (2002) reported that pupal weight was negatively related ($P < 0.01$) to lifespan and the current results confirm this report. Life span of the sterile flies was also negatively and significantly related to most CLIMEX indices. We infer that as summer approaches the life span shortens, or inversely as climate conditions become cooler and less favourable, that life span increases as a survival mechanism.

CLIMEX indices

The high number of significant relationships between production variables and CLIMEX indices was unexpected but indicates that the internal climate control is heavily influenced by conditions outside the facility. Temperature and moisture have long been recognized as primary environmental influences on Qfly. RAIN had seven significant relationships while EVAP had nine and we presume these are linked as they are both moisture related parameters. Tmax, Tmin and TI had seven, eight and seven significant relationships respectively and these temperature indices seem to be in accord. GI was a surprisingly poor performer under factory conditions but has been a useful indicator of fruit fly populations and survival in some field evaluations (Meats *et al.* 2003, Dominiak *et al.* 2003). DLNG had nine significant relationships and this was unexpected as we anticipated that the internal facility lighting to dominate over the outside day length. The adult colony and quality control rooms have sky lights however all other parts of the production facility have no outside light and are entirely lit by artificial light on timers. The complete absence of any relationship between percentage egg hatch and all CLIMEX indices is also unexpected.

Summary

Dominiak *et al.* (2002) reported on the concept that 'bigger is better' for the initial sterile Qfly production and reviewed other species which largely agreed with the concept. Pupal weight was a key parameter linked to most other quality variables. Dominiak *et al.* (2007a) subsequently found that there appeared to be a maximum pupal weight beyond which there seemed to be no increasing advantage. Regarding transport stress, Dominiak *et al.* (2007b) reported bigger was better as larger pupae were more tolerant of the stresses of transport from the production facility to release site in the Riverina.

In the present study, pupal weight was significantly ($P < 0.01$) and positively related to emergence and flight ability, and increasing pupal weight at the production facility would appear to be a positive strategy to producing better insects from a sterile release program perspective. Conversely, increasing the pupal weight decreases the proportion of desirable males available for release. Increasing pupal weight was significantly ($P < 0.01$) and negatively related to egg hatch, to shorter lifespan, and to higher weekly pupal yield.

The negative relationship with the key parameter of pupal weight with higher weekly pupal yields leaves us with a conundrum. What is the ideal level of production which results in a reasonable pupal weight? Perhaps there are procedures or processes which need to be revised to reverse some less desirable trends. As the EMAI facility is the only Qfly sterile production facility in the world, there are no other facilities to share the burden of production or research. Meza *et al.* (2005) reported that once larvae of *Anastrepha ludens* reached a critical weight, that adult performance depended more on genetic quality than on size. Competition for food by larvae within a production facility could cause reduced pupal weight and ultimately reduced sexual competitiveness.

In terms of the ideal pupal weight, our results indicate that producing heavier pupae results in a more vigorous fly (higher emergence and higher flight ability) with apparently a shorter lifespan. However the life span issue is not clear, and may have nothing to do with pupal weight. Pupal weight was positively and significantly linked to all CLIMEX indices while life span was negatively and significantly linked to the same CLIMEX parameters. It is possible that climatic factors determine life span and not pupal weight (Dominiak *et al.* 2002). Climatic factors, among others (e.g. egg loading on larval media trays and female fecundity) could also determine pupal weights. More research is required to determine which key factor determines pupal weight.

In a release program, our concerns about life span may also be unfounded. The

average LS50 in this study was about 10 weeks, with the lower range at six weeks. Adult flies become sexually mature within about one week, provided they find food and shelter, and would have sufficient life span to mate with wild females. Dominiak and Webster (1998) reported that 86% of recaptured flies were caught within four weeks after release. NSW release programs resupply flies every week (Dominiak unpublished data) therefore even a four week sexually active life span would be adequate in the field with a weekly resupply of sterile adults. Dominiak *et al.* (2003) also reviewed many programs and reported that the maximum length of lifespan of the last survivor ranged from 40 to 182 days with many programs resulting in a 70 days maximum survival. We conclude that current life span is likely to be adequate for our release programs.

Weekly pupal yield was a significant contributor to many variables however the relationship was not linear. Weekly production levels of up to 5 kg resulted in higher levels of most variables and usually reflect production levels in early spring as the production facility moves from winter non-production through to maximum summer production. Although the larval diets do not change, many quality parameter levels decline and then increase to stabilize after weekly production levels reach about 80 kg which is typical of normal weekly production levels. We have assumed that this was related to a lag in labour resources. As additional staff are hired for the increasing production levels, there is a period of training and familiarization when new staff are less skilled, compared with their skill level in the height of summer. This labour issue could be overcome by hiring and training staff earlier than when they are actually required.

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