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A Most Promising Bud-galling Wasp, *Trichilogaster acaciaelongifoliae* (Pteromalidae), Established Against *Acacia longifolia* in South Africa

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Abstract

Trichilogaster acaciaelongifoliae is one of many specialized natural enemies that suppress seed production by *Acacia longifolia* in Australia, and it was recently (1981) released against this weed in South Africa. Adults live for a few days, larvae gall buds, and the species is univoltine. The incidence of males in colonies from different sources in Australia may vary from rare to abundant, depending on the source. Damage by *T. acacialongifoliae* in Australia is infrequent and unimpressive because of high levels of parasitism. Surveys in Australia, and specificity tests in South Africa showed that the wasp is restricted to *A. longifolia* and *A. floribunda*. Once suitable collecting and shipping techniques were developed, establishment was easy and rapid. Observations at a few urban sites in Australia where this insect was found largely isolated from its parasitoids, and at release sites in South Africa indicated that it may be much more destructive to the host than would be anticipated from an agent acting primarily on inflorescence buds.

Evaluations at two release sites have shown that both seed production and vegetative growth of the weed are markedly reduced by galling.

Une Guêpe Qui Provoque la Gale des Bourgeons, *Trichilogaster acaciaelongifoliae* (Pteromalidae), Agent Efficace de Lutte Biologique Contre l'Arbuste Ligneux *Acacia longifolia* en Afrique du Sud

Trichilogaster acaciaelongifoliae est l'un des nombreux ennemis naturels spécialisés qui empêchent la formation des graines de *Acacia longifolia* en Australie, et cet insecte a récemment (1981) été introduit en Afrique du Sud pour lutter contre cette plante nuisible. Les adultes vivent quelques jours, les larves provoquent la gale des bourgeons et l'espèce est univoltine. Les mâles sont habituellement rares et peut-être inutiles. Les dommages causés par *T. acaciaelongifoliae* en Australie sont peu fréquents et négligeables en raison de hauts niveaux de parasitisme. D'après des études menées en Australie et des assais de spécificité effectués en Afrique du Sud, cette guêpe se limite aux plantes hôtes *A. longifolia* et *A. floribunda*. Dès que des techniques appropriées pour recueillir et transporter les insectes ont été mises au point, le'établissement a été facile et rapide. Les évaluations ont mis en évidence que, outre l'élimination quasi totale des graines, les insectes ont réduit de façon considérable la croissance et la vigueur des plantes, même lorsque le nombre de gales était limité. Ces résultats infirment les prévisions théoriques selon lesquelles les insectes galligènes constituent des agents biologiques inefficaces.

Introduction

Acacia longifolia (Andr.) Willd. (Leguminosae), a woody, perennial shrub to small tree from southeastern Australia has become naturalized in the southwestern and southeastern Cape where it is a serious and troublesome weed along watercourses and in valleys and on mountain slopes with deeper soils. It invades and replaces natural vegetation, forms dense thickets (Boucher and Stirton 1978), and affects normal water flow along streams. Control is expensive and difficult, perhaps largely because of the copious production of long-lived seeds accumulating in the soil, stimulated to germinate and to form dense stands after fires (Fig. 1) and constantly germinating next to watercourses after floods.

In its natural distribution in eastern Australia the plant is attacked by a variety of insects. Van den Berg (1982*a*, *b*, *c*) reported on stem- and root-borers, sap-suckers, leaf-miners, defoliators, and species developing in pods and seeds.

A subsequent study (unpubl.) revealed further natural enemies that may be useful in defoliating the plant; e.g. an apparently undescribed species of the genus *Rayieria* Odhiambo (Hemiptera: Miridae), and others that may suppress flowering and seeding, such as an eriophyid mite in young inflorescences, an unidentified cosmopterigid peduncle-boring larva, cecidomyiids developing in unopened florets (provisionally identified as *Asphondylia* sp. 1), in newly set podlets (?*Dasineura* sp.) (cf. '*Cecidomyia*' *acaciaelongifoliae* described by Skuse 1890) and in young pods (*Asphondylia* sp. 2) and an unidentified *Bruchophagus* sp. (Hymenoptera: Eurytomidae) developing in immature seeds.

The brachyscelidiphagine gall-wasp *Trichilogaster acaciaelongifoliae* (Froggatt) (Hymenoptera: Pteromalidae) described from *A. longifolia* in New South Wales (Froggatt 1892) and from Queensland (Girault 1913), was one of the several species recommended for further studies (Van den Berg 1977) and after specificity studies (Van den Berg 1980; Neser, unpubl. data) were completed, the first small releases were made in December 1981 (Dennill 1985).

The very short-lived females (most die within 2–3 days) emerge from the galls on a particular plant over a brief period (1–2 wks) in summer and immediately lay eggs (Fig. 2) in young axillary buds destined to develop into inflorescences during the following 8–10 months. At the time shortly before, during, and soon after flowering, the affected buds enlarge rapidly, to form round, single-celled, to larger, irregular, multicelled galls (Fig. 3), the contained larvae (Fig. 4) mature and pupate and the new generation of adults appear in November to January when the next season's inflorescence buds are present on the plant. The biology of the insect on its only three known hosts, now regarded as two varieties of *A. longifolia* (the typical variety, and var. *sophorae* [Labill.] F. Muell.) and *A. floribunda* (Vent.) Willd. (see Costermans 1981: 304–5) was carefully studied and reported by Noble (1940). Somewhat puzzling features he mentioned were the virtual to complete absence of males in populations on *A. longifolia* and the presence of about 50% of males in batches reared from *A. floribunda* (Noble 1940: 23). He also commented on the extreme patchiness of populations of the wasp: often only single plants in a group would be heavily galled with no galls on adjacent plants. Van den Berg (pers. comm., 1976) also noticed a very sparse and patchy occurrence of galls on *A. longifolia* in southeastern Australia. Noble (1940: 22) ascribed the phenomenon to poor powers of flight and the fact that the newly emerged females tended to lay eggs on the immediate vicinity of the galls from which they had emerged. He, however, also mentioned (p. 32) that the degree of parasitism and composition of associated and parasitoid species varied markedly between different plants in the same area.

Results and Discussion

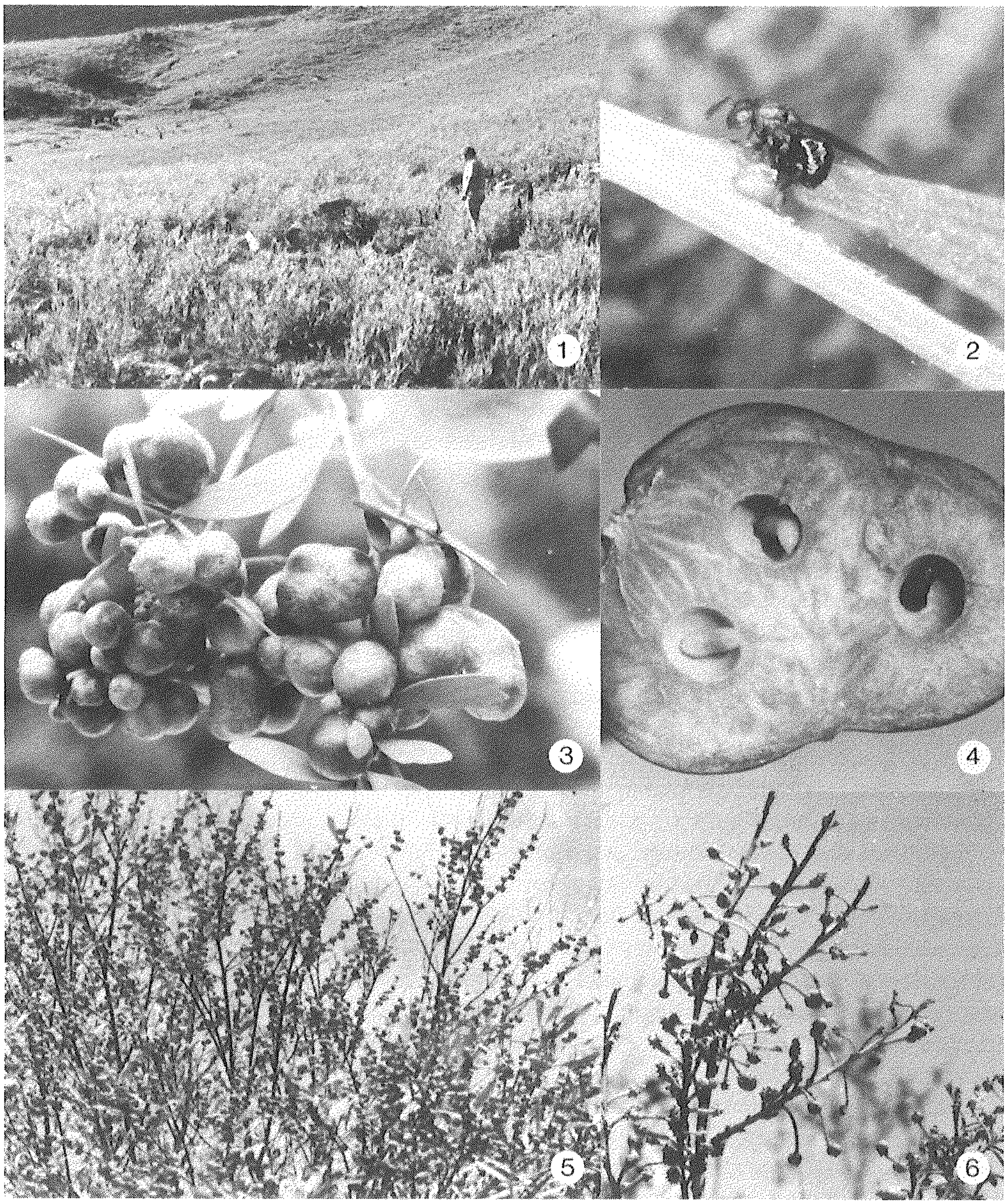
During collecting trips in New South Wales, Victoria and Tasmania during the summers of 1981 and 1982 to obtain large numbers of pupae of the wasp for shipment to South Africa, it was found that the proportion of larvae and pupae parasitized by mainly the two species of *Megastigmus* (Hymenoptera: Torymidae) and two *Eurytoma* spp. (Hymenoptera: Eurytomidae), or outcompeted by larvae of mainly *Acrocercops eumetalla* (Meyrick) (Lepidoptera: Gracillariidae) (most likely the species referred to by Noble 1940), was generally very high (70–90% and occasionally and locally approaching 100%). This was seen as part of the reason why heavily galled plants were so rare and why populations of the wasp appeared to be so localized: populations were probably founded by occasional females that dispersed into areas where the new colonies flourished until reached by the parasitoids, which then reduced the gall wasp populations to the generally observed very low levels. Parasitoids and secondary insects developing in the galls are therefore seen as the reasons why *T. acaciaelongifoliae* overall does not appear to be an important natural enemy of *A. longifolia* in Australia.

A shipment of about 1000 galls from *A. longifolia* collected near Melbourne in November 1980 and shipped to South Africa yielded only four weakened *T. acaciaelongifoliae* females and numerous parasitoids. Despite efforts to keep the galls as long as possible to allow maximal emergence, most of them decomposed. This illustrates some serious early problems experienced in shipping large numbers of this insect to South Africa: (1) once collected, the very succulent galls deteriorate and rot rapidly in humid conditions, and dehydrate quickly in drier conditions — both situations rendering the galls unsuitable for emergence by the short-lived, delicate adult females; (2) the galls should be collected and shipped only during the last 7–10 days before the adults emerge, to prevent massive mortality in transit and/or emergence of weakened wasps; and (3) because reliance had to be placed on field-collected rather than laboratory-reared specimens, sources relatively free from parasitoids had to be found.

For the large shipments planned for 1981–82, various possible collecting sites were visited and samples of galls from each were dissected from time to time to note degree of parasitism and developmental stage of larvae. This allowed early location of suitable collecting sites (or of individual suitable plants) and an estimated best collecting date for each site, group of plants in a general area, or even for individual selected plants. The periods of peak emergence of wasps in different parts of coastal and near-coastal southeastern Australia occurred from about mid-October to late January. For instance, near the coast between Newcastle and Gosford (50–120 km NNE of Sydney), peak emergence in 1981 and 1982 occurred during the last 2 wks of October; in and around Sydney (± 34°S, 151°E) it was about a week later (late October to early November); around Jervis Bay (140 km SSW of Sydney), it was around mid-November; and between Mittagong and Fitzroy Falls (about 100 km SW of Sydney and 40 km inland from the coast) it was a week later. Further southwest, in and around Melbourne (± 38°S, 145°E) peak emergence was expected to occur about mid-December 1982, and at Launceston (± 41°30′S, 147°E) in Tasmania emergence had not started by early January 1981 and was expected to occur in the second half of January. The growing cycle and maturation of inflorescences probably determine onset of rapid growth of larvae in galls, and emergence in an area (or at any particular site or during a particular year), may be closely tied to flowering time and prevailing growing conditions for the host plant.

For shipments it was endeavoured to collect the galls when about 10–15% of adults had emerged, which ensured that the majority of the remainder would emerge in the following week or two, before the galls deteriorated.

Parasitism was generally found to be much lower in galls on plants in towns and cities, compared to plants in relatively undisturbed situations. Thus *A. longifolia* planted in gardens and next to streets in urban areas (e.g. Sydney; the coastal town Moruya,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New South Wales; an industrial area in Geelong, Victoria; a bitumin-sealed parking area in Launceston, Tasmania; metropolitan Melbourne, where the plants were sooty from pollutants in the air; or some planted next to some major freeways), were found to be the best sources of largely unparasitized pupae for shipment to South Africa.

The first 265 females were released on 31 sleeved *A. longifolia* branches at two sites near Stellenbosch and the gauze sleeves were removed a week later (Dennill, 1985). Even with the high stocking rates (in hindsight) of 5–10 females/branch, establishment at these sites was readily accomplished, as shown by the effect of galling that occurred in the 2 yrs after the wasps were allowed to spread (Dennill 1985).

Larger releases (made by simply releasing females, newly emerged in quarantine from surface-sterilized galls shipped from Australia) were made possible by exploiting the collecting strategies outlined above. In November–December 1982, 14,800 females were released at several sites in the southwestern Cape, and in December 1983, galls were so abundant at the release sites that redistribution to 64 additional sites was possible. Establishment has also been achieved from an initial small release in December 1982 of a few females at Grahamstown in the eastern Cape, where further releases were made in 1983.

Where *A. longifolia* was heavily galled in urban sites in Australia (where parasitoids did not have the usual suppressing action on the gall wasp populations), it was possible to get an idea of the possible effect that this insect might have in South Africa. It was noticed that pods were absent on galled branches, which also displayed paucity of new side shoots (the following year's fruiting branches), and even die-back of the terminal growth. At one site (urban Geelong) galling was so heavy that many of the plants, further stressed by drought in November 1982, dropped most of their phyllodes (Fig. 5) and on particularly badly affected branches the galls were only a fraction of their normal size (Fig. 6) and contained only small insects, instead of the fully developed larvae and pupae which would be expected there in November. Die-back of terminal sections of these branches was pronounced.

In his evaluation of the wasp at the first two release sites in the Cape Province, Dennill (1985) showed that within two generations the wasps had reduced seed production on galled branches by 99% and on heavily infested trees by 95% at the two sites, and that seed production was reduced by an average of 89% when 50% or more of the branches on plants of different sizes had galls. He further clearly showed that galls caused abscission of phyllodes (an actual decrease in the number over the season, rather than a net increase) and a 66% reduction in the number of new lateral branches/galled branch, and eventually a much higher (100%) growth tip mortality than on ungalled branches. On heavily infested trees, the same suppressing effect on growth tips and seed production was observed, whether there was only one or up to 72 galls/branch.

Figs. 1–6. *Acacia longifolia* (Andr.) Willd. and the gall-forming wasp, *Trichilogaster acaciaelongifoliae* (Froggatt). *1.* Dense regeneration of *A. longifolia* after a fire on the lower slopes of the Banhoek Mountains near Stellenbosch in the southwestern Cape. *2.* Female of *T. acaciaelongifoliae* ovipositing in a bud destined to develop into inflorescences 8–10 months later. *3.* Single and composite galls formed in axils where flower spikes would have developed. Fruiting on galled branches is usually entirely prevented. *4.* Section through a compound gall showing larvae and a pupa of *T. acaciaelongifoliae*. Up to 19 adults have been reared from a single, large, compound gall. *5. A. longifolia* heavily galled by *T. acaciaelongifoliae* at Geelong, Victoria (November 1982). Drought stress enhanced defoliation. *6.* Retarded galls on a heavily galled, largely defoliated plant (Geelong, November 1982). Similar levels of galling have been observed on odd branches at one release site at Stellenbosch (January 1984).

Observations on the very local and patchy distribution of the wasp in Australia may suggest that the species may be limited as an effective biological control agent by its supposed poor powers of dispersal. Noble (1940: 22) said: '... the adults are rather sluggish and degenerate in appearance. They crawl rather than fly and not uncommonly fall over and find difficulty in regaining their normal upright position.' Observations of newly emerged females on plants in the laboratory and in a glasshouse in 1981 and 1982 indicated that they are likely to disperse quite well, and may be capable of strong, and even directed flight in search of hosts. Newly emerged females, very distended with eggs, did not fly successfully, but after a few hours of egg-laying, and especially in the warmer part of the day, they readily took off on characteristic spiralling flights of many metres high, often returning to the *A. longifolia* plants in the vicinity. It is therefore quite likely that older females may fly, or be carried far during windy days and that with the high population densities anticipated, dispersal may be very effective.

In the population of *T. acaciaelongifoliae* from *A. longifolia* in Sydney studied by Noble (1940) males were rare, and absent in samples of galls from some plants. Flanders (1945), considering that the incidence of males was about 50% when apparently the same species from the same population developed in the vegetative and inflorescence buds on *A. floribunda*, suspected some form of 'environmental' control on the sex ratios.

During the present work, males were also found to be abundant in galls on *A. floribunda* collected in Victoria and Tasmania (in both instances the *A. floribunda* was planted together with, also galled, *A. longifolia*). However, the galls from *A. longifolia* from Launceston yielded unexpectedly large numbers of males. Another, larger sample (5 kg of galls) collected there in January 1984 yielded 887 females and 865 males. A colony established on *A. longifolia* on the slope of Stellenbosch Mountain from Launceston material collected January 1982, seems to perpetuate the phenomenon, as a sample of second generation galls collected there in December 1983 yielded 116 males and 64 females (but this last sample was taken when most wasps had emerged, and there is a possibility that males may tend to emerge later).

The males show interest in, and were seen to perform a relatively simple dance towards females, attempting copulation, and some observed attempts may have been successful. Noble (1940) showed that female offspring were produced by virgin females, but the effect of fertilization on the sex ratios in offspring has apparently not been studied.

Conclusions

On theoretical grounds, an insect developing in flower buds of a woody, long-lived legume growing at moist sites without much competition, and producing a staggering superabundance of inflorescences (usually two or more in nearly each phyllode axil on 1-yr-old branches on vigorously shooting plants) may not be readily seen as a very significant potential biological control agent, unless if used as a part of a complex complementing each other. Its potential value may even look less significant in the light of the longevity and the known formidable seed store in the soil in the infested areas (P.J. Pieterse, P.P.R.I. Stellenbosch, pers. comm.). However, the dramatic effect that this insect has been observed to have at such an early stage after release on seed production and vegetative growth (which would be expected to be enhanced by other adverse factors such as drought stress, as observed on the plants at Geelong in November 1982), and the fact that it may attack and multiply on young plants as soon as they start producing flower buds, indicate that this species by itself may in time be sufficient to cause a reduction in the density of infestations of the weed. The gradual expected suppression of the vigour of the plants and the accompanying thinning out of the otherwise dense canopies, may give other species a chance of establishing, and growing amongst the affected plants, and even to compete more successfully with them, thus adding another stress factor which may help to tip the balance in favour of the original vegetation in invaded areas.

The anticipated (and already observed) very heavy galling of plants in South Africa in the rather abnormal situation in the absence of its usual Australian parasitoids and competing species, may from time to time cause dramatic 'crashes' in the population of the wasp especially when the stressed host plant will not have sufficient resilience and reserves to allow full development of the galls and maturation of the larvae. The dynamics of the wasp populations and their effects on the plants and their populations in the next few years are likely to be most interesting, as will be comparisons of colonies in which the incidence of males differs.

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