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Seasonal phenology of the gall-making fly, *Fergusonina* sp. (Diptera: Fergusoninidae) and its implications for biological control of *Melaleuca quinquenervia*

John A. Goolsby[1], Jeffrey Makinson[2] & Matthew Purcell[2]

[1]United States Department of Agriculture, Agricultural Research Service, Australian Biological Control Laboratory, 120 Meiers Rd., Indooroopilly, QLD, Australia 4068 (email: john.goolsby@brs.ento.csiro.au)

[2]CSIRO Entomology, 120 Meiers Rd., Indooroopilly, QLD, Australia 4068

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Send correspondence to:
Dr. John A. Goolsby
USDA-ARS-ABCL (CSIRO)
120 Meiers Rd., Indooroopilly, QLD
Australia, 4068

Abstract A gall-making fly, *Fergusonina* sp. is under study as a potential biological control agent of *Melaleuca quinquenervia*, an invasive weed in Florida, USA. The seasonal phenology of *Fergusonina* sp. and its host *M. quinquenervia* was studied over a two-year period in northern New South Wales and southeast Queensland. *Fergusonina* sp. populations followed an annual cycle with gall numbers peaking in August/September. Gall density was strongly correlated with bud density and temperature, but not rainfall. Comparison of climates in Australia across the native range of *Fergusonina* sp. with Miami, Florida, predicts that climate should not be a limiting factor in its establishment. The fly/nematode complex of *Fergusonina/Fergusobia* sp. is compared with other gall-making agents used in biological control programs. The gall has many of the attributes of a moderately powerful metabolic sink. High gall densities could potentially suppress seed production and reduce vigor of the tree, making this insect species an effective biological control agent of *M. quinquenervia*.

Key words weed biological control, Australia, Florida, Myrtaceae

INTRODUCTION

Insects which induce galls on plants have been used in many biological control programs to combat weeds (Diatloff & Palmer 1987, Dennill & Donnelly 1991, Harris & Shorthouse 1996, Julien & Griffiths 1999). Gall-making insects are often selected as biological control agents because of their narrow host specificity (Gagné 1989, Stilling & Rossi 1995, Kolesik & Peacock 1999). However, gall-making insects are not all physiologically capable of having a significant negative impact upon their hosts. For example, the leaf gall induced by the cecidomyiid *Cystiphora sonchi* (Bremi) acts as a sink, drawing nutrients away from its host, the sow-thistle, *Sonchus arvensis* L., but does not directly affect the reproduction of the plant (Peschken *et al.* 1989). In contrast, flower bud galls of *Trichilogaster acaciaelongifoliae* (Froggatt) severely limit seed production of its host, *Acacia longifolia* (Andr.) Willd, in addition to being a nutrient sink (Manongi & Hoffman 1995). Other factors, such as parasitism and climate, are also known to influence the impact of gall-making insects in biological control programs. The impact of the introduced gall fly, *Rhopalomyia californica* Felt, on *Baccharis halimifolia* L. in Australia, was greatly reduced by attack from native parasitoids (McFayden 1985, Palmer *et al.* 1993). Climatic differences between southern Canada and Western Europe were given as reasons for the apparently poor performance of the European gall-inducing tephritid fly, *Urophora cardui* (L.) on Canada thistle, *Cirsium arvense* (L) (Harris & Shorthouse 1996). *Urophora cardui* is poorly adapted to cope with moisture stress, common in the prairies of Saskatchewan, Canada, which was not a limiting factor in its native habitat. Field studies in the native range of an insect considered for biological control can be designed to investigate many of these factors, thereby enhancing the selection process of each agent.

The broad-leaved paperbark tree, *Melaleuca quinquenervia* (Cav.) S.T. Blake, was introduced into Florida, USA from Australia in the early 1900's. In the last 30-40 years *M. quinquenervia* has greatly expanded its range in southern Florida where it now infests over 200,000 hectares, including the ecologically sensitive Everglades, causing extensive environmental and economic damage (Ferriter 1994, Turner *et al.* 1998). *Melaleuca quinquenervia*, which can grow to 30 m in height, flowers and seeds prolifically forming dense forests which displace native plants and animals. A major Federal and State effort is underway to restore the Everglades. Biological control of exotic invasive weeds, including *M. quinquenervia*, figures prominently in this restoration program. To this end, over 450 insect herbivores have been collected on *M. quinquenervia* in Australia (Balciunas *et al.* 1994, 1995). One of these insects, the foliage feeding weevil *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae), is now established in Florida. A second agent, *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae) is pending release.

The gall-making fly, *Fergusonina* sp. Malloch (Diptera: Fergusoninidae), is under study as a potential biological control agent for *M. quinquenervia. Fergusonina* sp. and its obligate nematode, *Fergusobia* sp. Currie (Nematoda: Tylenchida: Sphaerulariidae), form galls in the leaf and flower bud tissue of *M. quinquenervia*. Preliminary data indicates that the nematode initiates gall formation before the *Fergusonina* sp. eggs have hatched. (Giblin-Davis unpublished data). Multiple fly larvae feed and develop from the gall tissue. Galls stop terminal growth of the stem and prevent formation of flowers. Reducing seed production could be important in the management of *M. quinquenervia* in Florida.

The original work on Fergusoninidae (Currie 1937) showed the symbiotic relationship of *Fergusonina* and its associated *Fergusobia* nematodes. Since then little research had been conducted on this group until Taylor *et al.* (1996) described the biology of *Fergusonina flavicornis* Malloch and its parasitoids on its host *Eucalyptus camaludensis* Dehnh in South Australia. Several new species of *Fergusonina* from the *Melaleuca leucadendra* complex, which includes *M. quinquenervia* and 10 of its close relatives, are currently being described. (G. Taylor pers. comm.). *Fergusonina flavicornis* is only known from *E. camaldulensis* (Malloch 1925). Similar host relationships have been predicted for species of Fergusoninidae in the *M. leucadendra* complex (Giblin-Davis, pers. comm.). This presumed high degree of host specificity makes *Fergusonina* sp. an ideal candidate for biological control. Very little is known about the field biology of Fergusoninidae. The purpose of our study was two-fold: 1) to gain a better understanding of the field population dynamics of the gall-making fly as it relates to the phenology of its host *M. quinquenervia* and 2) to evaluate the potential of *Fergusonina* sp. as a biological control agent.

MATERIALS AND METHODS

To study the seasonal phenology of *Fergusonina* sp. on its host, *M. quinquenervia*, three study sites were selected: Peregian, Queensland (QLD) (26° 30.37'S & 153° 05.47'E), Morayfield, QLD (27° 07.30'S & 152° 58.50'E), and Woodburn, New South Wales (NSW) (29° 12.79'S & 153° 15.76'E). The three study sites are typical of stands within the native range of both *M. quinquenervia* and *Fergusonina* sp. in subtropical, eastern Australia. Peregian and Woodburn are seasonally inundated sites, with standing water common during the summer months. Morayfield remains free of standing water year-round.

Monthly surveys of *Fergusonina* sp. galls on *M. quinquenervia* trees were conducted at each site from July 1997 to September 1999. Fifty trees were selected at intervals along a transect. The transect at Peregian was approximately 50 metres long and followed a walking path through the wetland. At Woodburn the transect was of similar length and followed a creek through open woodland forest. The transect at Morayfield was demarcated within a patch of dense regrowth in a paddock. The trees we selected at each of the sites were small, between the height of 0.5 and 4.5 metres, to allow us to survey whole trees. As a result our study was biased against larger, mature flowering trees.

The total numbers of active galls on each of the sample trees were counted. We were not always able to positively distinguish whether galls had arisen from flower or leaf buds. Therefore, numbers of galls per 50 trees reflects the total of both flower and leaf galls, though the number of flower bud galls were insignificant due to the small size of the tree that were sampled. Galls are generally active for two months after oviposition and have soft green tissue with developing insects. Old galls, which are hard, brown and have a full complement of fly and parasitoid holes, were not included in the study because they no longer had an impact on stem growth.

Leaf buds were used to estimate bud density, because flower buds were not common on the small sized trees selected for the surveys. Bud size and compaction are critical factors in the suitability of the site for oviposition by *Fergusonina* sp. Dormant, unexpanded buds with tight compaction were found to be unsuitable for oviposition, based on laboratory and field observations. Buds begin to be suitable for oviposition as they become slightly expanded and elongated with the new leaves still tightly held together (‘small’ < 25mm long), and continue to be suitable up to the point where leaves begin to elongate and unfurl (‘medium’ < 50 mm)

To rate bud density, small and medium sized buds were categorized separately on a monthly basis as rare, uncommon, common, or abundant. The abundance of small and medium sized buds were given numerical values: absent - 0, rare - 1, uncommon - 2, common - 3, and abundant - 4. The sum of the values for both size buds was used as a measure of bud density. For example, if both small and medium sized buds were 'abundant', the assigned value was eight. If both size classes were 'rare', the corresponding measure of bud density was two. Tree density was determined by counting the number of *M. quinquenervia* plants within a representative area of the transect. The area surveyed for tree density ranged from 75-225 m^2, due to differences between search areas at each site. The mean tree height was determined by measuring 30 trees at random within the search areas.

Mean daily rainfall and temperature records for all three sites were provided by the Queensland Department of Natural Resources using the Data Drill program. CLIMEX was used to compare climates in Wollongong, NSW; Brisbane and Cairns, QLD; with that of Miami, Florida, USA (Sutherst & Maywald 1985). Miami was the best available site in the CLIMEX database which was representative of the climate in South Florida. We chose the Australian locations because they represented the geographic range of *Fergusonina* sp. on *M. quinquenervia*. CLIMEX uses long-term meteorological data to make comparisons between target locations. It generates a match index that indicates the level of similarity in mean monthly figures for maximum temperature, minimum temperature, total rainfall, rainfall pattern, and relative humidity.

Analysis of co-variance was used to compare the effects of bud density, rainfall, temperature, and site on gall density. A square root transformation was required for gall density. Separate analyses were used to fit an annual cycle to bud and gall density. A simple sine curve common to all sites gave the best fit and was used to estimate the months of peak density. Because we observed a lag time between oviposition by the fly and subsequent mature gall formation of about two months, we regressed total number of galls on each collection date with measurements of bud density, rainfall, and temperature taken two months earlier. Forall was used for the statistical analyses (Kerr 1980).

RESULTS

Temperature and rainfall data for the three study sites: Peregian, Morayfield, and Woodburn are given in Table 1. Mean annual temperatures from July 1997 to August 1999 were similar for the two sites in QLD, with the third site in NSW, two degrees of latitude south, being one degree cooler. The lowest temperature (2^0C) was recorded at Morayfield on 26 Aug. 1997, while the highest temperature (39.5^0C) was at Woodburn on 27 Dec. 1998. Total rainfall was similar at all three study sites during the first year of the study, with a difference of 158mm. During the second year, rainfall was more variable, with a difference of 749 mm between the Peregian and Morayfield locations.

Density of *M. quinquenervia* trees and saplings was highest at the Peregian site (Table 2). Peregian is heathland, dominated by high-density short, stunted *M. quinquenervia* trees and *Banksia rogur* Cav. behind coastal sand dunes. Plants here are stunted, possibly due to the effect of salt spray. The stunted condition of the trees at Peregian is reflected in the mean height of the trees, with the *M. quinquenervia* trees being on average 2 to 3.5 times taller at the Morayfield and Woodburn sites, respectively (Table 2). *Melaleuca quinquenervia* comprises nearly 100% of the tree species at the Morayfield site, and are relatively uniform in size and age due to clearing of the paddock several years before the start of the study. The forest at Woodburn is comprised of a mixture of *Eucalyptus* spp. growing amongst *M. quinquenervia* trees along a small creek. All three study sites represent distinctly different ecological settings.

Fergusonina sp. abundance appears to be closely synchronized with the phenology of *M. quinquenervia*; positively correlated with the presence of new buds. Formation and growth of *M. quinquenervia* buds was seasonal, with the highest densities occurring during the colder months from May to September (Fig 1). Peak bud density generally occurred during July/August. Gall numbers were typically highest in August/September, approximately one to two months after peak bud density.

Mean gall and bud densities at the three study sites over the two-year study period are compared in Table 2. Morayfield had the highest mean bud and gall densities, although bud density was not significantly different from the Woodburn site. Peregian showed the strongest seasonal trends with very low bud and gall densities during the warmer months and sharp peaks during cooler months.

Gall densities followed a strong seasonal pattern at two of the three sites, Peregian and Morayfield (Fig 1). Gall density at the Woodburn site remained low for most of 1998 despite typical seasonal bud formation and temperatures. Gall densities for all sites fit the same sine curve indicating an annual cycle of gall formation ($F = 32.68$, $P < 0.0001$, df = 2, 77), even though mean gall densities varied by site ($F = 22.7$, $P < 0.0001$, df = 2, 77). In this analysis 59% of the variation in gall density was explained by the two factors, seasonal sine curve and site.

In a second analysis of gall density, the seasonal sine curve was replaced by the factors: bud density, current mean temperatures, and rainfall. Fifty-one percent of the variation in gall density was explained by this analysis. Bud density was highly significant ($F = 46.75$, $P < 0.0001$, df = 1, 70) with gall density increasing with bud density. Mean temperature was also significant ($F = 9.27$, $P < 0.003$, df = 1, 70) with higher temperatures associated with lower gall density. Rainfall was not a significant factor in gall density ($F = 0.12$, $P = 0.73$, df = 1, 70). There were no significant interactions with site.

Comparison of climates between Brisbane, QLD and Miami, FL using CLIMEX shows only a 59% match (Table 3). The greatest differences between the two climates are in minimum temperatures and RH. RH in Brisbane is much lower than Miami during the winter months. Mean monthly temperatures in Miami are consistently warmer than those recorded for Brisbane (Fig 2), with the greatest difference occurring during the winter months. Cairns, QLD represents the more northern tropical part of the range of *M. quinquenervia* and *Fergusonina* sp. in Australia. Cairns and Miami have nearly identical mean monthly temperatures. However, rainfall in Cairns during summer is more than twice that of Miami. Wollongong in temperate NSW represents the most southern distribution of

Fergusonina sp. and its host in Australia. Winter and summer temperatures in Wollongong are cooler than both Brisbane and Miami.

DISCUSSION

The field study of *Fergusonina* sp. shows a close ecological relationship between the gall-making insect/nematode complex and its host plant *M. quinquenervia*. Population dynamics follow an annual cycle with high densities of *Fergusonina* sp. occurring mainly during the winter months when there is an abundance of new bud growth. Summer temperatures negatively influenced both populations of *Fergusonina* sp. and new plant growth. Despite the significant effects of bud density and temperature, other factors must be playing an important role in population dynamics. This is evidenced by the significant fit of the seasonal sine curve with the density of *Fergusonina* sp. Biotic influences, such as plant canopy shading, nutrient cycling in the trees, and parasitism, are likely to be influencing population dynamics of *Fergusonina* sp. Rossi & Stilling (1998) found that plant nitrogen levels and shading had significant effects on population levels of the cecidomyiid gall, *Asphondylia borrichiae* Rossi & Strong on its host, the sea daisy, *Borrichia frutescens* (L.). Ehler (1978) found that parasitism of the gall-making cecid, *Rhopalomyia californica*, varied according to the parasitoid assemblage in the gall, with parasitism highest in mixed species samples. *Rhopalomyia californica* was later released in Australia against *Baccharis hamlimifolia* and parasitism varied widely in the different ecological areas of southeast Queensland (Melksham, unpublished data). Parasitism of *Fergusonina* sp. should be investigated further. Site differences in gall density could be due to the assemblage of species in the parasitoid guilds.

Ecological differences at the study sites may also be influencing the population dynamics of *Fergusonina* sp. Morayfield had the highest mean density of buds and galls over the two-year study period. Morayfield was the only site that had been significantly altered ecologically. *Melaleuca* *quinquenervia* had regrown from suckers at the site after it had been cleared several years before. The trees showed vigorous growth and had very little, if any, competition from other woody plants. It is interesting to note that stands of *M. quinquenervia* at this disturbed location are very similar to the seedling stands in Florida, USA. In comparison, competition from other tree species was greatest at Woodburn, and gall density was significantly lower. Ecological differences between sites were most evident at Peregian. Stunted *M. quinquenervia* growing in the coastal heath at the Peregian site showed the greatest fluctuations of bud and gall densities. Sharp peaks in gall density during Sep - Oct 1999 followed previous periods of high bud density indicating that *Fergusonina* sp. is able to quickly respond to localized increases in bud density.

Climate is an important factor that influences not only the establishment of a biological control agent, but its impact as well. Many gall-making insect species, while physiologically adapted to the host, are not capable of responding to the climatic regimes of their new environment. In our comparison using CLIMEX we do not foresee the climate of Florida to be a limiting factor for *Fergusonina* sp. However, our analysis is based on monthly averages, and does not take into account catastrophic freeze events which can occur in Florida. In Australia, *Fergusonina* sp. is found on *M. quinquenervia* throughout a range of climates, from Cairns in tropical north QLD to Wollongong in temperate NSW. The climate of Miami, Florida falls within the range of temperatures, humidities, and rainfall patterns found in the native distribution of *Fergusonina* sp.

The environment of south Florida may be advantageous for *Fergusonina* sp. Flushes of high-density young leaf and flower buds occur over longer periods of time in Florida than in Australia (Van *et al*. in press). However, despite perceived environmental advantages, *Fergusonina* will need to gall significant numbers of buds to have any effect on seed production and recruitment. Clearly, *Fergusonina/Fergusobia* sp. galls do not have a profound impact on *M. quinquenervia* at densities that occur in Australia. It is difficult to predict how *Fergusonina* sp. would respond to its introduced environment in Florida. It is most likely that parasitism would be lower, which could allow

Fergusonina sp. to reach the densities necessary to have a physiological impact on *M. quinquenervia*. A high density of galls acting as nutrient sinks could have a profound effect on the vigor and reproductive potential of the tree. *Fergusonina* sp. galls both leaf and flower buds. Our study was biased against flower bud galls because the trees in two locations, Woodburn and Morayfield, were younger trees, less likely to flower. Only one percent of the galls in the entire study were determined to be flower bud galls because they were associated with a flower triad, or had partial flower development. We do believe that flower bud galls would be common on older trees that produce more flower buds. Therefore, the impact of *Fergusonin*a sp. on the reproductive potential of *M. quinquenervia* would be both direct (galling of flower buds), which reduces seed production, and indirect (galling of leaf buds). The indirect effects on reproduction are due to the gall acting as a metabolic sink reducing the potential of the plant to flower, set and mature viable seeds.

The potential impact of the gall produced by *Fergusonina/Fergusobia* sp was compared with other species used in biological control programs. Several authors have reviewed the traits of gall-making insects and described what appear to be traits that increase their potential effectiveness as biological control agents. The success of the hymenopteran gall-maker *T. acaciaelongifoliae* on acacia in South Africa allowed Dennill (1988) to describe what he believed to be the attributes of an effective gall-maker in a biological control program. The attributes he described are: 1) the agent must live within the tissue which is galled; 2) the tissue which is galled should be primordial; 3) the organs galled must be produced in large numbers; 4) the dry mass of the developing galls must be substantially greater than that of the corresponding plant structures; 5) gall development must span the entire reproductive and/or growth phase of the plant; and 6) the dry mass of the developing galls must be relatively greater during the early part of the reproductive growth season. *Fergusonina/Fergusobia* sp. appears to have many but not all of these attributes. The fly and nematode do live within the tissue as the gall is being formed and the tissue being affected is primordial. *Fergusonina* oviposits into the flower and leaf buds, which are seasonally abundant, and gall development spans the entire reproductive and/or growth phase of *M. quinquenervia*. Attempts to quantify the difference in dry mass between the developing gall and the corresponding plant structures were beyond the scope of this study. In light of the attributes described by Dennill, it does not appear that smaller *Fergusonina/Fergusobia* sp. galls would have a similar impact as the massive galls produced by *T. acaciaelongifoliae.*

Harris & Shorthouse (1996) reviewed the biology, gall morphology, gall physiology and effectiveness of six insects and one nematode released in Canada for biological control. Effectiveness was based on impact of the biological control agent on the weed. The most effective gall-making biological control agents were powerful metabolic sinks, diverting substantial amounts of nutrient away from plant reproduction. The most effective galls either severed the vascular connection and persisted over the entire growing season, or developed a vascular system with a heavily lignified shell. In addition, the presence of enlarged stomata on the gall was considered to be detrimental to biological control if the gall was in a dry habitat where moisture was limiting. Analysis of the *Fergusonina* sp. gall using the attributes listed above shows that it has many of elements which may make it an effective metabolic sink. *Fergusonina/Fergusobia* sp. galls do not completely sever the vascular connection, but are weakly vascularized and are composed of parynchemal tissue with pockets of hypertrophied cells around developing fly larvae and nematodes. The gall has a highly lignified shell without enlarged stomata. Thus, they are adapted to dry habitats and have the potential to divert a considerable amount of plant nutrients into gall tissue. If gall numbers reached a high density on the plant their impact could be substantial, especially considering that the galls persist throughout the growing season. However, using the attributes of Harris and Shorthouse (1996) we would not classify the *Fergusonina/Fergusobia* gall as a powerful metabolic sink because of the weak vascularization of the gall.

Field data from this study indicates that *Fergusonina* sp. does respond well to increasing bud density, therefore it should be able to fully exploit the resources of the target plant in its new environment. The high bud densities found in the dense monocultures of the Everglades (Rayachhetry *et al.* 1998) may provide the ideal habitat for the gall fly. Parasitism of the galls is extremely high in Australia throughout the year (Goolsby, unpublished data). If parasitism in the introduced environment was significantly lower, as might be expected, population levels of *Fergusonina* sp. could increase dramatically. Because the *Fergusonina/Fergusobia* gall has many of the attributes necessary to be an effective metabolic sink, high densities could potentially suppress seed production and reduce vigor of the tree. Based on all these factors, *Fergusonina* sp. is a good candidate for further study as a biological control agent of *M. quinquenervia*.

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Table 1 Temperature and rainfall data*

Site Name	Mean T (C)	Min/Max T (C)	Rainfall Yr 1 (mm)	Rainfall Yr 2 (mm)
Peregian, QLD	20.4	6.0 / 34.5	1337	2664
Morayfield, QLD	20.2	2.0 / 37.0	1179	1915
Woodburn, NSW	19.4	3.5 / 39.5	1258	2435

* Data covers July 1997 to June 1999

Table 2 Physical characteristics of *M. quinquenervia* stands

Site Name	Description	Tree Density* / 100 M^2	Mean height +/- SE** (M)	Mean Bud Density Rating	Mean Gall Density***
Peregian, QLD	coastal heath	226.5	0.9 +/- 0.06[a]	4.3 [a]	15.6 [a]
Morayfield, QLD	regrowth on paddock	65.3	2.0 +/- 0.12[b]	6.2 [b]	34.6 [b]
Woodburn, NSW	lowland forest along stream	54.2	3.5 +/- 0.31[c]	5.7 [b]	19.1 [a]

* Tree density based on the mean of three counts at each site

**Means in each column of this table followed by the same letter are not significantly different ($p < .05$) from transformed data analysis

*** Mean based on number of galls per fifty trees, sampled monthly over a two-year period

Table 3 Comparison of selected Australian climates to Miami, FL using CLIMEX indices of similarity*

Site Name	All Indices	Max T	Min T	Rain Amount	Rain Pattern	RH
Cairns, QLD	46	81	89	70	36	57
Brisbane, QLD	59	74	50	80	71	26
Wollongong, NSW	49	42	35	94	67	51

*An index of 100 equals and exact match with Miami, FL

Fig. 1. Seasonal densities of *Fergusonina* sp. galls (—●—) and *Melaleuca quinquenervia* buds (bars) at sites in southeast Queensland and northern New South Wales.

Fig. 2. Comparison of temperature, humidity, and rainfall between Cairns and Brisbane, QLD, Wollongong, NSW, and Miami, FL. In the top part of the figure, bars represent rainfall amounts, Miami (Black), Brisbane (white), and Cairns (dark grey) and Wollongong (light grey). Mean monthly relative humidities are plotted for Miami —●—, Brisbane —▼—, Cairns —■—, and Wollongong —◆—. In the lower part of the figure, mean monthly maximum/minimum temperatures are plotted for Miami —●—/—○—, Brisbane —▼—/—▽—, Cairns —■—/—□—, and Wollongong —◆—/—◇— .