

The biology of *Dasineura dielsi* Rübsaamen (Diptera: Cecidomyiidae) in relation to the biological control of *Acacia cyclops* (Mimosaceae) in South Africa

Robin J Adair

Agricultural Research Council, Plant Protection Research Institute, Private Bag X5017, Stellenbosch, South Africa.

Abstract *Acacia cyclops* is an invasive Australian tree in South Africa and a target for biological control using seed-reducing agents. In southern Australia, two gall-forming Cecidomyiidae, *Dasineura dielsi* (Small Fluted Galler) and *Asphondylia* sp., develop on the flowers and seeds of *A. cyclops*, respectively. The larvae of *D. dielsi* form woody fluted galls on the ovaries of flowers and prevent the development of fruit. Immature *Asphondylia* sp. develop in the loculi of green fruit and destroy developing seeds. *Dasineura dielsi* was selected as a biological control candidate for *A. cyclops* in South Africa and was approved for official release after host specificity evaluation and consideration of potential conflicts of interest. *Dasineura dielsi* naturalised in South Africa in 2001 and after 3 years dispersed up to 450 km from a single population at Stellenbosch, Western Cape. At sites where *D. dielsi* has been present longest, high gall densities occur on *A. cyclops* during the peak flower season in summer. Four hymenopterans, ?*Synopeas* sp., *Mesopolobus* sp., *Torymus* sp. and an unidentified Platygasteridae, were reared from *D. dielsi* galls and are suspected parasitoids of the cecidomyiid, with incidence levels less than 10%. Monitoring is required to evaluate trends in the population status of *D. dielsi*, its parasitoids and seed production of *A. cyclops*. Importantly, field monitoring should determine the extent and nature of possible competitive interactions between *D. dielsi* and an introduced seed-feeding weevil, *Melanterius servulus*.

Key words Asphondylia, Australia, biocontrol, biological control agent, gall midge.

INTRODUCTION

Australian acacias are invasive in South Africa and disrupt ecological processes, threaten the conservation of biodiversity and reduce agricultural productivity (Versfeld & van Wilgen 1986; Versfeld *et al.* 1998; Henderson 2001). However, several species, particularly *Acacia mearnsii* and *A. cyclops*, are exploited commercially and contribute to the economic and social welfare of South Africa (Pieterse & Boucher 1997; de Wit *et al.* 2001). Balancing the need for suppression of invasive Australian acacias with the desire to preserve their economic benefits has been a controversial issue in South Africa for several decades (Stubbings 1977; Pieterse & Boucher 1997), but was largely resolved with the acceptance of specific, seed-reducing biological control agents as a means of suppressing the reproductive capacity of problematic *Acacia* species (Dennill *et al.* 1999; Adair 2002).

The western Australian tree *A. cyclops* was introduced into South Africa around 1835 (Roux 1961), primarily for sand stabilisation in the south-western Cape region (Shaughnessy

1980), but is now naturalised extensively in coastal regions across the southern Cape (Henderson 2001). Naturalised populations of *A. cyclops* also occur in western USA (USDA 2004), Portugal (Tutin *et al.* 1968) and eastern Australia (Virtue & Melland 2003). In South Africa, *A. cyclops* is widely used as source of fuel wood for domestic and small-scale commercial purposes and contributes to the local economies of the region.

Classical biological control of *A. cyclops* using Australian seed-reducing insects that cause minimal disruption to vegetative growth of the host plant has been adopted as the best means of suppressing broad-scale infestations of *A. cyclops* in South Africa (Dennill *et al.* 1999). The Australian seed-feeding beetle *Melanterius servulus* Pascoe (Curculionidae) was released in South Africa in 1991, is now widely established and destroys up to 95% of seed at some sites (Impson *et al.* 2000, 2004). However, seed destruction by *M. servulus* is variable and appears to be influenced by limited dispersal ability of the weevil, possible variations in annual seed production by the plant and disturbance of release sites (Impson *et al.* 2000, 2004). Additional compatible agents may reduce geographical and seasonal variation in seed reduction and increase total seed destruction to the near-complete levels required for the suppression of invasive weeds (Noble & Weiss 1989; Kriticos *et al.* 1999).

Present address: Department of Primary Industries, PO Box 48, Frankston, Vic. 3199, Australia (email: robin.adair@dpi.vic.gov.au).

Gall-forming Cecidomyiidae are mostly stenophagous and often restricted to a single plant species or its close relatives (Mani 1964; Ananthakrishnan 1986; Gagné 1989). Gall-forming cecidomyiids can disrupt growth patterns of the host species and consequently the guild has been utilised or considered as biological control agents for invasive plants (Caresche & Wapshere 1975; McFadyen 1985; Gordon & Nesper 1986; Palmer *et al.* 1993; Gagné *et al.* 1996, 1997; Gordon 1999; Hinz & Muller-Scharer 2000; Sobhian *et al.* 2000). A diverse phytophagous cecidomyiid fauna occurs on Australian acacias and several midge species are under consideration as potential biological control agents of invasive acacias in South Africa, including *A. cyclops* (Adair *et al.* 2000, Adair 2004; Kolesik *et al.* 2005).

In this paper, the cecidomyiid species associated with the inflorescences of *A. cyclops* in Australia are reported. The biology and distribution of a flower-galling midge *Dasineura dielsi* Rübsaamen is described and the insect is evaluated as a potential biological control agent of *A. cyclops*.

MATERIALS AND METHODS

Surveys in Australia for cecidomyiids of *A. cyclops* and their natural host range

In Australia, the cecidomyiid fauna of the reproductive organs of acacias was surveyed by haphazardly selecting samples sites where at least three sexually mature plants of each of one or more species of *Acacia* were present. Sites were located at latitudes greater than 25°S as this is approximately the northern limit of problematic Australian *Acacia* infestations in South Africa (Henderson 2001). At each site, plants were visually searched for up to 10 min, depending on size, for the presence of cecidomyiid galls. Cecidomyiid species were recorded or where identification was not possible or uncertain, samples were collected and larvae, pupae and adults were extracted or reared. Adults were preserved and mounted following the methods of Gagné (1989). All acacias surveyed were identified and voucher specimens were lodged with national herbaria at Melbourne, Sydney or Perth when field identifications were uncertain.

Source of insects used for biological and host specificity studies

Mature gall clusters of *D. dielsi* were collected from *A. cyclops* at Moonta, South Australia (34°03'S, 137°33'E) and Cheyne Beach, Western Australia (34°49'S, 118°19'E) in 1999 and 2000 and exported to quarantine laboratory facilities at Stellenbosch, South Africa (33°57'S, 18°50'E). Adult *D. dielsi* were reared in gauze emergence cages held at 15–25°C with natural lighting received through double-glazed windows. A gall cluster consists of an aggregation of galled flowers contained on a single flower head. These are now referred to as 'galls' and where required, individual galls derived from single flowers within a flower head will be referred to as 'flower galls'.

Oviposition

No-choice oviposition tests were used to determine the stage of inflorescence development of *A. cyclops* utilised by adult *D. dielsi*. Tests were undertaken in a quarantine laboratory where newly emerged *D. dielsi* adults were aspirated directly into transparent plastic cylinders (12 cm × 8.5 cm) containing an inflorescence or infructescence of *A. cyclops* held in a small vial of water. Stems were categorised into five phenological stages: bud initials, early bud, late bud, open flowers and early fruit, and there were three to seven replicates for each phenological stage. Adult *D. dielsi* were retained in the test cylinders for 3 d at 20°C before removing the stems for egg counts and sexing the test flies. Each cylinder contained between 18 and 23 adults of mixed gender. Egg counts were made by removing 20 flowers from all flower-heads and dissecting each to aid detection of eggs. Oviposition on fruits was determined by searching the pod surface and ovules for the presence of *D. dielsi* eggs.

In a separate study, oviposition specificity was determined using methods similar to those described above. In plastic cylinders, stems with one or two open flower-heads of eight *Acacia* species were provided separately to groups of between 14 and 31 newly emerged adults of *D. dielsi*. After 2 d, 20 flowers were selected, dissected and the number of *D. dielsi* eggs was counted. Adults were sexed after all had died. There were two to four replicates for each of eight *Acacia* species tested.

Adult life span and fecundity

Adult *D. dielsi* between 3 and 7 h old were aspirated into ventilated plastic cylinders (12 cm × 8.5 cm) each containing a stem with fresh flowers of *A. cyclops*. One to seven adult *D. dielsi* were added to each cylinder. These were maintained in controlled environment cabinets at 20°C with a 12 h photoperiod from fluorescent lamps. Each day, a fine water aerosol was applied to cylinders, and the number and gender of dead flies were recorded.

A two-sample Student's *t*-test ($\alpha = 0.05$) was used to detect differences between the mean life span of male and female *D. dielsi*.

The fecundity of female *D. dielsi* was determined by counting the number of eggs from dissected ovaries. Egg counts were undertaken on freshly emerged flies held in plastic cylinders for approximately 24 h without host bouquets. The abdomen of each fly was slit open and the ovaries were extruded in a drop of water on a glass microscope slide. Eggs were separated by drawing the egg mass across the slide with a fine paintbrush. The slide was dried at room temperature and eggs were counted against a black background.

Adult emergence patterns

Mature *D. dielsi* galls collected at Moonta on 7 October 2000 were held in laboratory emergence cages and all adult cecidomyiids and hymenoptera were collected every 1–3 d until emergence ceased. Adult *D. dielsi* were sexed and suspected

hymenopteran parasitoids were identified. Galls were then dissected to check for diapausing stages that could result in emergence the following season.

A chi-square goodness of fit calculation was used to test the null hypothesis that the proportion of female to male *D. dielsi* was equal.

In a separate experiment, the voltinism and duration of generations of *D. dielsi* was determined by confining newly emerged adults in gauze sleeves on flowering branches of *A. cyclops* in the field at Stellenbosch, South Africa. Prior to the introduction of *D. dielsi*, buds and senesced flowers were removed from test branches. Gall development was monitored weekly by dissecting several flower galls from each cohort. When final instar larvae or pupae were found in cocoons, galls were collected and held in cages at room conditions until adults emerged. Adults that emerged within 1–7 d of each other were returned to flowering branches of *A. cyclops* in the field. This process was continued for 12 months. Mean weekly maximum and minimum temperature records were obtained from Fleurbaix weather station at Elsenberg, Stellenbosch (33°57'S, 18°50'E).

A Pearson's correlation coefficient for mean weekly maximum and minimum temperatures and the number of days to first emergence of each generation was determined.

Physiological host range for gall development

Adult *D. dielsi* were collected every 1–2 d from emergence cages and released in polyester sleeves (80 cm × 30 cm, 417 µ mesh) tied onto flowering branches of seven Australian and seven African *Acacia* species in the field. Sleeves were retained on the test plants for 8–10 d after which time all adults had died. The number of adults released in each sleeve ranged from 9 to 62 as the availability of *D. dielsi* varied over the emergence period and the flowering period of the test acacias. Branches were labelled and retained on the host plant for 1–4 months, after which branches were removed and the number of galled flower-heads and the number of galled flowers per flower-head were counted. There were three to eight replicates for each test plant species, but only one replicate was completed for *Acacia robusta*. Control branches of *A. cyclops* were also sleeved with *D. dielsi* throughout the testing period. Host tests were undertaken on African acacias within the National Botanical Gardens at Kirstenbosch, Worcester and Pretoria, and on Australian acacias at the Plant Protection Research Institute's Vredenburg laboratory at Stellenbosch, South Africa.

Energy status and biomass of galls

Dasineura dielsi galls were collected from Moonta, South Australia and three South African sites in the Western Cape: Strand Beach (34°06'S, 18°48'E), Somerset West (34°03'S, 18°51'E) and De Hoop Nature Reserve (34°21'S, 20°32'E). *Acacia cyclops* fruit were collected in South Africa at Strand Beach, Langebaanweg (32°58'S, 18°05'E), De Hoop Nature Reserve and Yzerfontein (33°20'S, 18°10'E). Samples were oven dried at 80°C for 5 d then ground to a powder using an

electric food processor. Three subsamples of approximately 0.5 g of processed material were taken from each site and used for calorific determinations using an Auto Bomb Calorimeter. Subsample calorific readings were used to produce mean site values and these were used for subsequent statistical analysis. A two-sample Student's *t*-test for samples with unequal variance was used to test the significance of differences in mean calorific value of *D. dielsi* galls and fruit of *A. cyclops*.

The dry biomass of mature *D. dielsi* galls and *A. cyclops* fruit was compared. Galls were haphazardly collected at Moonta, South Australia and the number of galled flowers in each gall cluster were recorded. Similarly, mature fruit of *A. cyclops* were collected at Strand Beach, Western Cape and the number of fruit per flower-head and the number of ovules per fruit were recorded. Gall and fruit samples were dried at 80°C for 5 d before being weighed.

Parasitoids

At four field sites in Western Australia (Cheyne Beach, D'Entrecasteaux National Park) and South Australia (Moonta), *D. dielsi* galls were collected from *A. cyclops*, trimmed to remove leaves and stems, then stored in ventilated plastic containers at room conditions. Emergent hymenoptera were collected and preserved in 70% ethanol before mounting following the techniques of Prinsloo (1980). The feeding mode of hymenoptera species associated with *D. dielsi* was determined by dissecting flower galls and removing immature parasitoids for adult emergence in small vials capped with cotton wool plugs. Vouchers of all hymenoptera reared from *D. dielsi* galls were lodged with the South African National Insect Collection (Pretoria).

In South Africa, 200–500 mature *D. dielsi* galls were collected in April 2003 from *A. cyclops* at each of three sites in the Western Cape: Strand Beach, Somerset West and Lyndoch (33°58'S, 18°46'E). Leaves and stems were removed and galls were held in sealed cardboard emergence boxes. Insects were collected, identified and counted after emergence had finished. Potential parasitoids of *D. dielsi* were submitted for identification and voucher specimens lodged with the South African National Insect Collection (Pretoria). Species of hymenoptera, particularly those with multiple accessions, were assumed parasitoids of *D. dielsi*, but their precise relationship with *D. dielsi* was not determined.

Dispersal in South Africa

Dasineura dielsi was found naturalised at single site near Stellenbosch, Western Cape in June 2001. The extent of the population and rate of dispersal of *D. dielsi* was determined using systematic surveys of *A. cyclops* in south-western South Africa between 2001 and 2003. Populations of *A. cyclops* were searched for the presence or absence of *D. dielsi* galls at approximately 20 km intervals along highways and roads radiating from the founder population of *D. dielsi* at Stellenbosch. At each site, up to 20 sexually mature *A. cyclops* plants were searched for galls of *D. dielsi*. Surveys were undertaken annually between March and June when galls were at maximum

density on host trees. In each year, surveys were discontinued when *D. dielsi* was absent for three or more locations (i.e. >50 km) in the same general direction after the last recorded occurrence.

RESULTS

Surveys in Australia for cecidomyiids of *A. cyclops* and their natural host range

In southern Australia, 500 field sites and 141 *Acacia* species, six infraspecific taxa and two hybrids were surveyed for gall-forming cecidomyiids between 1998 and 2003 (Adair 2004). Surveyed acacias were predominantly from the subgenus *Phyllodineae* and the sections *Phyllodineae* (72 species), *Botrycephalae* (27 species) and the *Juliflorae* (19 species) with lesser numbers from the *Plurinerves* (11 species), *Pulchellae* (5 species) and the *Alatae* (1 species).

Acacia cyclops was surveyed at 34 sites in Western Australia and South Australia. Two gall-forming Cecidomyiidae species were found on the reproductive structures of *A. cyclops*; *D. dielsi* that induces woody 'fluted galls' (Kolesik *et al.* 2005) on the ovaries of flowers, and an undescribed *Asphondylia* sp. that feeds on developing seeds and causes fruit to become stunted and slightly swollen.

Dasineura dielsi was found at 22 (65%) survey sites across the natural distribution of *A. cyclops* in southern Australia (Fig. 1) where the insect ranged from rare (one to several galls per plant or survey site) to extremely abundant (>200 galls per plant on most plants surveyed). Five *Acacia* species were recorded as hosts of *D. dielsi* in southern Australia, three from the *Plurinerves* (*A. cyclops*, *A. oswaldii*, *A. papyrocarpa*), one each from the *Phyllodineae* (*A. ligulata*) and *Juliflorae* (*A. sophorae*). *Acacia cyclops* was the primary host of *D. dielsi* as this cecidomyiid was usually only found on *A. cyclops* at sites where multiple acacia species occurred

sympatrically, and at sites where *A. cyclops* was the sole acacia species present. Alternative host acacias of *D. dielsi* (*A. sophorae*, *A. oswaldii*, *A. papyrocarpa*, *A. ligulata*) were found at five sites in South Australia (Moonta Beach 34°03'S, 137°33'E, Milnaton 34°37'S, 137°35'E, Ardrossan 34°30'S, 137°52'E; 34°19'S, 137°52'E, Aldinga 35°17'S, 138°26'E) where *A. cyclops* with *D. dielsi* occurred, in most cases, in close proximity (<10 m).

The fruit-galling *Asphondylia* sp. was found at four (12%) survey sites in Western Australia on *A. cyclops* where the insect was rare, but could have been overlooked as gall symptoms were often cryptic. *Asphondylia* sp. is unlikely to be monophagous as a cecidomyiid with similar gall symptoms and adult morphology occurs on *A. littorea*, *A. meissneri*, *A. truncata*, *A. sphenophylla* and *A. rostelifera*, but formal taxonomic assessment is required to determine whether the same or separate taxa occur on these hosts.

Asphondylia sp. develops on the seeds of *A. cyclops* in association with the Coelomycete fungus *Camarosporium* sp. (Adair 2004). The rarity of *Asphondylia* sp. on *A. cyclops* in Australia together with difficulties in establishing laboratory cultures of this fungus-dependent cecidomyiid prevented further assessment of its potential for biological control.

Oviposition

Female *D. dielsi* only oviposited in open flowers of *A. cyclops* where 1875 eggs were recovered from 140 flowers. The mean number of eggs (\pm SE) laid per female in each flower was 1.03 ± 0.2 ($n = 7$). No *D. dielsi* eggs were found in the buds or fruit of *A. cyclops*.

In no-choice tests with eight *Acacia* species, *D. dielsi* oviposited in open flowers of six Australian acacias from four sections and one African acacia, *A. robusta*. The highest mean number of eggs (\pm SE) laid per 20 flowers per female was on *A. cyclops* (*Plurinerves*) with 28.6 ± 2.3 eggs ($n = 3$), followed by *A. longifolia* (*Juliflorae*) with 15.9 ± 1.2 eggs ($n = 2$),

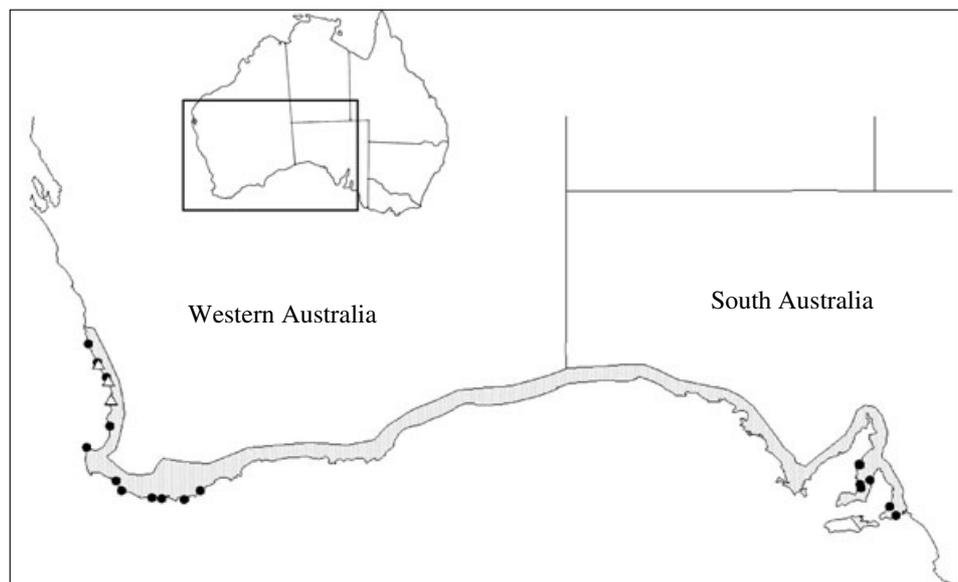


Fig. 1. Distribution of gall-forming Cecidomyiidae from *Acacia cyclops* in Australia: (●), *Dasineura dielsi*; (▲), *Asphondylia* sp. The shaded area denotes the distribution of *A. cyclops*.

A. melanoxylon (*Plurinerves*) with 8.1 ± 3.4 eggs ($n = 3$), *A. saligna* (*Phyllodineae*) with 6.9 ± 4.3 eggs ($n = 4$), *A. robusta* with 5.6 ± 2.4 eggs ($n = 4$), *A. mearnsii* (*Botrycephalae*) with 0.70 ± 0.70 eggs ($n = 4$) and *A. decurrens* (*Botrycephalae*) with 0.31 ± 0.20 eggs ($n = 4$). No eggs were laid in the flowers of *A. dealbata* (*Botrycephalae*) ($n = 3$).

Adult life span and fecundity

Adult *D. dielsi* are short-lived with a mean (\pm SE) life span of 1.35 ± 0.2 d for males ($n = 9$) and 1.66 ± 0.2 d for females ($n = 16$). There was no significant difference in the life span of male and female *D. dielsi* ($P > 0.5$). Female *D. dielsi* had a mean (\pm SE) of 233.3 ± 13.0 eggs ($n = 16$).

Adult emergence patterns

Male and female *D. dielsi* emerged simultaneously from Australian field-collected galls with the main emergence period lasting 169 d (Fig. 2a). However, 24 *D. dielsi* adults emerged between February and April 2002, 16–18 months after collection together with one specimen each of a *Synopeas* sp. and

a *Gastrancistrus* sp. No *D. dielsi* or hymenopteran parasitoids emerged during summer or autumn of 2003.

The total number of female *D. dielsi* was higher than males with a female:male sex ratio of 1.5:1 ($\chi^2 = 19.7$, $P < 0.001$, $n = 497$).

Ten species of hymenopteran parasitoids were reared from galls of *D. dielsi*, which emerged over the same period as *D. dielsi* adults (Fig. 2b).

Dasineura dielsi from *A. cyclops* was multivoltine with up to five generations per annum. The duration of development of *D. dielsi* generations was correlated with mean weekly maximum temperature ($r^2 = -0.938$, $P < 0.001$) and minimum temperature ($r^2 = -0.886$, $P < 0.01$) (Fig. 3). The developmental period from oviposition to adult emergence of field populations of *D. dielsi* ranged from 41 to 120 d.

Physiological host range for oviposition and feeding

In no-choice host specificity tests in sleeve cage with 14 *Acacia* species, *D. dielsi* induced gall formation on three species

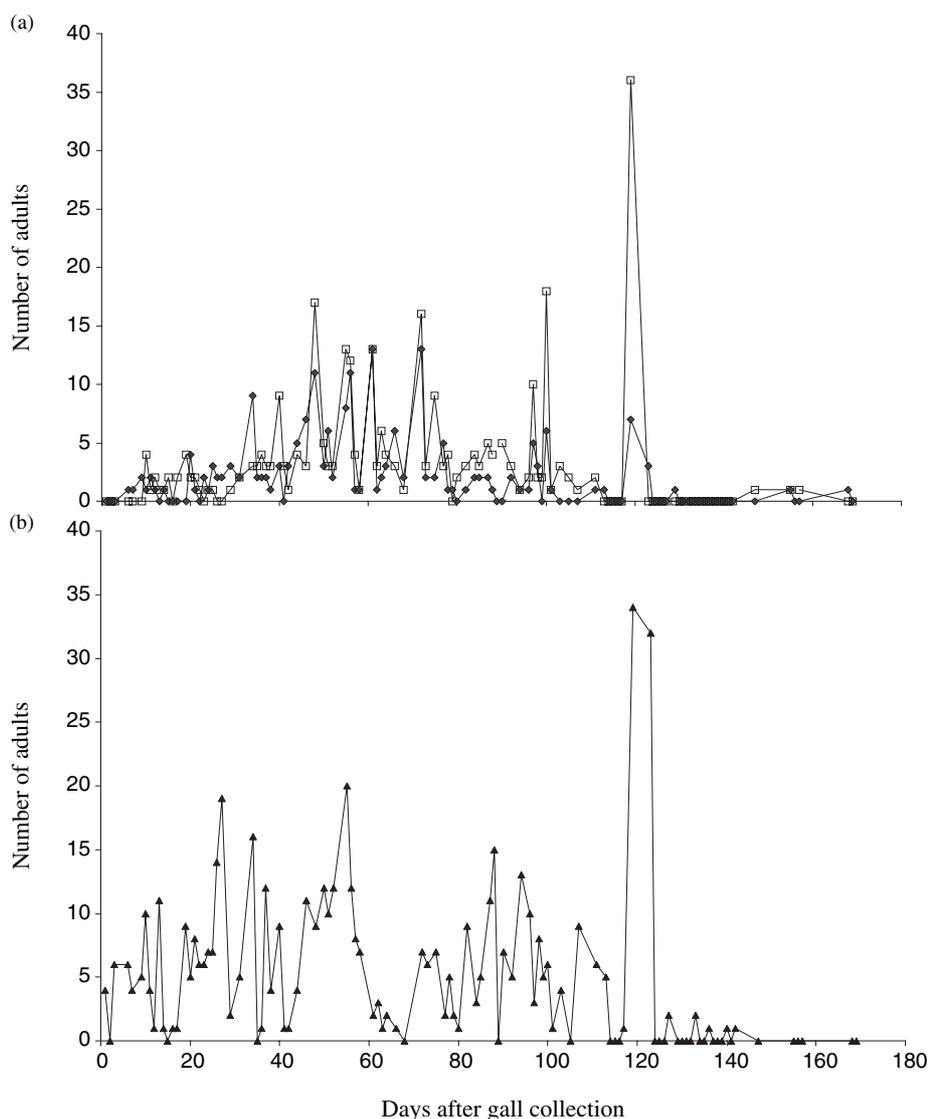


Fig. 2. Emergence of insects associated with *Dasineura dielsi* galls from *Acacia cyclops*: (a) (◆) ♂ *D. dielsi*; (□) ♀ *D. dielsi*; (b) hymenoptera parasitoids.

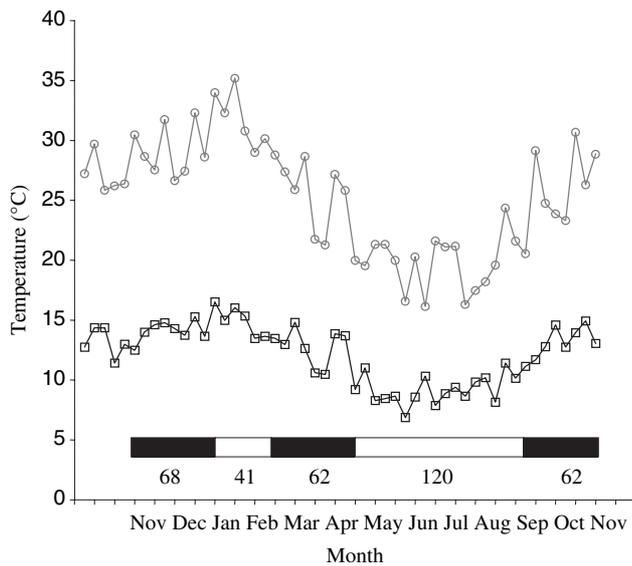


Fig. 3. Duration of development (days) of five generations of *Dasineura dielsi* as represented by the horizontal bar at Stellenbosch, South Africa with mean maximum temperature (○) and mean minimum temperatures (□) between 2000 and 2001.

of Australian acacias, *A. cyclops*, *A. implexa* and *A. elata* (Table 1). The most galls occurred on *A. cyclops*, the primary Australian host of *D. dielsi*, with minor gall formation on *A. elata* and *A. implexa*, where only one and two gall clusters developed, respectively. No African acacia test species were galled by *D. dielsi*.

Energy status and biomass of galls

Mature galls of *D. dielsi* had a mean (\pm SE) calorific value (kJ g^{-1}) of 18.37 ± 0.3 and was slightly, but significantly ($P = 0.009$), lower than the calorific value of *A. cyclops* fruit which was $19.97 \pm 0.3 \text{ kJ g}^{-1}$.

The dry weight of *A. cyclops* fruit increased linearly with the number of seeds per flower-head ($y = 0.1474x - 0.1237$, $r^2 = 0.861$, $y = \text{dry biomass}$, $x = \text{number of seeds}$) and had a significantly steeper slope ($P < 0.001$) than the dry weight of *D. dielsi* flower galls per flower-head ($y = 0.592x - 0.1882$, $r^2 = 0.8039$ where $y = \text{dry biomass}$, $x = \text{number of galls}$) (Fig. 4).

Parasitoids

In Australia, 11 species of Hymenoptera were reared from mature galls of *D. dielsi*, with five species confirmed to be primary or secondary parasitoids of *D. dielsi*. The ectoparasitoid *Gastrancistrus* sp. and the primary larval endoparasitoid *Synopeas* sp. 1 were the most abundant species reared from galls (Table 2).

At sites in South Africa where *D. dielsi* has been present for approximately 12 months, four species of Hymenoptera were reared from gall clusters of *D. dielsi*. The most abundant species (11.7% of the total number of insects) were the platygastriids *Synopeas* sp. 2 and specimens in an unidentified

Table 1 No-choice host specificity test results for *Dasineura dielsi*

Test plant origin	Acacia subgenus	Acacia section	Test species	<i>n</i>	Mean no. of adults per test	Range of adults per test	No. of gall clusters per branch (mean \pm SE)	Total no. of gall clusters	No. of flower galls per gall cluster (mean \pm SE)
Australia	Phyllodineae	Plurinerves	<i>Acacia cyclops</i>	8	23.7	9–40	5.5 \pm 2.29	44	18.9 \pm 2.5
			<i>A. implexa</i>	3	35	35	0.6 \pm 1.1	2	6.5 \pm 6.3
	Botrycephalae		<i>A. elata</i>	4	35	30–40	0.25 \pm 0.5	1	1
			<i>A. decurrens</i>	4	51.5	40–62	0	0	0
	Phyllodineae		<i>A. mearnsii</i>	3	45	37–58	0	0	0
<i>A. podalyrifolia</i>			4	34	17–45	0	0	0	0
<i>A. cultrifomis</i>			4	50	50	0	0	0	0
South Africa	Acacia		<i>A. karroo</i>	7	25.1	17–40	0	0	0
			<i>A. gerrardii</i>	4	45	40–50	0	0	0
			<i>A. fleckii</i>	3	50	40–60	0	0	0
			<i>A. robusta</i> ssp. <i>clavigera</i>	1	30	30	0	0	0
			<i>A. sieberiana</i> var. <i>woodii</i>	4	25.7	10–40	0	0	0
Aculeiferum		<i>A. ataxacantha</i>	7	22.5	20–25	0	0	0	
		<i>A. schweinfurthii</i>	4	27.5	19–40	0	0	0	

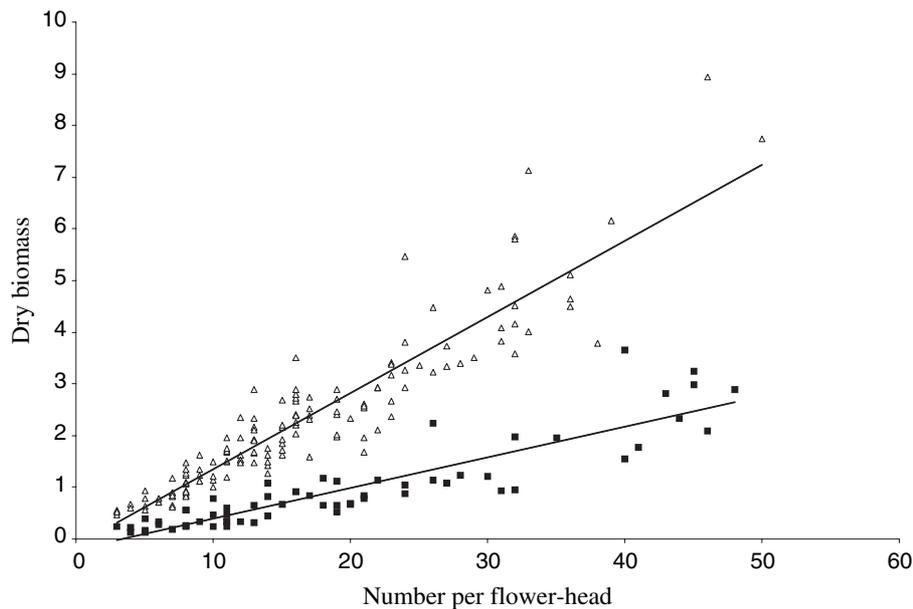


Fig. 4. Dry biomass (g) of mature *Acacia cyclops* fruits (Δ) and flower galls of *D. dielsi* per flower-head of *A. cyclops* (\blacksquare).

Table 2 Hymenopteran parasitoids reared from galls of *Dasineura dielsi* collected in Australia and South Africa

Country	Family	Species	Feeding mode	Accession number	Comment
Australia	Pteromalidae	<i>Gastrancistrus</i> sp.	ecto	2571/2 3023/1	A dominant larval-pupal parasitoid of <i>D. dielsi</i>
		<i>Systasis</i> sp. 1	?ecto	2598/2 2883/3	
		<i>Systasis</i> sp. 2	?ecto	2883/3	
	Torymidae	<i>Torymoides</i> sp.	ecto	3023/2	Widespread but not abundant and occurs in many other Australian gall-forming <i>Dasineura</i>
		<i>Megastigmus</i> sp.	ecto	2883/1 2571/1 2883/2 3023/5	
		Genus indet.		3023	
	Eupelmidae	<i>Aprostocetus</i> sp.	?ecto	3023	
	Elasmidae	<i>Euderus</i> sp.	?	3023/6	Uncommon
		<i>Elachertus</i> sp.	?	3023/6	Uncommon
		<i>Elasmus</i> sp.	?	3023/6	Uncommon
<i>Synopeas</i> sp. 1		endo	2598/1 2883/4	A primary larval parasitoid, which can be abundant	
South Africa	Encyrtidae	<i>Inostemma</i> sp.	endo	2883/4	
		<i>Homalotylus</i> sp.	?endo	3023/4	
	Pteromalidae	<i>Mesopolobus</i> sp.	?	3306/1	
Torymidae	<i>Torymus</i> sp.	?	3306/2	Rare	
Platygastridae	? <i>Synopeas</i> sp. 2	endo	sn	Dominant parasitoids at one coastal site in the Western cape	
Genus indet.	endo	sn			

ecto, ectoparasitoid; endo, endoparasitoid; sn, no accession number.

genus, but these were restricted to the Strand Beach site. No insects other than *D. dielsi* and hymenopterans were collected from emergence cages; however, a few small spiders were also collected at some sites. Emergence of Hymenoptera occurred with adults of *D. dielsi* over 6 weeks and commenced within several days after collecting galls from the field. The pteromalid *Mesopolobus* sp. was less common (0.6–1.6% of the total number of insects), but occurred at all three sample sites (Table 3).

Dispersal in South Africa

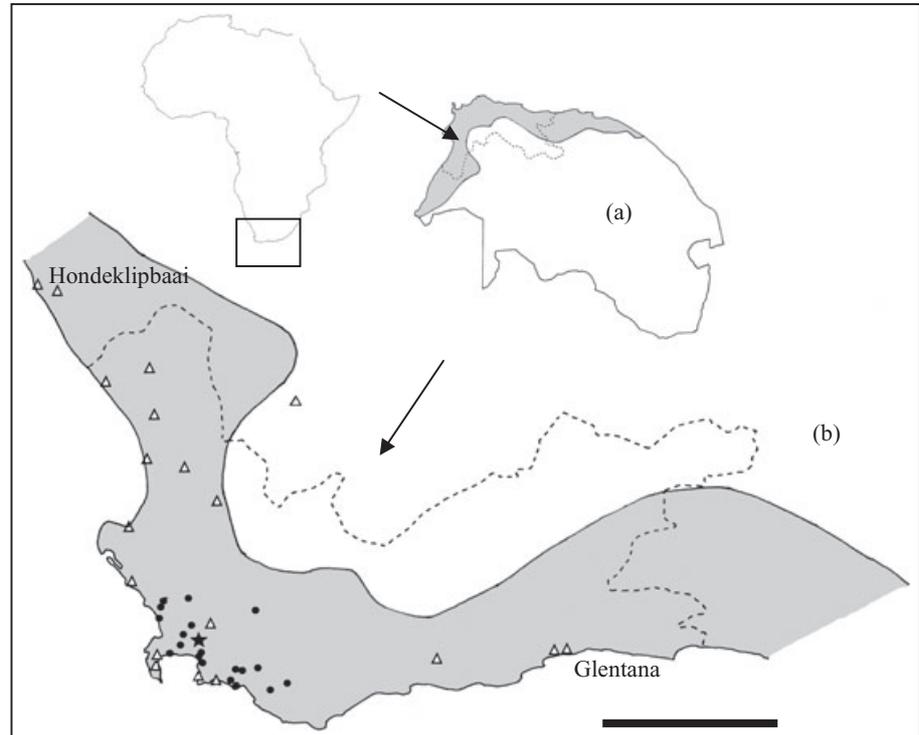
Dasineura dielsi spread rapidly within the distribution of *A. cyclops* in the Western Cape following naturalisation at Stellenbosch in 2001 (Fig. 5). Dispersal occurred predominantly north-west and south-east of Stellenbosch within the first year with galls detected up to 100 km from the initial site of establishment. In 2003, the most northerly occurrence of *D. dielsi* was at Hondeklipbaai (30°32'0"S, 17°27'0"E), 450 km

Table 3 Number of hymenopteran and cecidomyiids reared from *Dasineura dielsi* galls from three locations in Western Cape, South Africa

Site	Number of <i>D. dielsi</i>	Total number of parasitoids	Platygastridae†	<i>Torymus</i> sp.	<i>Mesopolobus</i> sp.
Stellenbosch	865	6	0	1	5
Somerset West	751	12	0	0	12
Strand Beach	921	136	124	1	11

†Includes ?*Synopeas* sp. and an undetermined genus. Numbers of adults were combined because of difficulties in distinguishing these species.

Fig. 5. Distribution of *Dasineura dielsi* in South Africa: (a) South African distribution of *Acacia cyclops* (shaded); (b) distribution of *D. dielsi* in the Western Cape (broken line) with original release point (★), 2002 distribution records of *D. dielsi* (●) and 2003 distribution records (△). The scale bar in map (b) is 100 km.



north-northwest of Stellenbosch and the most easterly occurrence was at Glentana (34°041'S, 22°325'E), 390 km from Stellenbosch. Galls of *D. dielsi* were readily detected in the canopy of *A. cyclops*, particularly following the peak flowering period in summer–autumn. At the edge of the invasion front, *D. dielsi* gall densities were low, often only 1–10 galls per 10–20 sample trees. However, at sites within 20 km of Stellenbosch, where populations had been present for 1–2 years, gall densities were higher with several thousand galled flower-heads often present on a single mature tree.

DISCUSSION

Gall-forming insects can have a debilitating impact on their hosts and have been utilised successfully for biological control of Australian acacias in South Africa (Dennill *et al.* 1999; Hoffmann *et al.* 2002). Cecidogenic agents usually develop close physiological relationships with their hosts (Floate *et al.* 1996), which can constrain the potential range of host plant species. As narrow host ranges are a general requirement of

modern classical biological control programs (Harley 1992), gall-forming agents generally meet host specificity standards.

Although *D. dielsi* was found on five *Acacia* species in Australia (*A. cyclops*, *A. sophorae*, *A. papyrocarpa*, *A. oswaldii*, *A. ligulata*), *A. cyclops* was the primary host and galling on other hosts only occurred when they were in close proximity to *A. cyclops*, indicating this was likely to be opportunistic feeding. Oviposition by *D. dielsi* appears to be largely independent of subgeneric boundaries within *Acacia*, but larval development and gall formation are restricted to Australian acacias, and primarily to species in the section *Plurinerves*. As African acacias and Australian acacias used in plantation forestry in South Africa are at low risk from attack by *D. dielsi*, this cecidomyiid was considered suitable as a biological control agent for *A. cyclops*. In South Africa, superficial galling on *A. melanoxylon* (*Plurinerves*) has occurred where *A. cyclops* and *A. melanoxylon* occur sympatrically. Flowering of *A. melanoxylon* occurs as a single pulse in late winter to early spring. As *D. dielsi* is multivoltine and requires a continuous source of open flowers for its persistence in high numbers, isolated populations of *A. melanoxylon* are unlikely

to sustain this midge in South Africa. Sporadic galling by *D. dielsi* on *A. longifolia* and *A. implexa* in South Africa is also likely where these acacias occur with or near *A. cyclops*, such as on the lower slopes of coastal mountain ranges in the western and eastern Cape provinces. The expected ephemeral or sporadic occurrence of *D. dielsi* on *A. melanoxylon*, *A. implexa* and *A. longifolia* in South Africa is unlikely to make significant contributions to the biological control of these invasive species.

The galls of *D. dielsi* have lower unit biomass and calorific values than mature fruit of *A. cyclops*. As a large proportion of *A. cyclops* flower-heads are not shed after anthesis and produce fruit clusters, *D. dielsi* is unlikely to adversely disrupt vegetative growth patterns of *A. cyclops*, even at high gall densities. This view is further supported by the ephemeral nature of gall duration, which varies from 1 to 3 months per flower-head and is considerably less than the 8–12 months required for fruit development of *A. cyclops* (F Impson pers. comm. 2004). Although flower production of *A. cyclops* in relation to gall or pod production was not determined in this study, it is unlikely that greater flower production because of *D. dielsi* colonisation will occur. No such effect was detected on a similar midge, *Dasineura rubiformis* Kolesik that forms super-galling densities on *A. mearnsii* in Western Australia (Adair 2004). In these respects, *D. dielsi* appears unlike other galling agents released for the biological control of Australian acacias that induce a process of 'resource commitment' and cause a substantial decline in host vigour (Dennill 1988; Hoffmann *et al.* 2002).

The interactive impacts of biological control agents utilising the same host and similar feeding niches is rarely examined in weed biological control programs. Although additive effects of multiple agent introductions are documented (Hoffmann & Moran 1998), direct competition for food resources can limit agent efficacy (Woodburn 1996). *Dasineura dielsi* and *M. servulus* feed on inflorescence structures that are phenologically separated, and therefore avoid direct competition for food resources. However, indirect competitive effects may become apparent in areas where *D. dielsi* and *M. servulus* are sympatric. *Dasineura dielsi* prevents the development of fruit, which are used by *M. servulus* adults and larvae as a source of food. As a consequence, reduced fruit loads of *A. cyclops* are likely to constrain *M. servulus* population densities, but declines in populations of the weevil may only be consequential, if reduced seed production achieved by a combination of *D. dielsi* and *M. servulus* is less than reduction levels currently obtained by *M. servulus* alone. Detailed field monitoring of *M. servulus* at sites before and after the arrival of *D. dielsi*, and the respective contributions of the two agents to seed reduction, will reveal the nature of the interactions between these species.

The temporal-spatial dispersal dynamics of biological control agents can influence the success or otherwise of pest suppression programs. Rapid dispersal is a desirable trait as it reduces the time taken to expose the pest population to the controlling agent (Fagan *et al.* 2002). In south-western South Africa, *D. dielsi* has spread rapidly throughout populations of

A. cyclops. This rapid dispersal is attributed to the insect's small body weight and predisposition to wind dispersal and the strong winds experienced along the southern African coastal region over most of the year. This is augmented by the apparently proficient host finding abilities of *D. dielsi*, evident from its frequent presence on isolated plants of *A. cyclops* in South Africa. In addition to this, *D. dielsi* is multivoltine with up to five generations per year, providing the potential for faster dispersal than most other *Dasineura* species from Australian acacias, which are univoltine or bivoltine (Adair 2004; Kolesik *et al.* 2005).

Classical biological control agents often acquire parasitoids in their country of introduction within several years (Hill & Hulley 1995), but the full complement of species may accrue gradually and over a much longer period of time (Cornell & Hawkins 1993). The level and nature of parasitism of biological control agents can influence the success or otherwise these programs (e.g. Dodd 1961; Julien & Griffiths 1998; Pratt *et al.* 2000) by affecting establishment, dispersal (Fagan *et al.* 2002) and impact on the host plant. The galls of *D. dielsi* were rapidly detected and utilised by four species of South African parasitoids, but in the first 2 years since the establishment of *D. dielsi*, they appear to have had no adverse impact on the dispersal and colonisation success of this cecidomyiid. Two endoparasitic Platygastriidae, including a ?*Synopeas* sp., and the pteromalid *Mesopolobus* sp. dominate the early parasitoid fauna of *D. dielsi* in South Africa. This has similarities to the Australian parasitoid fauna of *D. dielsi*, where although more species rich, the platygastriid ?*Synopeas* sp. and the pteromalid *Gastrancistrus* sp. are the dominant parasitoids (Adair 2004). In South Africa, gall-forming cecidomyiids occur on African acacias, including several species on *A. mellifera* with similar gall structure to *D. dielsi*. These cecidomyiids are utilised by an unidentified platygastriid, and the pteromalids *Systasis* sp. and *Gastrancistrus* sp. (Adair 2004) and represent a striking similarity to the composition of parasitoids of *D. dielsi* in Australia. Longer-term monitoring of the parasitoid composition of *D. dielsi* in South Africa could determine parasitoid recruitment rates and host utilisation patterns, which may be helpful in assessing the feasibility of parasitoid predictions for classical biological control agents. Furthermore, such studies could establish whether the spectacular spread and establishment of *D. dielsi* is a short-term event, resembling the rise and fall of *Rhopalomyia californica* Felt in Queensland (McFadyen 1985; Julien & Griffiths 1998), or whether high population densities can be sustained to render *D. dielsi* an effective biological control agent for *A. cyclops* in South Africa.

In Australia, *A. cyclops* is naturalised in south-eastern South Australia (Virtue & Melland 2003), western Victoria and the Belarine Peninsula, Melbourne (AVH 2001; Cowan & Maslin 2001). In South Australia, *D. dielsi* has followed the spread of *A. cyclops* where it occurs in coastal areas of the Yorke and Fleurieu Peninsulas. The possible expansion of *A. cyclops* into the Adelaide Hills, South Australia and Victoria is likely to facilitate exposure of *D. dielsi* to potential eastern Australian acacias, particularly *A. melanoxylon* and

A. implexa leading to the possible occurrence of new cecidomyiid-acacia records.

ACKNOWLEDGEMENTS

The South African Department of Water Affairs and Forestry through the Working for Water Program generously funded this project in collaboration with the Plant Protection Research Institute (PPRI) of the Agricultural Research Council, South Africa. The staff of PPRI are gratefully acknowledged for their assistance, in particular Keith Appollis, Abraham Adonis and Lulu Masihyi for laboratory and field assistance and Lesley Henderson for the production of South African distribution maps. Ottilie Nesor (PPRI) was generous with her time and patience in identifying parasitoids of *D. dielsi* from Australia and South Africa. Judy Moore (PPRI) provided invaluable assistance during the preparation of this paper and her cooperation is very much appreciated. Liesl Barnes (University of Cape Town) kindly operated the bomb calorimeter for calorific determinations. Jim Backholer and Les Bould (Victorian Department of Primary Industries) helped with the final preparation of figures. Peter Kolesik (University of Adelaide) confirmed the identification of *D. dielsi*. My colleagues Stefan Nesor, John Hoffmann and Fiona Impson generously provided constructive review of an early draft of this paper.

This work was undertaken as part of a PhD study in the Zoology Department, University of Cape Town, South Africa.

REFERENCES

- Adair RJ. 2002. Black wattle: South Africa manages conflict of interest. *Biocontrol News and Information* **23**, 5N–7N.
- Adair RJ. 2004. *Seed-reducing Cecidomyiidae as potential biological control agents for invasive Australian wattles in South Africa, particularly Acacia mearnsii and A. cyclops*. PhD Thesis, University of Cape Town, Cape Town, South Africa.
- Adair RJ, Kolesik P & Nesor S. 2000. Australian seed-preventing gall midges (Diptera: Cecidomyiidae) as potential biological control agents for invasive *Acacia* spp. in South Africa. In: *Proceedings of the X International Symposium on Biological Control of Weeds*, Bozeman, Montana, 4–14 July 1999 (ed. NR Spencer), pp. 605–614. Montana State University, Montana, USA.
- Ananthakrishnan TN, ed. 1986. *Biology of Gall Insects*. Edward Arnold, London, UK.
- AVH (Australia's Virtual Herbarium). 2001. *Australia's Virtual Herbarium*. Council Heads of Australian Herbaria. Available from URL: <http://www.anbg.gov.au/avh/>
- Caresche LA & Wapshere AJ. 1975. The *Chondrilla* gall midge (*Cystiphora schmidti*) II. Biology and host specificity. *Bulletin of Entomological Research* **65**, 55–64.
- Cornell HV & Hawkins BA. 1993. Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. *American Naturalist* **141**, 847–865.
- Cowan RS & Maslin BR. 2001. *Acacia cyclops*. In: *Flora of Australia* Vol. 11B, *Mimosaceae, Acacia. Part 2* (eds AE Orchard & AJG Wilson), pp. 138. ABR/CSIRO, Melbourne, Australia.
- Dennill GB. 1988. Why a gall former can be a good biocontrol agent: the gall wasp *Trichilogaster acaciaelongifoliae* and the weed *Acacia longifolia*. *Ecological Entomology* **13**, 1–9.
- Dennill GB, Donnelly D, Stewart K & Impson F. 1999. Insect agents used for the biological control of Australian *Acacia* species and *Paraseri-*
- anthes lophantha* (Willd.) Nielsen (Fabaceae) in South Africa. *African Entomology Memoir* **1**, 45–54.
- Dodd AP. 1961. Biological control of *Eupatorium adenophorum* in Queensland. *Australian Journal of Science* **23**, 356–365.
- Fagan WF, Lewis MA, Neubert MG & van den Driessche P. 2002. Invasion theory and biological control. *Ecology Letters* **5**, 148–157.
- Floate KD, Fernandes GW & Nilsson JA. 1996. Distinguishing intrapopulation categories of plants by their insect faunas: galls on rabbit-bush. *Oecologia* **105**, 221–229.
- Gagné RJ. 1989. *The Plant-Feeding Gall Midges of North America*. Cornell University Press, Ithaca, USA.
- Gagné RJ, Balciunas JK & Burrows DW. 1997. Six new species of gall midges (Diptera: Cecidomyiidae) from *Melaleuca* (Myrtaceae) in Australia. *Proceedings of the Entomological Society of Washington* **99**, 312–334.
- Gagné RJ, Sobhian R & Isidoro N. 1996. A review of the genus *Psectrosema* (Diptera: Cecidomyiidae), Old World pests of tamarix (Tamaricaceae), and description of three new species. *Israel Journal of Entomology* **30**, 53–69.
- Gordon AJ. 1999. Biological control of Australian myrtle, *Leptospermum laevigatum* (J. Gaertn.) F. Muell. (Myrtaceae), in South Africa. *African Entomology Memoir* **1**, 139–143.
- Gordon AJ & Nesor S. 1986. The seasonal history of the gall midge, *Zeuxidiplosis giardi* Keiffer (Diptera: Cecidomyiidae), an introduced natural enemy of St John's Wort, *Hypericum perforatum*. *Journal of the Entomological Society of Southern Africa* **49**, 115–120.
- Harley KLS. 1992. *Biological Control of Weeds: A Handbook for Practitioners and Students*. Inkata, Melbourne, Australia.
- Henderson L. 2001. *Alien Weeds and Invasive Plants: A Complete Guide to Declared Weeds and Invaders in South Africa*. Agricultural Research Council, Pretoria, South Africa.
- Hill MP & Hulley PE. 1995. Host-range extension by native parasitoids to weed biocontrol agents introduced to South Africa. *Biological Control* **5**, 297–302.
- Hinz HL & Muller-Scharer H. 2000. Influence of host condition on the performance of *Rhopalomyia* n. sp. (Diptera: Cecidomyiidae), a biological control agent for scentless Chamomile, *Tripleurospermum perforatum*. *Biological Control* **18**, 147–156.
- Hoffmann JH, Impson FAC, Moran VC & Donnelly D. 2002. *Trichilogaster* gall wasps (Pteromalidae) and biological control of invasive golden wattle trees (*Acacia pycnantha*) in South Africa. *Biological Control* **25**, 64–73.
- Hoffmann JH & Moran VC. 1998. The population dynamics of an introduced tree, *Sesbania punicea*, in South Africa, in response to long-term damage caused by different combinations of three species of biological control agent. *Oecologia* **114**, 343–348.
- Impson FAC, Moran VC & Hoffmann JH. 2004. Biological control of an alien tree, *Acacia cyclops*, in South Africa: impact and dispersal of a seed-feeding weevil, *Melanterius ?servulus*. *Biological Control* **29**, 375–381.
- Impson FAC, Moran VC, Hoffmann JH, Donnelly D & Stewart K. 2000. Recent developments in the biological control of invasive *Acacia* in South Africa: *Melanterius ?servulus* (Coleoptera: Curculionidae) Against *Acacia cyclops*. In: *Proceedings of the X International Symposium on Biological Control of Weeds*, Bozeman, Montana, USA, 4–14 July 1999 (ed. NR Spencer), pp. 729–734. Montana State University, Montana, USA.
- Julien M & Griffiths MW, eds. 1998. *Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds*, 4th edn. CAB International, Wallingford, UK.
- Kolesik P, Adair RJ & Eick G. 2005. Nine new species of *Dasineura* (Diptera: Cecidomyiidae) from flowers of Australian *Acacia* (Mimosaceae). *Systematic Entomology* (in press).
- Kriticos D, Brown J, Radford I & Nicholas M. 1999. Plant population ecology and biological control: *Acacia nilotica* as a case study. *Biological Control* **16**, 230–239.
- Mani MS. 1964. *The Ecology of Plant Galls*. Junk, The Hague, Netherland.
- McFadyen PJ. 1985. Introduction of the gall fly, *Rhopalomyia californica* from the USA into Australia for the control of the weed *Baccharis halimifolia*. In: *Proceedings of the VI International Symposium on*

- Biological Control of Weeds*, Vancouver, Canada, 19–25 August 1984 (ed. ES Delfosse), pp. 779–796. Agriculture Canada, Ottawa.
- Noble IR & Weiss PW. 1989. Movement and modelling of buried seed of the invasive perennial *Chrysanthemoides monilifera* in coastal dunes and biological control. *Australian Journal of Ecology* **14**, 55–64.
- Palmer WA, Diatloff G & Melksham J. 1993. The host specificity of *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) and its importation into Australia as a biological control agent for *Baccharis halimifolia*. *Proceedings of the Entomological Society of Washington* **95**, 1–6.
- Pieterse PJ & Boucher C. 1997. A.C.A.C.I.A. (A case against controlling introduced Acacias) – 19 years later. *Southern African Forestry Journal* **180**, 37–44.
- Pratt PD, Coombs EM & Croft BA. 2000. Predation and interference by Phytoseiid mites on the Spider Mite *Tetranychus lintearius* (Acari: Tetranychidae), an established biological control agent of Gorse (*Ulex europaeus*). In: *Proceedings of the X International Symposium on Biological Control of Weeds*, Bozeman, Montana, USA, 4–14 July 1999 (ed. NR Spencer), pp. 729–734. Montana State University, Montana, USA.
- Prinsloo GL. 1980. *An Illustrated Guide to the Families of African Chalcidoidea (Insecta:Hymenoptera)*. Department of Agriculture and Fisheries Science Bulletin No. 395. Pretoria, South Africa.
- Roux ER. 1961. History of introduction of Australian acacias on the Cape flats. *South African Journal of Sciences* **57**, 99–102.
- Shaughnessy GL. 1980. Historical ecology of alien woody plants in the vicinity of Cape Town, South Africa. PhD Thesis, University of Cape Town, Cape Town, South Africa.
- Sobhian R, Littlefield J, Cristofaro M & Mann K. 2000. Biology and host specificity of *Spurgia capitigena* (Bremi) (Diptera: Cecidomyiidae), for the biological control of *Euphorbia escula* L. in North America. *Journal of Applied Entomology* **124**, 333–338.
- Stubbings JA. 1977. A.C.A.C.I.A. (A case against controlling introduced acacias). *South African Forestry Journal* **102**, 8–14.
- Tutin TG, Heywood VH, Burges NA *et al.*, eds. 1968. *Flora Europaea*. Vol. 2. Cambridge University Press, London, UK.
- USDA NRCS. 2004. *The PLANTS database*, Version 3.5. National Plant Data Centre, Baton Rouge, USA. Available from URL: <http://www.plants.usda.gov>
- Versfeld DB, le Maitre DC & Chapman RA. 1998. Alien invading plants and water resources in South Africa: A preliminary assessment. *Water Research Commission Report No. TT99/98*. Pretoria, South Africa.
- Versfeld DB & van Wilgen BW. 1986. Impacts of woody aliens on ecosystem properties. In: *The Ecology and Control of Biological Invasions in South Africa* (eds IAW Macdonald, FJ Kruger & AA Ferrar), pp. 239–246. Oxford University Press, Cape Town, South Africa.
- Virtue JG & Melland RL. 2003. *The environmental weed risk of revegetation and forestry plants*. South Australia. Department of Land, Water and Biodiversity Conservation. Report DWLBC 2003/02.
- de Wit MP, Crookes DJ & van Wilgen BW. 2001. Conflicts of interest in environmental management: estimating the costs and benefits of a tree invasion. *Biological Invasions* **3**, 167–178.
- Woodburn TL. 1996. Interspecific competition between *Rhinocyllus conicus* and *Urophora solstitialis*, two biocontrol agents released in Australia against *Carduus nutans*. In: *Proceedings of the IX International Symposium on the Biological Control of Weeds*, Stellenbosch, South Africa, 19–26 January 1996 (eds VC Moran & JH Hoffmann) pp. 409–415. University of Cape Town, Cape Town, South Africa.

Accepted for publication 27 January 2005.