

SESSION 8

Host Selection and Specificity

Australian Seed-Preventing Gall Midges (Diptera: Cecidomyiidae) as Potential Biological Control Agents for Invasive *Acacia* spp. in South Africa

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Abstract

In Australia, bud, flower, fruit and seed-feeding Cecidomyiidae occur on all Australian *Acacia* invasive in South Africa, except for *A. saligna* (Labill.) H.L. Wendl. In southern Australia, *Dasineura* and *Asphondylia* are the main genera that cause damage to the reproductive organs of *Acacia*. *Dasineura* spp. commonly form clusters of galls on inflorescences and thereby suppress seed production. There is considerable variation in gall morphology, and numerous *Acacia* hosts, suggesting a rich assemblage of closely allied taxa. Detailed morphological examination of adults, pupae and larvae will resolve their taxonomic status, but comparison of the DNA in some groups may be required to clarify taxonomic relationships. *Asphondylia* spp. develop in galls in unopened florets, or on seeds in developing pods. At least four species have been reared from a range of *Acacia* spp. and all are associated with a fungus that also grows in the galls. The larvae are in close contact with fungal hyphae and there is possibly a symbiotic relationship between the two organisms. There are two main life strategies in seed-preventing Cecidomyiidae on *Acacia*. The most abundant is a univoltine life cycle with the cecidomyiid passing from one flowering season to the next as larvae in galls on the host. A smaller number of taxa are multivoltine and produce galls on specific organs. They mostly have short generation times and can switch from one host species to another during the year, or switch to the utilisation of different reproductive organs on the same host.

Specificity testing and taxonomic determinations are required to assess the risk to African *Acacia* spp. and other Mimosaceae to attack by Australian Cecidomyiidae. Cropping for non-floral products of *Acacia* in South Africa could continue if vegetative growth of the host is not adversely affected by seed-preventing gall midges. Research into the potential of these insects as biological control agents for *Acacia* in South Africa may have ramifications in other countries where Australian acacias are invasive or are being promoted as crops.

Keywords: *Acacia*, Cecidomyiidae, *Asphondylia*, *Dasineura*, Australia, South Africa

Introduction

The Australian wattles, *Acacia mearnsii* De Wild. and *A. melanoxylon* R. Br. are commercially important trees in South Africa and are used mainly for the production of tannin, timber and pulpwood products (New 1984). Both are also invasive weeds in non-plantation areas and are responsible for reduced water production, loss of biodiversity and reduced agricultural production. Other *Acacia* species also have negative environmental impacts in South Africa, particularly *A. dealbata* Link, *A. decurrens* Willd., *A. cyclops* A. Cunn. e.c. G. Don, *A. saligna* (Labill.) H.L. Wendl., *A. longifolia* (Andrews) Willd. and *A. pycnantha* Benth., but these have limited or no commercial value.

Destruction of seeds or reduction of copious seeding using host-specific biological control agents would allow commercial *Acacia*-based industries to be maintained, while reducing the rate of spread and regeneration success of the acacias. Four host-specific, seed-feeding species of *Melanterius* (Coleoptera: Curculionidae) have been released in South Africa on *A. longifolia*, *A. mearnsii*, *A. melanoxylon* and *A. cyclops*. While seed production has been reduced on some hosts, the beetles have either spread slowly or are still not effective over the entire range of the targets. Additional agents are required to complement the seed reduction already induced by *Melanterius* and by 2 species of *Trichilogaster* (Hymenoptera: Pteromalidae), which form galls on developing inflorescences (Dennill *et al.* 1999).

In Australia, bud, flower, fruit and seed-feeding Cecidomyiidae have been found on all Australian *Acacia* spp. invasive in South Africa, except for *A. saligna*. All are gall-inducing and most are undescribed. The only two described species are *Dasineura dielsi* Rübsaamen from *A. cyclops* (Rübsaamen 1916) and *D. acaciaelongifoliae* (Skuse) from *A. longifolia* (Gagné and Marohasy 1993), both of which form conspicuous woody gall clusters on developing infructescences. Cecidomyiidae that feed on the reproductive organs of Australian acacias are under evaluation as potential biological control agents in South Africa as all appear to be specific to the genus, and are capable of causing substantial reductions in seed production. A program has commenced to describe all relevant taxa, determine the life strategies and host specificity of species considered to have the highest potential as biological control agents, and measure their impact on the vegetative and reproductive growth potential of *Acacia* hosts.

Life Strategies

Two life strategies occur in seed-preventing Cecidomyiidae on Australian acacias. The dominant strategy is a univoltine life cycle with insects passing from one flowering season to the next in galls on infructescences. Oviposition mostly occurs at flowering and eggs are deposited on the surface of the ovary. Larvae induce host tissue to evaginate around them leading to gall formations that contain one to several chambers per gall. Feeding and gall development usually takes place for a few weeks to several months before pupation occurs in cocoons within the gall chamber. Most galls remain on the host plant until the emergence of adults. In several species, larvae emerge from the gall after the cessation of feeding and pupate in the soil close to the host tree. The duration of the pupal stage is several weeks. Adults are short lived, surviving only for several days.

Multivoltinism has been observed in several cecidomyiid species on *Acacia* in south-

ern Australia, with generation times lasting several months. A podlet galler (*Dasineura* sp.) that forms non-woody gall clusters on developing fruits, often emerges when the host is phenologically out of synchrony with the oviposition requirements of the female. Females lay eggs in open flowers and podlet galls develop in place of normal fruits. If flowers are not present at the time of emergence searching for alternative hosts must occur for local populations to persist. At least one other host is required for this cecidomyiid to persist on *A. mearnsii*, but acacias that produce flowers during all months, such as *A. retinoides* Schldl., host independent populations of this insect. Two Bud Gallers (*Asphondylia* spp.) produce almost identical galls on the buds and fruits of a range of *Acacia* spp. Larvae develop on immature seeds within pods and in the buds of the same or related hosts. In most acacias these organs are not simultaneously present on the host tree (except for a group of bipinnate acacias) and these cecidomyiids are believed to alternate development on these host organs, depending on availability. This life strategy enables the insects to avoid long gaps in the phenological cycle their hosts. Although these *Asphondylia* spp. are recorded from a range of *Acacia* hosts, it is not known whether the species' are truly oligophagous or consists of a number of host-specific biotypes.

Associations with Fungi

Several *Asphondylia* species gall the buds and seeds of a range of acacias in southern Australia in association with an unidentified fungus. The cecidomyiid larvae live in contact with mycelium and in the later stages of development, the fungus forms a darkened casing around the pupa. Sporulation has not yet been observed and attempts to culture the fungus on potato dextrose agar media have failed. In sectioned gall tissue from buds of *A. mearnsii* galled by an *Asphondylia* sp., hyphae are packed around the stamen bundle in the centre of the bud, but do not seem to develop any inter- or intracellular connections with the plant host. In older galls, the stamen bundle and gynoecium are reduced to stubs and the hyphae cover the inner walls of the gall. As cecidomyiid larvae have no chewing mouth parts, it is likely that enzyme secretions by the fungus may be the main means by which host metabolites are made available to the fungus and hence to the larva. Fungi appear obligatory in all galls of *Asphondylia* (Meyer 1952, Gagné 1989, and Kolesik et al. 1997) and partially constitute the food of those midges. However, the cecidomyiid/fungus relationship may not be obligatory. Ross (1932) considered the fungi as inquilines in galls of Cecidomyiidae, as more than one species of fungus can be found in one gall. In the early stages of establishment of a seed-feeding cecidomyiid (*Asphondylia* sp.) in the immature pods of *A. mearnsii*, first instar cecidomyiid larvae occur without any signs of fungi, but fungal development occurs in more advanced stages of pod/cecidomyiid maturation. If the relationship between *Asphondylia* on *Acacia* and the fungus is symbiotic, then the introduction of both organisms into South Africa may need to be undertaken to establish laboratory and field populations. While *Asphondylia* are known from *Acacia* in Africa (Kenya) (Gagné and Marohasy 1993) and have been observed on *Dichrostachys* (Mimosaceae), there is no clear record of their association with fungal symbionts. A comparison of associated fungi, if present, with *Asphondylia* on African acacias and related Mimosaceae in South Africa with those on *Acacia* spp. in Australia may clarify whether deliberate importation of Australian fungi is required.

Host Specificity

Most Cecidomyiidae gall midges are monophagous or oligophagous, but a few species are known to be polyphagous on a range of unrelated hosts (Gagné 1989). Seed-preventing Cecidomyiidae on *Acacia* spp. in southern Australia use a range of hosts, but all taxa appear to be restricted to this genus. Oligophagy seems to be dominant in Australian Cecidomyiidae on *Acacia* with closely related hosts being utilised (table 1). For example, the Tiny Podlet Galler (*Dasineura* sp.) is only known from *A. mearnsii* and the closely related *A. irrorata* Sieber ex Spreng. and *A. deanei* (R.T. Baker) Welch, Coombs and McGlynn. Similarly, a univoltine cecidomyiid that causes distinctive inflated podlets in tight ball-like clusters, is often found on several bipinnate wattles including *A. dealbata*, *A. decurrens*, *A. baileyana* F. Muell., *A. blayana* Tind. and Court, *A. filicifolia* Cheel and Welch, but not *A. mearnsii*. Occasionally, this cecidomyiid is also found on *A. paradoxa* DC. and *A. podalyriifolia* A. Cunn. ex G. Don. A highly distinctive cecidomyiid that forms small round, moss-like galls on flowers is only known from *A. irrorata*. The Common Bud Galler (*Asphondylia* sp.) is very widespread across southern Australia and develops small, pumpkin-like galls on the buds of many *Acacia* species. Hosts are known from most sections of the subgenus *Phyllodineae*.

Most *Acacia* species have short flowering periods once a year. Therefore, host selection for cecidomyiids that oviposit on specific reproductive organs, particularly flowers, would be expected to be governed by the availability of oviposition sites and host compatibility. This may be the situation where the South African tree *A. karroo* Hayne grows in association with Australian *Acacia* at a few sites in gardens in Victorian. *A. karroo* flowers in summer while local native species (*A. melanoxydon*, *A. paradoxa*, *A. dealbata*, *A. mearnsii*) produce flowers in late winter to late spring. A Fluted Galler (*Dasineura* sp.), which forms conspicuously lobed, woody galls, occurs on *A. melanoxydon*, but fails to gall neighbouring *A. karroo*. Whether this is the result of "phenological protection" due to the lack of flowering and hence oviposition sites at the time of adult emergence or physiological incompatibility is unknown. Similarly, in Western Australia *A. sophorae* (Labill.) R. Br., an introduced species from eastern Australia, and the local native *A. cyclops* occasionally grow intermingled. While *A. cyclops* is utilised by a Fluted Galler (*Dasineura* sp.) that forms small highly lobed galls, *A. sophorae* is not, despite there being an overlap in flowering periods. As most Australian cecidomyiids show narrow host ranges in their country of origin they are very unlikely to develop on African acacias that are phylogenetically separated from the native Australian *Acacia* flora (Guinet 1969, Vassal 1972). However, evaluation of host specificity using non-choice oviposition tests is required to determine the susceptibility of African acacias to Australian seed-preventing Cecidomyiidae.

Parasitoids

Hymenopterans (Chalcidoidea) are the main parasitoids of Cecidomyiidae and are either generalist or specialist species (Hawkins and Goeden 1984). Hymenopteran parasitoids can be extremely abundant in populations of seed-preventing cecidomyiids, to the point that collection of unparasitised larvae, or adults from galls can be difficult. Higher parasitoid levels seem to occur during the autumn rather than the early spring period. While a detailed analysis of the parasitoid fauna has not yet been undertaken on

Table 1.
Preliminary census of seed-preventing Cecidomyiidae
on *Acacia* in southern Australia

Cecidomyiid	Common Name	Host
<i>Dasineura</i> sp.	Hairy Podlet Galler	<i>A. baileyana</i> , <i>A. blayana</i> , <i>A. dealbata</i> , <i>A. decurrens</i> , <i>A. filicifolia</i> , <i>A. irrorata</i> , <i>A. paradoxa</i> , <i>A. podalyriifolia</i>
<i>Dasineura</i> sp.	Hairy Podlet Galler	<i>A. o'shanesii</i>
<i>Dasineura</i> sp.	Fluted Galler	<i>A. maidenii</i> , <i>A. melanoxyton</i> , <i>A. pendula</i> , <i>A. sclerophylla</i> , <i>A. stricta</i>
<i>Dasineura</i> sp.	Podlet Galler	<i>A. mearnsii</i> , <i>A. melanoxyton</i> , <i>A. pycnantha</i> , <i>A. retinoides</i> , <i>A. schinoides</i>
<i>Dasineura</i> sp.	Smooth Podlet Galler	<i>A. cochlearis</i> , <i>A. divergens</i> , <i>A. littorea</i> , <i>A. truncata</i> , <i>A. urophylla</i> , <i>A. verticillata</i>
<i>Dasineura</i> sp.	Convuluted Podlet Galler	<i>A. acinacea</i>
<i>Dasineura</i> sp.	Fruit Galler	<i>A. irrorata</i> , <i>A. mearnsii</i>
<i>Dasineura acaciaelongifoliae</i>	Fluted Galler	<i>A. implexa</i> , <i>A. longifolia</i> , <i>A. sophorae</i>
<i>Dasineura dielsii</i>	Fluted Galler	<i>A. cyclops</i>
<i>Dasineura</i> sp.	Keeled Podlet Galler	<i>A. polybotrya</i>
<i>Dasineura</i> sp.	Mossy Podlet Galler	<i>A. irrorata</i>
<i>Dasineura</i> sp.	Tiny Podlet Galler	<i>A. deanei</i> , <i>A. irrorata</i> , <i>A. mearnsii</i>
<i>Asphondylia</i> sp.	Seed/bud Cecid	<i>A. baileyana</i> , <i>A. cardiophylla</i> , <i>A. dealbata</i> , <i>A. decurrens</i> , <i>A. mearnsii</i> , <i>A. parvipinnula</i> , <i>A. schinoides</i> , <i>A. trachyphloia</i>
<i>Asphondylia</i> sp.	Seed/bud Cecid	<i>A. buxifolia</i> , <i>A. floribunda</i> , <i>A. gladiiformis</i> , <i>A. melanoxyton</i> , <i>A. obtusata</i> , <i>A. oxycedrus</i> , <i>A. paradoxa</i> , <i>A. penninervis</i> , <i>A. piligera</i> , <i>A. pravissima</i> <i>A. retinoides</i> , <i>A. salicina</i> , <i>A. sophorae</i> , <i>A. uncinata</i> , <i>A. verticillata</i>
<i>Asphondylia</i> sp.	Seed/bud Cecid	<i>A. divergens</i> , <i>A. truncata</i> , <i>A. pulchella</i> , <i>A. cochlearis</i> , <i>A. cyclops</i> , <i>A. littorea</i>
<i>Asphondylia</i> sp.	Glabrous Bud Galler	<i>A. deanei</i> , <i>A. irrorata</i> , <i>A. mearnsii</i>
<i>Asphondylia</i> sp.	Pointy Bud Galler	<i>A. parvipinnula</i> , <i>A. pulchella</i>

Cecidomyiidae from Australian *Acacia* spp., at least several families are involved and both endo- and ectoparasitic Hymenoptera are present.

Distribution of Seed-preventing Cecidomyiidae

All seed-preventing Cecidomyiidae of key targets for biological control in South Africa (*A. mearnsii*, *A. dealbata*, *A. decurrens*, *A. longifolia*, *A. cyclops*, *A. melanoxylon*, *A. pycnantha*) have been found over most of the natural range of their hosts. These *Acacia* species have broad distributions in Australia covering a diverse range of habitats, latitudes and climatic zones. Therefore, the Cecidomyiidae associated with them also tolerate considerable climatic variation. This will be important for the implementation of biological control because invasive Australian *Acacia* occur over most biogeographical regions in South Africa, especially *A. mearnsii*, which is widespread and problematic in all provinces (Henderson 1995, Versfeld *et al.* 1998).

The western slopes of the Great Dividing Range and the tablelands of northern New South Wales and southern Queensland have the closest climate match (match index > 7.0 using CLIMEX[®] for windows, version 1.1, Sutherst *et al.* 1999) with high altitude areas of Gauteng, Mpumalanga, Eastern Cape and KwaZulu-Natal, South Africa that have severe invasions of *A. mearnsii*, *A. dealbata* and *A. decurrens*. Both *A. mearnsii* and *A. decurrens* are not native to this region of Australia. Consequently, seed-preventing Cecidomyiidae from these hosts are not available from this region. However, closely related species such as *A. irrorata*, *A. filicifolia* and *A. deanei* support seed-preventing Cecidomyiidae and some of these (Glabrous Bud Galler, Hairy Podlet Galler, Common Bud Galler) appear to be the same taxa that attack *A. mearnsii*, *A. decurrens* and *A. dealbata* in more southern areas of Australia. Comparison of DNA profiles of these insects may be required to clarify their taxonomic relationships.

In Western Australia, several eastern Australian *Acacia* species have naturalised as a result of deliberate introductions for ornamental or utility purposes (Hussey *et al.* 1997), including *A. dealbata* and *A. decurrens*. The Tiny Podlet Galler (*Dasineura* sp.), known from *A. mearnsii*, *A. deanei* and *A. irrorata* in eastern Australia, is well established on *A. mearnsii* in south-west Western Australia and can be extremely abundant. This cecidomyiid has not been observed on indigenous *Acacia* in Western Australia, but it causes massive reductions in seed production of *A. mearnsii* and has prevented this wattle from becoming naturalised and invasive in the region. The Hairy Podlet Galler (*Dasineura* sp.) is also present at several sites in south-west Western Australia on *A. dealbata* and *A. decurrens*. Gall densities and health appear to be higher, and levels of parasitism lower than those occurring on the same hosts in eastern Australia.

Impact on Growth

Gall-forming agents can seriously reduce the growth potential of their host by creating resource “sinks” (Dennill 1988). The success in South Africa of a gall-forming Pteromalidae on *A. longifolia* (Dennill *et al.* 1999) and the systemic rust fungus *Uromycladium tepperianum* on *A. saligna* (Morris 1996) can be attributed to this phenomenon. While the diversion of plant growth resources to gall formation may be desirable for target species that have little or no commercial value, a conflict of interest would occur with the tannin, timber and paper industries in South Africa, if galls formed growth

sinks on *A. mearnsii*, *A. dealbata*, *A. decurrens* and *A. melanoxylon*. The Tiny Podlet Galler (*Dasineura* sp.) and the Common and Glabrous Bud Gallers (*Asphondylia* spp.) on *Acacia mearnsii* produce galls approximately 2-4mm diameter in clusters of up to around 50 on a single flower. Although gall numbers can be high, gall biomass is low and certainly less than if the same flower produced even a single pod. The impact of seed-preventing cecidomyiids on the vegetative growth of *Acacia* hosts will be evaluated quantitatively to determine whether commercial industries are at risk from the possible release of these insects. This will be done by insecticide exclusion experiments (Adair and Holtkamp 1999) both in South Africa under quarantine conditions, and in Australia.

Most Australian *Acacia* spp. produce copious numbers of flowers, but only a small proportion of these develop to form fruit. Cecidomyiidae that feed on the reproductive organs of *Acacia* do not attack seeds directly, except for some *Asphondylia* spp. and many flowers are likely to be galled that wouldn't have produced fruits in the absence of these insects. The lack of direct target-organ action, namely seed destruction, could hamper their effectiveness as biological control agents unless extremely high densities are achieved and most flowers are infested. In Australia, even with parasitoids present, several cecidomyiids do just this and are likely to make very good biological control agents in South Africa. The Tiny Podlet Galler (*Dasineura* sp.), the Glabrous Bud Galler (*Asphondylia* sp.) and Podlet Galler (*Dasineura* sp.) on *A. mearnsii*; the Fluted Galler (*Dasineura* sp.) on *A. cyclops*, and the Hairy Podlet Galler (*Dasineura* sp.) on *A. dealbata*, *A. decurrens* and *A. baileyana* fall into this category.

Integrated Control of *Acacia*

Australian *Melanterius* seed-feeding weevils are established on *A. mearnsii*, *A. longifolia*, *A. cyclops* and *A. melanoxylon* in South Africa and in some areas are causing substantial reductions in seed production (Dennill *et al.* 1999). *Melanterius* larvae feed on developing seeds in pods, and adults feed on green pods and young pinnules. Some *Melanterius* in South Africa show a density independent relationship with the availability of host pods (Dennill *et al.* 1999), suggesting that they may be compatible with additional agents that reduce pod formation, such as seed-preventing Cecidomyiidae. Destruction of buds and flowers by Cecidomyiidae followed by damage caused by seed-feeding *Melanterius* is likely to result in higher seed reduction levels than the actions of one of these groups alone.

In Australia, seed-preventing cecidomyiids have strong host finding abilities as it is not uncommon to find isolated trees or stands of acacias with cecidomyiids present. The insects' readiness to take flight and their light weight facilitate effective dispersal by wind. In weed clearing programs in South Africa, manual clearing of Australian *Acacia* is being undertaken on a large scale under the "Work for Water" scheme (Boucher and Marais 1995). Reduction of *Acacia* densities by clearing could weaken the impact of *Melanterius*, which have poor dispersal abilities, if the distance between trees exceeds the maximum dispersal distance of the insect. While this would also be true for Cecidomyiidae, the dispersal range of seed-preventing cecidomyiids is expected to be considerably higher than that for *Melanterius*. The planned preservation of infested trees in areas to be cleared should allow biological control to be compatible with and complementary to manual clearance programs. Empirical determination of minimum host densi-

ties and maximum inter-tree distances to maintain populations of biological control agents is required before tree clearing guidelines for manual control programs can be developed.

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