THE HAKEA FRUIT WEEVIL, *ERYTENNA CONSPUTA* PASCOE (COLEOPTERA : CURCULIONIDAE), AND THE BIOLOGICAL CONTROL OF *HAKEA SERICEA* SCHRADER IN SOUTH AFRICA

BY

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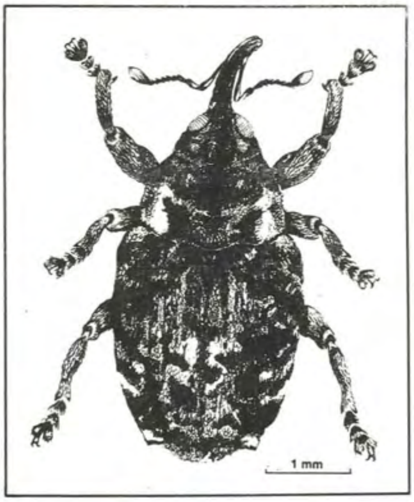
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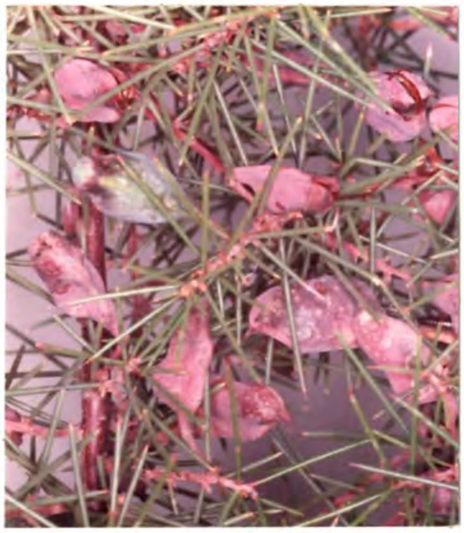

FRONTISPIECE

TOP: Mountains in the south-western Cape with typical, dense infestations of Hakea sericea on the slopes in the background. In the foreground is the typical, low-growing, indigenous mountain-fynbos vegetation with grey bushes of Protea neriifolia R.Br. prominent, and a small clump of H. sericea in the lower left-hand corner. The picture is framed by a H. sericea branch on the right.

MIDDLE LEFT: A larva of the hakea fruit weevil, Erytenna consputa tunnelling in a developing fruit.

MIDDLE RIGHT: The adult hakea fruit weevil, E. consputa.

BOTTOM LEFT & RIGHT: Developing H. sericea fruits before and after attack by larvae of E. consputa.

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1. RÉSUMÉ

The south and south-western Cape with its unique macchia or "fynbos" vegetation is regarded as one of the eight floral kingdoms of the world, primarily because seven plant families are endemic to the region. Physiognomically, fynbos is characterised by three floristic elements, restioid, ericoid and proteoid, and also by its extreme species richness; it is of immense scientific and aesthetic value.

A number of aggressive, alien invasive weeds, including Hakea sericea from Australia, now pose a serious threat to the preservation of the fynbos. H. sericea is a proteaceous shrub, well-adapted to the region, which, largely because of its copious seed production, has invaded about 480 000 hectares of mountain fynbos, forming ultimately dense, impenetrable thickets that totally suppress the fynbos species.

Although a certain amount of success has been achieved in controlling H. sericea mechanically, the overall control strategy has many short-comings, some of which are soluble by means of biological control. In the current programme three insects have been introduced from Australia to try and reduce the seed production of the plant. One of these, the hakea fruit weevil, Erytenna consputa, that attacks the young fruits, is the subject of this thesis. The main purpose of the study was to verify the establishment of the weevils in South Africa, and to evaluate their impact on the plant.

Basic biological and ecological information of the insect under South African conditions, was collected. Studies on the fecundity, adult feeding behaviour, and the survival of different stages in the field are included. A partial life-table was drawn up from which the rate of population increase was determined, and from which population growth could be predicted.

Colonisation of *E. consputa* was followed in the field, and the performance of *E. consputa* from different climatic regions in Australia were compared. The impact of *E. consputa* on a population of *H. sericea* was determined, and from the pattern of attack certain inferences about the behaviour of *E. consputa* relevant to its effectiveness as a biological control agent were made.

Despite variable colonisation by the different "strains" of *E. consputa*, some strains have established successfully. From these studies *E. consputa* can be seen to be a superbly adapted biological control agent which should achieve, and consistently maintain, levels of fruit attack approaching 100 per cent. The effect of high seed mortality on plant density in the long-term, must still be demonstrated, but all indications are that *E. consputa* will make a substantial contribution to the control of *H. sericea*.

2. INTRODUCTION

THE PLANT

Hakea sericea Schrader, known commonly as needlebush or hakea, is a shrub that is endemic to south-eastern Australia. It was probably introduced into South Africa in the 1830's (Neser & Fugler, 1978). Since then it has become an aggressive weed in the natural vegetation (frontispiece) of the south-western, southern and eastern parts of the Cape Province. It has been declared a noxious weed in terms of the Weed Act No. 42 of 1937.

The plant grows to a height of approximately four meters, and is characterised by its needle-like leaves, and by the round, rough, woody follicles or fruits, each of which contain two winged seeds. During flowering-time the plant is covered by a mass of small, cream-coloured inflorescences which are borne in the leaf axils. The pattern of events in the life cycle of *H. sericea* is summarized in Figure 1.

One of the most important features of the plant's autecology is its adaptation to fire. The woody, heat-resistant follicles are accumulated on the plant throughout its entire lifetime; following the death of the plant, usually after a fire, the follicles dehisce and release all the seeds within a few days. A combination of the massive seed production of *H. sericea*, together with the absence of natural seed predators in South Africa, results in estimated seed densities of up to 7 500 seeds per m^2 in the ash bed following fires (Siebert, *pers. comm.*).

The genus *Hakea* belongs to the family Proteaceae. It is a large genus comprising some 140 species, with over half the species confined to the south-west regions of Western Australia (Wrigley, 1979). *Hakea* species however occur in all the major

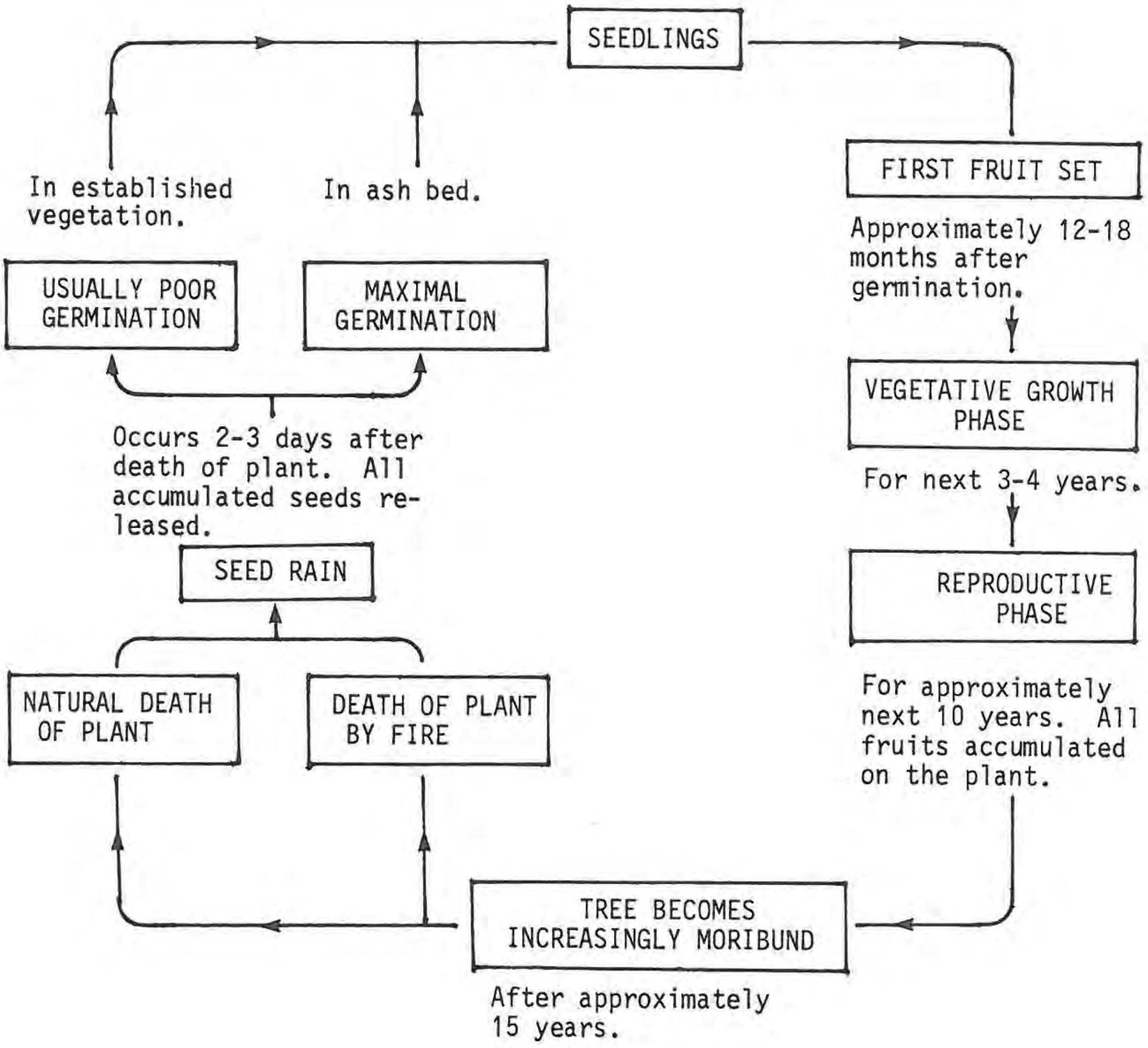


Fig. 1: A summary of the life cycle of Hakea sericea (based on the data of Neser, 1968; and Fugler, 1979).

phyto-geographical zones of Australia (Neser, 1968). The genus is characterized by the extraordinary variety of leaf and follicle shapes. In Australia, apart from the popularity of certain species as garden subjects, none of the Hakea species are of more than academic importance.

THE PROBLEM OF H. SERICEA AS A WEED

In South Africa H. sericea is primarily a problem in the conservation of the so-called mountain fynbos vegetation (Taylor, 1978). Certain characteristics of this vegetation such as its lack of species dominance (Taylor, 1978), and the general lack of trees or shurbs (frontispiece) (Moll, et al., 1980) make it vulnerable to invasion by aggressive weeds such as H. sericea. The soils in which the fynbos occurs are mostly acid, which suits the growth requirements of H. sericea (Neser, 1968). Although the fertility of these soils is generally low, H. sericea is still able to grow well because of its proteoid roots (Fugler, 1979). Proteoid roots are clusters of rootlets of limited growth that occur on lateral roots of plants in the Proteaceae (Purnell, 1960); it is widely accepted that these roots are specialized structures which have evolved in response to extreme nutrient deficient soils (Dell et al., 1980).

The areas in which the mountain fynbos occurs have a predominantly Mediterranean-type climate with the rainfall varying from 300-2 500 mm per annum (Taylor, 1978). The western part receives over 50 per cent of its rain in the winter. Towards the eastern parts, the rainfall is distributed more evenly throughout the year (Fig. 2).

Under the conditions described above, and together with its adaptation to fires, which occur frequently during the dry, summer months, H. sericea, with its massive seed production, is able to invade the fynbos vegetation forming dense, impenetrable thickets which almost totally suppress the indigenous species (frontispiece).

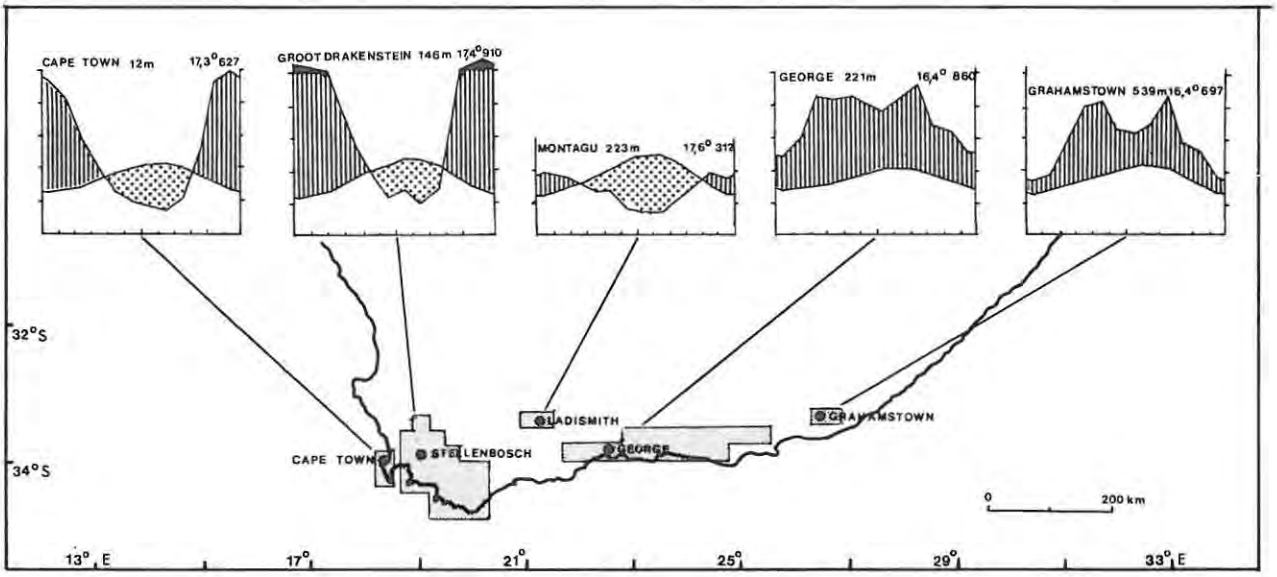


Fig. 2: Climadiagrams (see Fig. 4 for details) representative of the climate in each of the most important areas in South Africa which are affected by Hakea sericea (shaded areas).

The threat posed to fynbos by H. sericea is serious for a number of reasons. The fynbos is of immense scientific value. Because of its rich species diversity, and also because of the distinctiveness of the vegetation, it is regarded by some as a distinct floral kingdom (Good, 1974). The variety and beauty of the plants also make the fynbos aesthetically and commercially valuable. Fynbos is important to the wild flower industry which has an annual turn-over of about R4,5 million (Britz, pers. comm.); this includes many of the indigenous Proteaceae in the genera Protea, Leucospermum and Leucodendron which are prized for their blooms. The fynbos is of little agricultural value. Although it is not yet fully understood, the replacement of fynbos by dense stands of weeds, especially in the water catchment areas, may seriously upset the delicate hydrological balance which normally exists there.

At present, H. sericea has invaded a wide area from Tulbagh in the west to Grahamstown in the east (Fig. 2). The total area of the H. sericea infestations on both state-owned and private land is approximately 480 000 hectares (Fig. 3).

THE CONTROL OF H. SERICEA

Up until the start of the 1960's, hope for controlling H. sericea had centered mainly on mechanical clearing, chemical control and repeated burning. Research had been done up until then, and also subsequently, with various herbicides (Schutte, 1953; Jooste, 1966/67). Herbicides have however never found wide application in H. sericea control due mainly to problems involving application, selectivity and cost. When no real solution was found to the problem, consideration was given to biological control, which was initiated in 1961 by Dr J.W.C. Geyer, who was then Chief, Division of Entomology in the Department of Agricultural Technical Services.

Subsequently, foresters have evolved a very effective procedure for clearing the existing stands of H. sericea. The plants are felled and then burnt after eight to twelve months. In this way nearly all the seed is destroyed. One or two follow-up operations are sometimes required to remove, manually, any seedlings that survive. Because H. sericea cannot reproduce vegetatively, up to 100 per cent control is possible in some areas. This form of control has now been successfully incorporated into the new conservation plan which is being applied by the Department of Environment Affairs and Fisheries in all mountain catchment areas. Compartments of vegetation

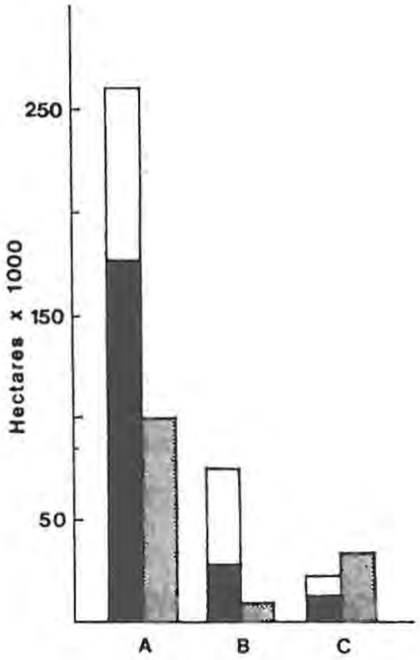


Fig. 3: The approximate areas of Hakea sericea in South Africa on state- and privately-owned mountain catchment areas (black), and on privately-owned non-catchment areas (hatched), that had been cleared mechanically (unshaded) by September, 1982,in each of the three worst-affected regions of the Department of Environment Affairs and Fisheries namely, (A) the south-western Cape, (B) the southern Cape, and (C) the Tsitsikamma regions. (From minutes, Hakea Working Group, 1981 & 1982).

of between 200 and 500 hectares are first cleared of all H. sericea, and other alien vegetation, before being burnt. The vegetation in these compartments is burnt on a twelve-year rotation.

Up until 1982, 143 000 hectares of fynbos have been mechanically cleared of H. sericea (Fig. 3). In 1979 it cost between US $3,90 to US $63,50 per hectare to clear H. sericea depending on the density of the plants. Follow-up operations cost up to US $4,50 per hectare (Fenn, 1980). The total expenditure on *H. sericea* control in the south-western Cape during 1979 was US $120 600.

Although a fungal gumosis disease has been known on *H. sericea* since the late 1960's (Petzer, *pers. comm.*), it has become increasingly important recently. Large stands of *H. sericea* have already been destroyed by the fungus, which has been identified as *Colletotrichum gloeosporioides* (Penz.) Sacc. (Morris, 1982). This disease may still have a significant impact on *H. sericea* control.

Despite the measure of success achieved so far with hakea control, there are shortcomings in the overall strategy which could be met by a successful biological control program. Mechanical control is labour intensive and expensive; it is therefore dependent on regular funding. Any cut-back hampering the present twelve-year clearing programme before 1990 could seriously jeopardize the overall success of the undertaking. In such an event biological control could help maintain the progress that has already been made, and reduce the probability of reinfestation.

An immediate priority is to eliminate the need for the time-consuming and costly follow-up work. The suppression, by means of biological control, of young hakea plants that survive the felling and burning procedure would make this possible. Biological control is also potentially the most efficient method that will remove the threat of reinfestation posed by isolated and inaccessible *H. sericea* plants.

THE BIOLOGICAL CONTROL OF *H. SERICEA* AND THE INTRODUCTION OF THE HAKEA FRUIT WEEVIL, *ERYTENNA CONSPUTA*

Exploration for insects associated with *H. sericea* started with a survey of potential biological control agents that was made around Sydney by Moore (1964), and by Webb in Australia between 1962-1964 (Webb - unpublished report 1965). Both singled out the hakea fruit weevil, known now as E. consputa, as one of the most promising biological control agents. Between 1964-1968 Neser studied the biology, phenology and host-specificity of some of the insects associated with H. sericea in Australia, including E. consputa. Following these studies E. consputa was introduced into South Africa under quarantine in 1970, and released in the field for the first time in 1972 (Neser and Annecke, 1973).

Because of the problems of rearing E. consputa, adults from Australia were released directly into the field after being screened in quarantine (Neser, pers. comm.). A record of all the E. consputa weevils that were introduced is given in Table 1. Initially, introductions were made from different climatic regions in Australia (Fig. 4) to match the different local climatic conditions (Fig. 2) as closely as possible. This was in keeping with the generally accepted view in biological control, prevalent at the time, which holds that the effectiveness of biological control agents may be maximized by using eco-climatically adapted agents (Wilson, 1964; Wapshere, 1973). As can be seen by comparing Figures 2 and 4, the problem was to find organisms that would be suited to the more prolonged and severe arid summers in South Africa.

Neser (pers. comm.) found that viable E. consputa colonies could be started with approximately fifty adults. Because of the threat posed by fires, a large number of these small releases were made initially, in a wide range of climatically different areas (Fig. 5).

The original objective in using E. consputa in South Africa was to reduce the massive seed production of H. sericea so that the indigenous vegetation would be better able to compete. To this end a second agent, the hakea seed moth, Carposina autologa

Origin of Material	Year of Introduction											
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	Total
Nerriga Area, New South Wales					1 648 (28)		2 161 (40)	243 (6)			850 (10)	4 902 (84)
Mittagong, New South Wales					309 (6)	212 (3)		118 (2)		30*		669 (11)
Cann River, Victoria				120 (1)		84 (1)		79 (1)				283 (3)
Wilson's Promontory, Victoria	274 (2)			20 (1)	1 032 (14)					239 (1)		1 565 (18)
Grampians, Victoria					762 (10)			30*				792 (10)
Total	274 (2)	-	-	140 (2)	3 751 (58)	296 (4)	2 161 (40)	470 (9)	-	269 (1)	850 (10)	8 211 (126)

(Number of releases given in brackets)
(* = Liberated at previous release sites)

Table 1: Total number of hakea fruit weevils, Erytenna consputa, from different regions in Australia (see Fig. 4), that were released on Hakea sericea in South Africa. The Nerriga area refers to material collected around Nerriga towards Oallen Ford in the east, Braidwood in the south and Nowra in the west. All the Mittagong material was collected on the outskirts of the town. The "Grampians" material was collected along a circular route south of Hall's Gap in The Grampians mountain ranges. "Cann River" refers to material collected between Eden and Orbost. All the collecting on the Wilson's Promontory was done at various localities within the reserve.

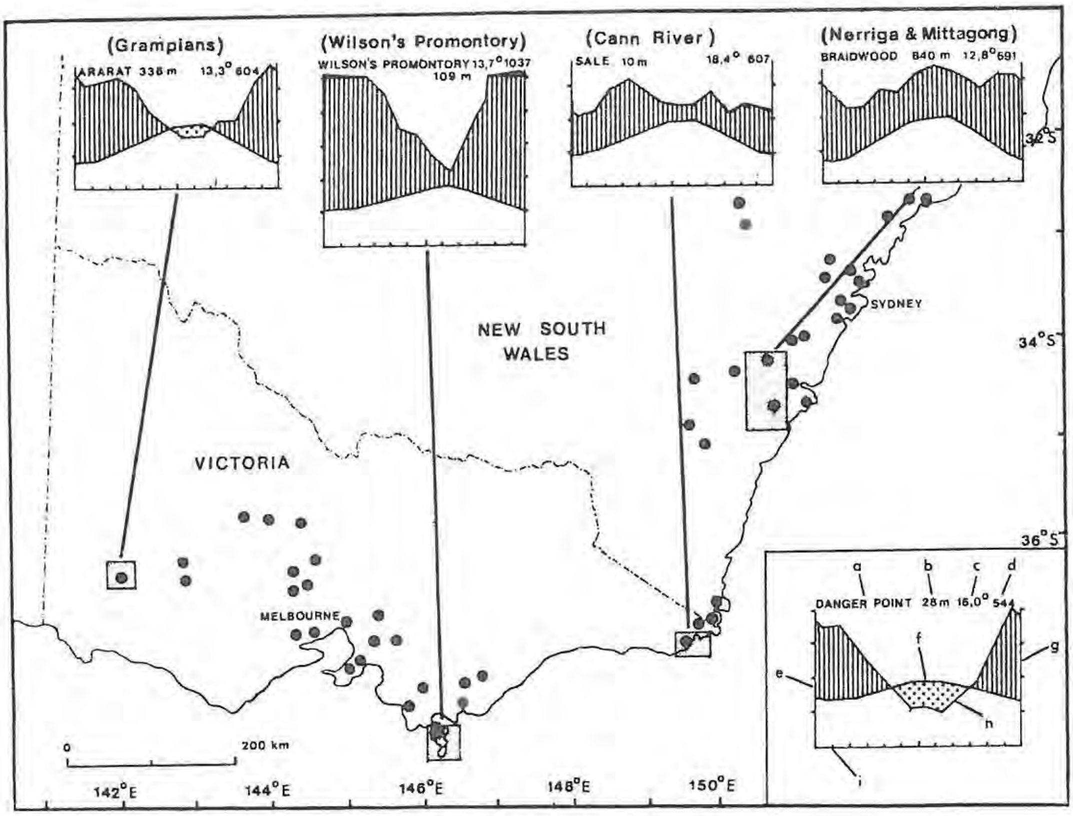


Fig. 4: A map of south-eastern Australia showing (A) the distribution of Hakea sericea in Australia (dots) as recorded by Webb (1964) from 12 herbaria in Australia, and (B) the most important areas (named in brackets - see Table 1) where the hakea fruit weevil, Erytenna consputa, was collected, together with climadiagrams representative of each area. Legend to climadiagrams (Walter, H. & H. Lieth, 1960 - see inset): a = station name; b = altitude; c = mean annual temperature in degrees centigrade; d = mean annual subtotal of precipitation in mm; e = temperature axis in degrees centigrade at ten degree intervals; f = mean monthly temperature; g = rainfall axis in mm at 20 mm intervals; h = mean monthly precipitation (precipitations above 100 mm are printed in black in the case of Wilson's Promontory); humid period i.e. precipitation exceeds temperature (hatched area); arid period i.e. precipitation goes below temperature curve (dotted area); i = monthly intervals starting from July.

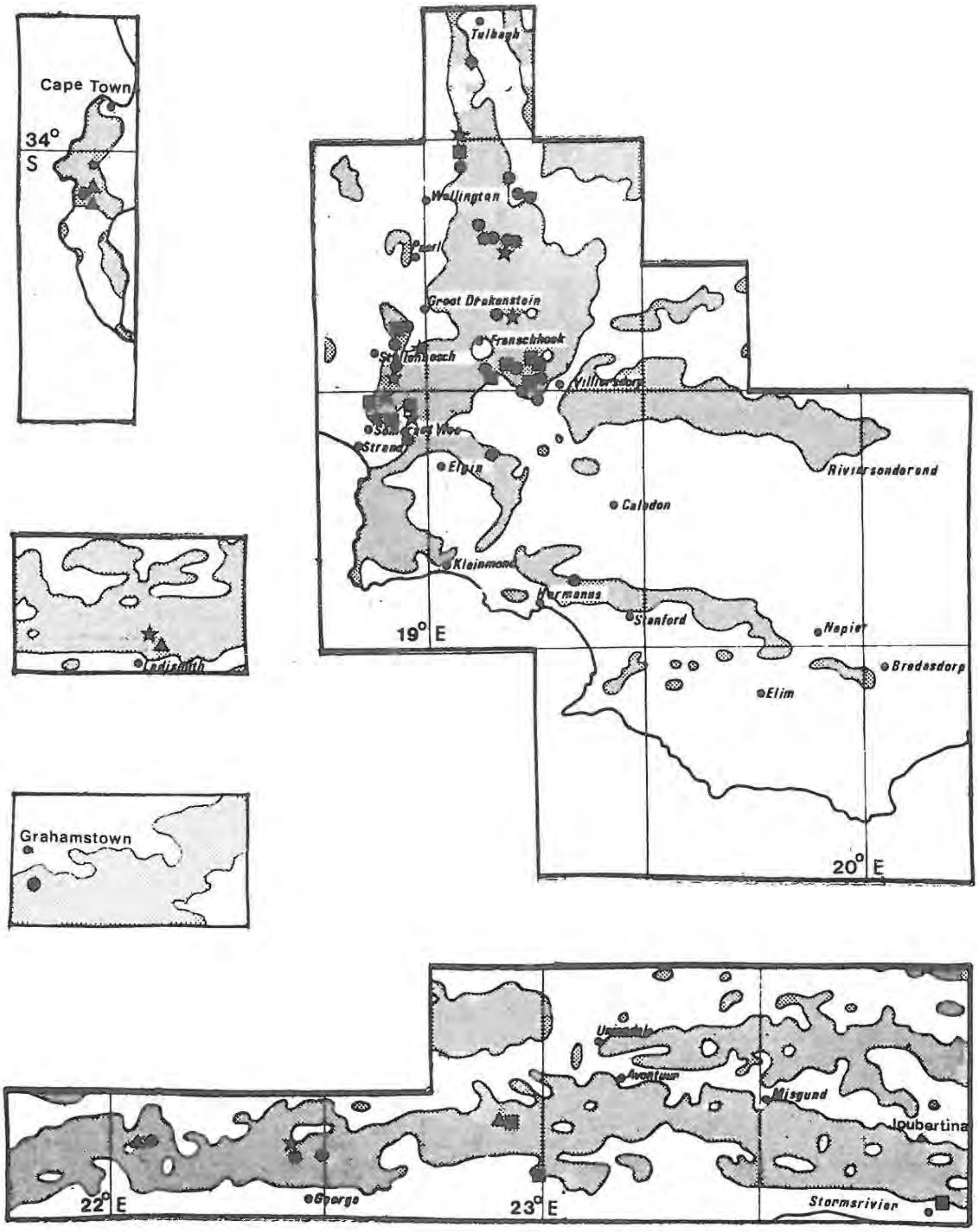


Fig. 5: Enlargements of the shaded areas from Figure 2 showing the distribution of the first important releases (Table 1) made in South Africa of the hakea fruit weevil, *Erytenna consputa*, from four different areas in Australia namely, Nerriga (●) and Mittagong (▲) in New South Wales, and Wilson's Promontory (■) and the Grampians (★) in Victoria, between August and September, 1975. About 50 adults were released at each site. The release of the Nerriga stock made at Kareedouw (32 km east of Joubertina) is not shown. The shaded areas represent non-arable, hilly and mountainous country as classified by Buys (1971).

Meyrick, whose larvae enter mature fruits and destroy the seeds accumulated on the plants, was also introduced (Neser, 1968). More recently a third insect, the hakea leaf weevil, *Cydmaea binotata* Lea, which attacks the young foliage of *H. sericea* has been established (Kluge and Siebert, *in litt.*, 1979). This study however, deals only with *E. consputa*.

THE SCOPE AND PURPOSE OF THIS STUDY

This study started shortly after the first important release of *E. consputa* had been made in South Africa in 1975. Its main purpose was to monitor establishment and to determine the impact of *E. consputa* on the fruit production of *H. sericea*.

Although Neser (1968) had done a detailed study on *E. consputa* in Australia, some additional information on the biology of *E. consputa* was needed for these studies (Chapter 3); most attention was given to the adult and larval stages. Adult feeding activity, fecundity and the seasonal egg-laying pattern were studied. Aspects of the larval phenology were also studied including the number of fruits that each larva destroyed, and the synchronisation of this stage with the fruiting season.

In Chapter 4, information on the mortality of the different stages of *E. consputa* in the field in South Africa is given, and this, together with data on fecundity from Chapter 3 is used to make an estimate of the finite rate of increase (λ) of *E. consputa* populations in South Africa. This information is used to predict the probable increase of *E. consputa* populations after release (Chapter 4).

The colonisation and the spread of *E. consputa* was monitored and is reported in Chapter 5. Apart from verifying establishment this also compared the success of the releases of *E. consputa* from different climatic regions in Australia, under South African conditions.

In Chapter 6 a partial life-table for H. sericea fruits is given to show the importance of E. consputa as a mortality factor of the fruits. The impact of E. consputa on a population of fruits over a three year period is described. Some information on the efficiency of E. consputa as a seed-predator was also derived from these data.

Finally in Chapter 7, the results of the present study, and information from the literature are used to predict the possible success of E. consputa as a biological control agent in the long-term. The general feasibility of using seed predators in biological control of weeds is discussed, and the future role of biological control in the control of H. sericea is considered.

3. BIOLOGICAL STUDIES ON THE HAKEA FRUIT WEEVIL, E. CONSPUTA

A comprehensive study which covers the taxonomy, distribution, biology and phenology of the hakea fruit weevil, E. consputa, in Australia has been done by Neser (1968). The main purpose of that work was to demonstrate the host-specificity of E. consputa. The biology of E. consputa in relation to H. sericea is summarized in Figure 6 which shows the interaction between the reproductive cycle of the host plant and the immature stages of E. consputa.

The aim of the various studies reported here was to gather the information required for subsequent observations on the colonization of the weevils, and the evaluation of their impact on the fruit production of H. sericea. These studies were concerned mainly with the feeding behaviour, fecundity and egg-laying of the adults. Emphasis was placed on the biology and mortality of the larval stage since much of the evaluation work has centred on this stage of the life cycle.

Most of the work done on the biology of E. consputa by Neser (1968) was done at Wilson's Promontory, or with Wilson's Promontory material (Fig. 4). All the present work, unless specifically stated otherwise, was done with E. consputa that originated from the Nerriga area in New South Wales. The significance of the origin of the material becomes apparent in Chapter 5. Also, unless otherwise stated, all studies were done in H. sericea stands at Florabult outside Stellenbosch (details are given in Appendix 1).

THE ADULT AND ADULT FEEDING

E. consputa is a weevil with a pronounced, curved, slender rostrum (frontispiece). Its is 4,0 - 5,0 mm in length, and 2,3 - 2,7 mm at the widest part of the elytra (Neser, 1968). The general colour of the adult varies with age (Neser, 1968), but

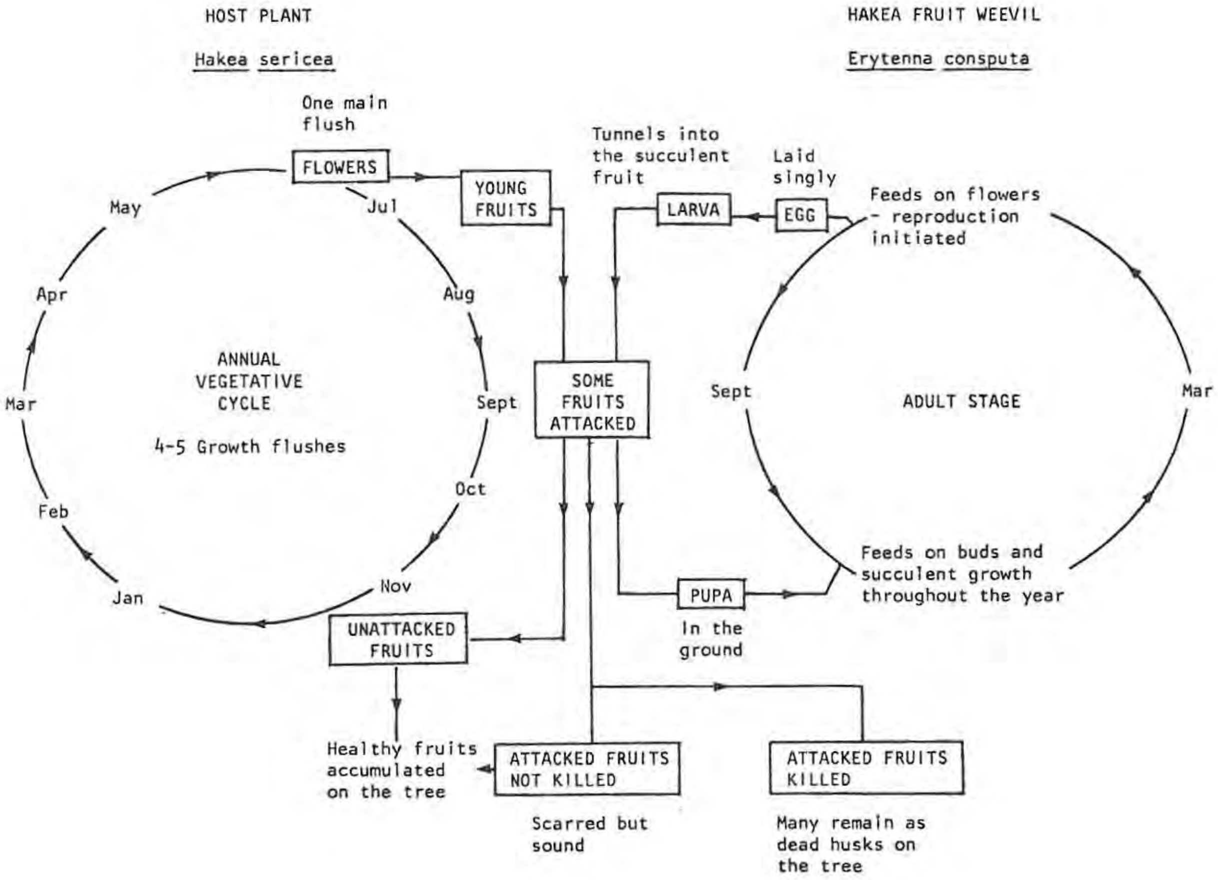


Fig. 6: A diagrammatic representation of the interaction between the phenology of the hakea fruit weevil, Erytenna consputa, and Hakea sericea showing the importance of the larval stage in reducing the fruit production of its host.

E. consputa from the Nerriga area in New South Wales is generally mottled grey, black and shades of brown above, with a grey underside. The weevils have a distinct blueish-black band along the proximal margin of the elytra (Fig. 30).

The adults may live for up to three years (see Chapter 4). Neser (1968) consistently found a slight preponderence of males in all field-collected samples from Wilson's Promontory. The sex ratio in his samples varied from 1:0,79 - 1:0,92 (n = 488). Counts from five local populations showed a slight preponderence of females with an overall sex ratio of 1:1,33 (range 0,81:1 - 1:1,53)(n = 552).

The E. consputa weevils can be found on H. sericea bushes throughout the year, and when they are not feeding or laying eggs they usually shelter in the husks on the tree.

In a feeding trial, the E. consputa adults were caged singly in 400 x 120 mm, 42 gauge Nybolt, gauze sleeves, which were placed over selected "sample" branches on the H. sericea plants. Feeding damage was recorded at weekly intervals between 3 January, 1977, and 1 December, 1978. The "sample" branch was selected so that it had an excess of all the categories of food that were present on the plant at that particular time, and the weevils were transferred weekly to new branches. The sample branches were up to 250 mm in length, and were examined under a stereomicroscope for feeding damage.

Feeding incidence, irrespective of the amount of feeding, was recorded on the various parts of the plant. The different feeding sites, as described by Neser (1968), were grouped into four main categories as follows:

a. Dormant buds. No distinction was made between vegetative and reproductive buds at this stage, and this category included axillary, apical and "additional" buds. The latter is a reproductive bud found at the base of the developing fruit, and it is usually aborted after the fruit reaches a certain stage of development (Neser, 1968). As a consequence of E. consputa feeding, the buds were hollowed out through a single hole at the apex.

b. Lesions on the vegetative growth. This included feeding on vegetative buds from bud burst to a stage when the new shoot was no longer succulent or suitable for feeding. Also included here was limited surface feeding on older stems, especially at the base of the fruits.

c. Flowers. This included feeding on reproductive buds up to a stage when the developing ovary was classified as a "small fruit".

d. Small fruits. This only included developing fruits less than 10 mm in length i.e. less than 0,1 ml in volume. Each fruit is usually only punctured once.

Because of the inevitable change in the number of individual weevils during the course of the trial, and because of the slight variation in the intervals between counts, the data were compared by considering the mean feeding rate in each category; this was calculated by the

$$\frac{\text{Total number of feeding spots in each category over a period}}{\text{Number of females x Number of days}}$$

The seasonal feeding pattern is shown in Figure 7.

Males and females feed throughout the year on a diet of dormant buds and succulent vegetative growth. There was an intensive period of feeding following emergence from the pupae in January and February. The feeding activity is least towards the middle of winter and increases dramatically with the start of flowering of H. sericea. The weevils immediately start feeding almost exclusively on the bursting buds. The significance of this change in the weevil's diet is that it synchronizes egg-laying with fruit development (Neser, 1968).

H. sericea has one main flush of flowers each season, sometimes with a much smaller second flush later in the season (Fugler, 1979). As the number of available flowers decreases, and the egg-laying season progresses, feeding activity on the dormant buds and vegetative parts increases to a peak in November. This coincides with the end of the egg-laying season (Fig. 8). Feeding activity then continues to decrease gradually as winter approaches.

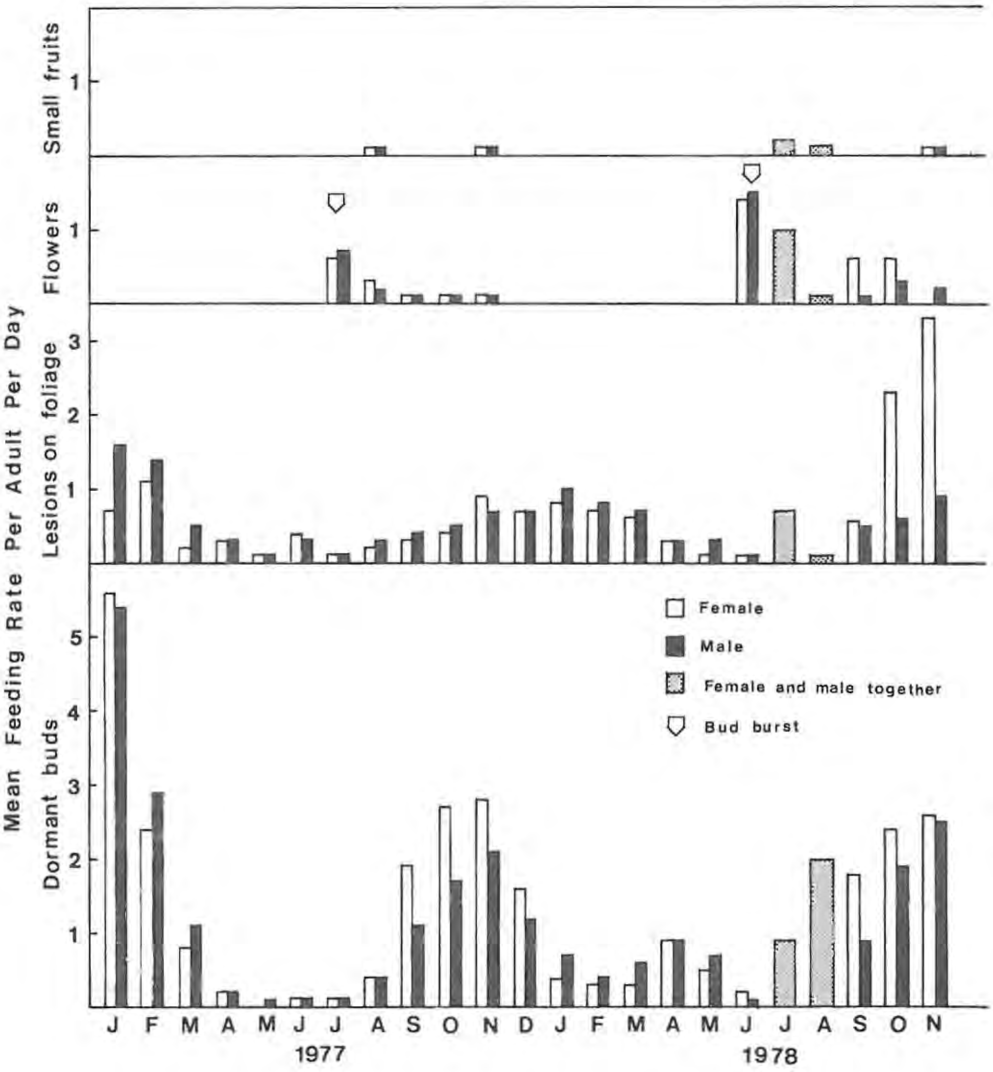


Fig. 7: The seasonal feeding pattern of four female and six male weevils, Erytenna consputa, on the different parts of their host plant, Hakea sericea, over a two year period, in sleeve cages in the field. The calculation of "mean feeding rate" is explained in the text.

These results elaborate the observations made by Neser (1968), who was aware that "the females in the field continued feeding throughout the non-breeding period", they (the weevils) came out to feed at irregular intervals throughout the year","that definite changes occurred in the feeding pattern" and "that the rate of ingestion in laboratory adults increased markedly towards midwinter".

Few fruits larger than 10 mm in length i.e. larger than 0,1 ml in volume, were eaten by the adults. Neser (1968), in the course of food preference studies in the laboratory, found "newly-set" fruit to be the preferred type of food. Allowing for some discrepancy in the term "newly-set" fruit, the results in Figure 7 suggest that Neser's results can be ascribed to some laboratory artifact, such as the condition of the H. sericea boquets.

THE EGG AND FECUNDITY

Newly-laid eggs are yellow, and turn a transparent grey towards the end of their development. They have a soft, membranous chorion. The duration of the egg stage in the field varied from approximately 28 days at the start of the season in September (n = 30), to approximately 15 days later in the season (n = 30). Neser (1968) recorded egg incubation times of 10 - 20 days for an undisclosed number of eggs at room temperatures of approximately 18 - 22°C, and a mean of 15 days (range 13 - 19 days for 132 eggs) at a constant temperature of about 20°C.

In egg-laying trials the females were caged singly (see below), or together with males, in sleeves on branches. Each branch was selected so that it had at least four fruits that were suitable for egg-laying. The adults were transferred to fresh branches at weekly intervals, and these branches were examined under a stereomicroscope in the laboratory for egg-laying sites. The position of each egg-laying site, which was easily recognised by the excretal plug covering the opening (Neser, 1968), was recorded as shown in Table 2. Each was carefully checked to make sure that it contained an egg.

Field-collected females from the previous season's generation were used. These "young" females were distinguished by means

No	Dry weight mg	First Season						Second Season						Total Fecundity
		% Eggs in each locality					Total eggs	% Eggs in each locality					Total eggs	
		Axb	Apb	Adb	Lt&Ml	H		Axb	Apb	Adb	Lt&Ml	H		
1	-	41	11	17	30	1	83	21	1	12	41	25	166	249
2	-	17	3	6	46	28	78	34	3	11	43	9	170	248
3	-	44	3	9	43	1	91	29	0	9	44	18	111	202
4	-	24	14	4	56	2	122	48	20	8	13	11	150	272
5	6,18	46	21	6	24	3	114	52	15	12	17	4	144	258
6	5,84	37	4	4	46	9	118	27	4	13	35	19	124	242
7	5,74	35	18	7	40	0	81	35	43	14	7	1	74	155
8	-	12	3	1	83	1	110	20	6	6	61	7	114	224
9	7,76	6	1	2	75	16	84	15	1	7	50	27	153	237
10	7,06	41	5	1	53	0	121	45	6	20	28	1	157	278
11	5,06	18	7	0	68	7	44	16	9	2	73	0	44	88
12	6,68	10	3	1	78	8	118	29	9	8	48	6	155	273
Total		28	8	5	53	6	1 164	29	8	12	38	13	1 562	2 726

Table 2: The individual egg-laying record of 12 hakea fruit weevils, Erytenna consputa, for both egg-laying seasons, showing the distribution of the eggs in the different egg-laying sites, and the dry weights of some of the females. (Axb = Axillary bud; Apb = Apical bud; Adb = Additional bud at base of fruit; Lt = Leaf tip; Ml = Mid-leaf; H = Horn on fruit).

of characters described by Neser (1968), and it is certain that they had not yet laid any eggs. The mean fecundity for 12 of the females that completed two full seasons was 227,1 ± 16,1 eggs (range 88 - 278) (Table 2). This was much higher than the low numbers of eggs that were recorded from E. consputa in the laboratory by Neser (1968). There was a significant positive correlation (r = 0,71) between fecundity and the dry weights of the females, which partly accounts for the large variation between the individual fecundities shown in Table 2.

The number of eggs laid during the second season (130,2 ± 11,2; range 44 - 170) was significantly more than that laid during the first season (97,0 ± 7,0; range 44 - 157) (P = 0,01) according to the Wilcoxon test for paired observations (Van Ark, 1981). As explained below these results can probably be attributed to the longer egg- laying season during 1978.

Two procedures were followed to investigate the effects of mating on fecundity and fertility. Firstly the four females from the feeding trial were kept virgin for the first season, and were then mated just before the start of the second season. Three of these females died early in the second season, but the fourth female completed a full season and laid 106 eggs which were viable. Seven other females were separated from males just before the start of their first egg-laying season, and were never brought into contact with males again. These females laid a mean of 118,0 ± 2,7 eggs (range 110 - 132) in their first season, and the four that survived, 137,5 ± 10,9 eggs (range 114 - 157) in the second season. The total mean fecundity of these four females was 254,3 ± 12,9 eggs (range 224 - 278), which is not significantly different ($P = 0,05$) from that of the females above that were always attended by males.

The results in Table 3 show that the overall fertility and viability of all the eggs laid in these studies were high, and that there was little difference between the seasons and between mated females kept with and without males. Although Neser (1968) found active spermatozoa in the spermathecae of "old" adults during the non-breeding season, the above results clearly show that an E. consputa female does not require regular mating between or during egg-laying seasons in order to produce normal quantities of fertile eggs.

SEASONAL EGG-LAYING PATTERNS AND OVIPOSITION PREFERENCE

The seasonal egg-laying patterns of E. consputa for two seasons are shown as fluctuations in the egg-laying rate (Fig. 8), derived from twelve female weevils. Egg-laying in the 1978 season started almost four weeks earlier than during the

Season	Period	Treatment	Number of females	Number of eggs sampled	% Hatched
1977	21 Jul. - 26 Dec.	With males	12	293	94,5
1978	21 Aug. - 26 Dec.	With males	12	353	94,6
	25 Jul. - 26 Dec.	Without males	7	176	93,2

Table 3: The viability of eggs of the hakea fruit weevil, Erytenna consputa, for females kept at room temperature with and without males after mating. Egg samples were collected at approximately two-weekly intervals throughout both seasons, and kept in 25 x 50 mm glass phials with cotton-wool stoppers. Each phial contained a piece of Carpobrotis edulis leaf for moisture.

previous year. This can be ascribed to the earlier flowering season of H. sericea during that year. Such seasonal variations in the flowering of H. sericea and E. consputa egg-laying were also recorded by Neser (1968) in south-eastern Australia.

In the middel of the egg-laying season, from September to October, there was a peak period when egg-laying averaged 1 - 1,5 eggs per female per day. This was preceded by a period of gradual increase in the egg-laying rate, following the start of egg-laying in July, and was followed by a period of gradual decline, and ultimately the cessation of egg-laying during December (Fig. 8).

During the peak egg-laying period, the females laid up to three eggs a day. E. consputa has four ovarioles which, according to Neser (1968), carry four apparently mature eggs at any one time. The maximum egg-laying rate under optimal conditions is therefore probably determined largely by the rate of oogenesis, and modified by the time taken by a female

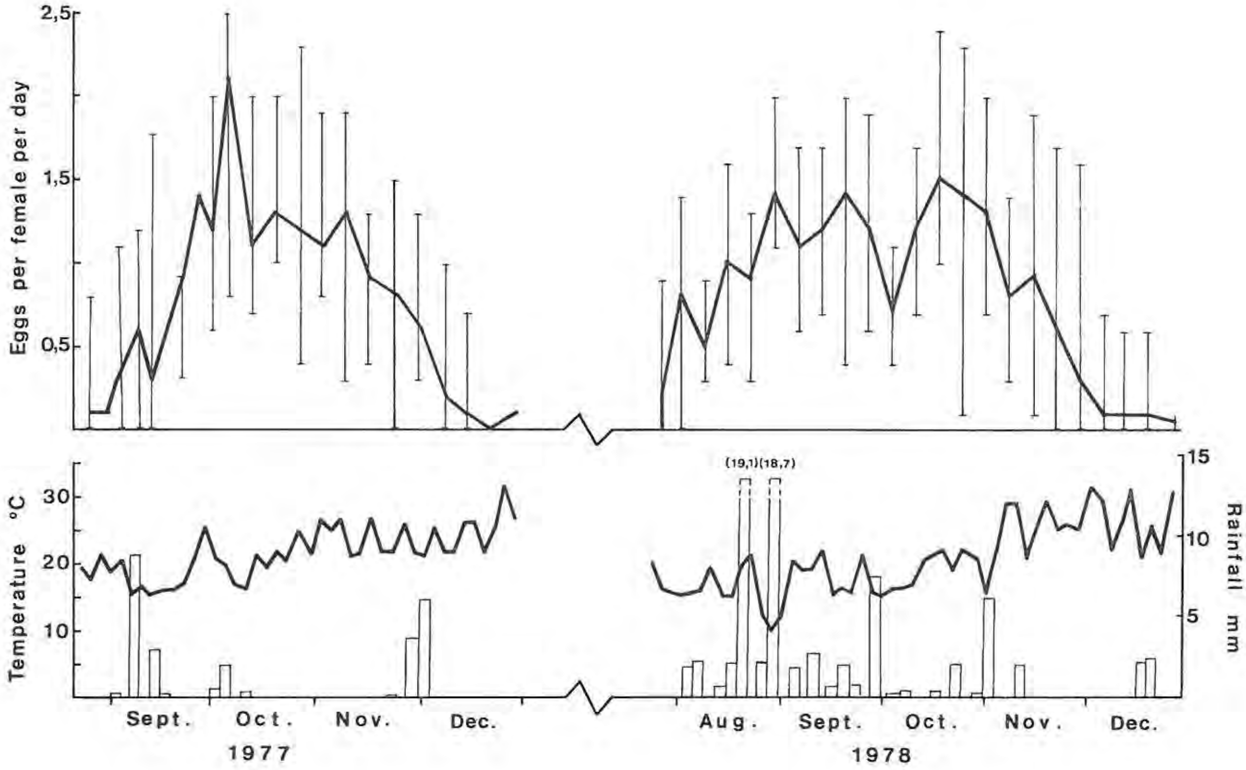


Fig. 8: The seasonal egg-laying pattern of 12 hakea fruit weevils, Erytenna consputa, (means and ranges) that were kept in sleeve cages on Hakea sericea in the field at Florabult from July, 1977, to December, 1978, together with data on rainfall, and the mean maximum temperature at three-day intervals as obtained from the Welgevallen Experimental Station in Stellenbosch.

to find and excavate a suitable egg-laying site.

For one week, from the 5th to the 12 th of October, 1982, half the cages (randomly chosen) were changed daily to see if the limited number of fruits in the sleeves suppressed the egg-laying rate. As a result of changing the cages daily, the females in that group were offered a total of between 28 - 56 fruits instead of the usual 4 - 14 fruits as was normal when the cages were changed weekly. The number of eggs laid was not increased by this procedure, and a total of 91 eggs was laid by each group of females.

The egg-laying season in 1978 was longer (approximately 160 days) than it was in 1977 (approximately 126 days) because of the earlier flowering time in 1978. Despite this the decline in the egg-laying rate at the end of both seasons was the same (Fig. 8). The shorter egg-laying season (about 27 per cent shorter during 1977), probably accounts for the lower fecundity of the E. consputa females during their first season (about 34 per cent less eggs being laid than during the second season).

The eggs are laid singly in excavations in leaf-tips, additional buds, and the horn-like protrusions on the fruits and in axillary and apical buds. A small proportion of the eggs (less than 2 per cent) were also laid along the length of the leaf (Table 2). These counts were included with the leaf tip counts. Each egg was laid in the immediate vicinity of a suitable fruit. Most of the eggs are laid in the leaf tips (Table 4). This confirms Neser's (1968) observations of Goulburn in New South Wales.

Season	Percentage eggs laid on different parts of the plant					Total Eggs
	Axillary Buds	Apical Buds	Additional Buds	Leaf Tips	Horns	
1977	28	8	5	53	6	1 164
1978	29	8	12	38	13	1 562

Table 4: The overall preference by the hakea fruit weevil, Erytenna consputa, for egg-laying sites in sleeve cages on Hakea sericea over two seasons in the field at Florabult, Stellenbosch.

The overall seasonal preference of E. consputa for the different egg-laying sites was similar for both seasons as shown in Figure 9. This preference is to some extent determined by the availability, during the season, of individual oviposition sites. As described above, the additional buds at the base of the developing fruits, for example, are aborted when the fruits reach a certain stage of development, while the horns on the fruits are only suitable for egg-laying for a limited period.

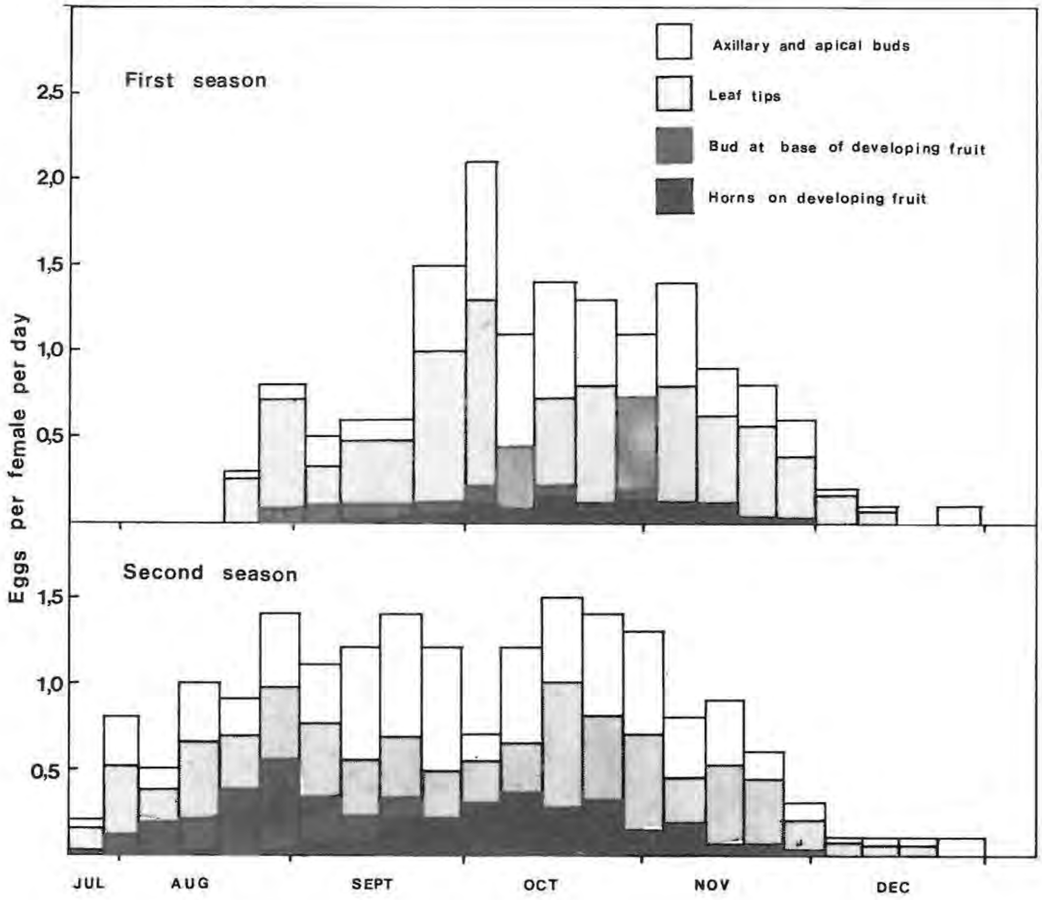


Fig. 9: The seasonal pattern in the preference of the hakea fruit weevil, Erytenna consputa, for the different egg-laying sites on its host plant, Hakea sericea, for two seasons.

It is likely that differences in the phenology of the plant (and the availability of egg-laying sites) explains the differences between the 1977 and 1978 seasons recorded in Table 4.

THE LARVA AND PUPA

The larva of E. consputa is a typical, apodous curculionid larva (frontispiece). Newly-hatched larvae are approximately 1,5 mm in length, and the mature larvae are about 5 - 8 mm in length. In the present study, four instars were recorded in the field before the larva leaves the fruit to pupate. Three pairs of mandibles can be recovered from the frass produced by a larva in the fruit(s) in which it has completed its development.

The development time of the larva in the fruit lasted from approximately 25 days at the start of the season (n = 30) to approximately 20 days during October (n = 30). According to Neser (1968) the feeding period varied around a mean of 22 days, but extended up to 40 days in some cases.

Because of the careful selection of an egg-laying site by the female in, for example, a leaf tip close to or touching the fruit, the larva, after hatching, usually has to crawl only a short distance to find a suitable fruit (Fig. 10). It eats its way into the fruit, making a small hole on the cheek, or somewhere along the suture of the fruit (Fig. 10). The larva then tunnels into the seed cavity and into the pericarp around the seed cavity (frontispiece). Both developing seeds are destroyed.

The attacked fruit turns a reddish colour at first, and starts to yellow as it desiccates (Fig. 11 B and C). This tends to cause the fruit to split open along the suture (Fig. 11 D). When the fruit is no longer suitable, the larva leaves it by

Fig. 10: A young Hakea sericea fruit that has been attacked by a first instar larva of the hakea fruit weevil, Erytenna consputa. The small entrance hole of the larva is visible on the suture (a), and opposite it the egg-laying site (b).

eating an exit hole through one side (Fig. 11 D), or sometimes by way of the gaping suture. A larva may require from one to three fruits to complete its development, depending on the size of the fruits (Table 5).

The attacked fruit remains on the tree as a dry, brown husk (Fig. 11 D). The larval entrance and exit holes, and the larval frass distinguish these husks from those which look similar, but which have died from other causes, mainly natural abortion.

Late in the season (double arrow Fig. 12) there were no more fruits which could be penetrated by E. consputa larvae. Larval attack only resulted in the scarring of fruits as described above and the fruits were not killed. Larvae still continued to hatch for a long time after this, but they died without penetrating fruits.

On completion of development in the fruit, the larva eats a large exit hole in the side of the fruit, or it crawls out through the gaping suture, and then drops to the ground to pupate (Neser, 1968). Although this has not been verified in the field, counts done in the laboratory (Table 6) show

Fig. 11: Unattacked and attacked fruits of Hakea sericea: (A) a healthy, developing fruit; (B & C) developing fruits that have discoloured following attack by the larva of the hakea fruit weevil, Erytenna consputa; (D) the dry husk that remains after successful attack by E. consputa; (E) a mature fruit with mucilagenous scars following an unsuccessful attack by an E. consputa larva; (F) a healthy, mature fruit.

Date	Larvae n	Number of fruits required by larvae to complete development: Three young fruits	Two young fruits	One young fruit	One young and one hardened fruit	One or two hardened fruits
		Percentage				
Early season up until 29 Sept.	13	38,5	61,5	0	0	0
Mid season up until 16 Nov.	59	1,7	67,8	23,7	5,1	1,7
Late season up until 12 Dec.	10	0	0	80,0	0	20,0
Total	82	7,2	59,0	26,5	3,6	3,6

Table 5: The number of young and hardened fruits of Hakea sericea used by larvae of the hakea fruit weevil, Erytenna consputa, to complete their development at different times from the start of the 1978 season at Coetzenburg, Stellenbosch.

that the majority of the larvae leave the fruits at night. One of the advantages in this would be to escape the high soil temperatures that occur during the day. Temperatures of up to 32°C have been measured. Larvae placed on the soil at this temperature succumbed within minutes.

At night the mature larvae exit from the fruits, drop to the ground, and burrow downwards into loose soil or plant litter, crevices or under stones. If the substrate is suitable the larvae burrow and disappear from sight within about 15 minutes. Otherwise they spend up to an hour actively moving over the surface of the soil until they find a suitable site for burrowing and pupation.

Period over which larvae collected	Total number of larvae recovered	Percentage larvae emerging from	
		17h00–08h00	08h00–17h00
2-7 Nov. 1981	262	88,5	11,5
15-22 Nov. 1981	493	96,1	3,9
Total	755	93,5	6,5

Tabel 6: A comparison made in the laboratory of the time of day that larvae of the hakea fruit weevil, Erytenna consputa, leave attacked fruits to pupate.

The development of woody tissue in the pericarp of the maturing fruit later in the season, prevents the larvae from penetrating into the seed cavities. Consequently they are forced to tunnel superficially in the outer, softer layers of the pericarp, leaving the fruit with mucilagenous scars (Fig. 11 E). These fruits remain intact and the seeds are not harmed (Neser, 1968). Depending on the degree of woodiness, some larvae are able to complete their development on two or more of these woody fruits. This is relatively rare and becomes less probable as the season progresses (Table 5) and as the fruits harden further.

The pattern of larval attack during the season was derived from the study of fruit mortality, fully described in Chapter 6, in which the mortality of a fixed cohort of developing fruits was recorded at weekly intervals. The first sign of larval attack usually occurred when the fruit population had reached a mean fruit volume of about 0,2 ml; the largest fruits are by then 0,3 ml in volume or about 15 mm in length. During this period, which lasted from 34 - 36 days, all the fruits were succulent and green, and vulnerable to attack by E. consputa larvae.

Figure 12 shows that the high incidence of larval attack coincided exactly with the availability of young fruits during all three seasons. The incidence of larval attack shown in Figure 12 includes attack by both newly-hatched larvae and developed larvae that were moving over from an attacked fruit to a fresh fruit. Between the end of October and the start of November, the first fruit pericarps started to become woody (single arrow Fig. 12), and over a period of 22 - 36 days the number of fruits that were vulnerable to attack decreased and there was a simultaneous decrease in the incidence of larval attack.

The larvae pupate in the soil, although they have not yet been found in the field. In the laboratory, the fragile pupal cell, constructed of sand particles that are glued together, is constructed from 10 - 40 mm below the soil surface. The period from the cessation of feeding until pupation varied from 9 - 29 days in the laboratory (Neser, 1968).

The pupa is exarate and soft, and in the laboratory at ambient temperatures the pupal duration was from 18 - 19 days (Neser, 1968), with the teneral adult spending a further 4 - 15 days in the pupal cell before emerging. The whole period from the time that the larvae leave the fruit, until the young adults emerge above ground lasted from approximately 44 - 68 days.

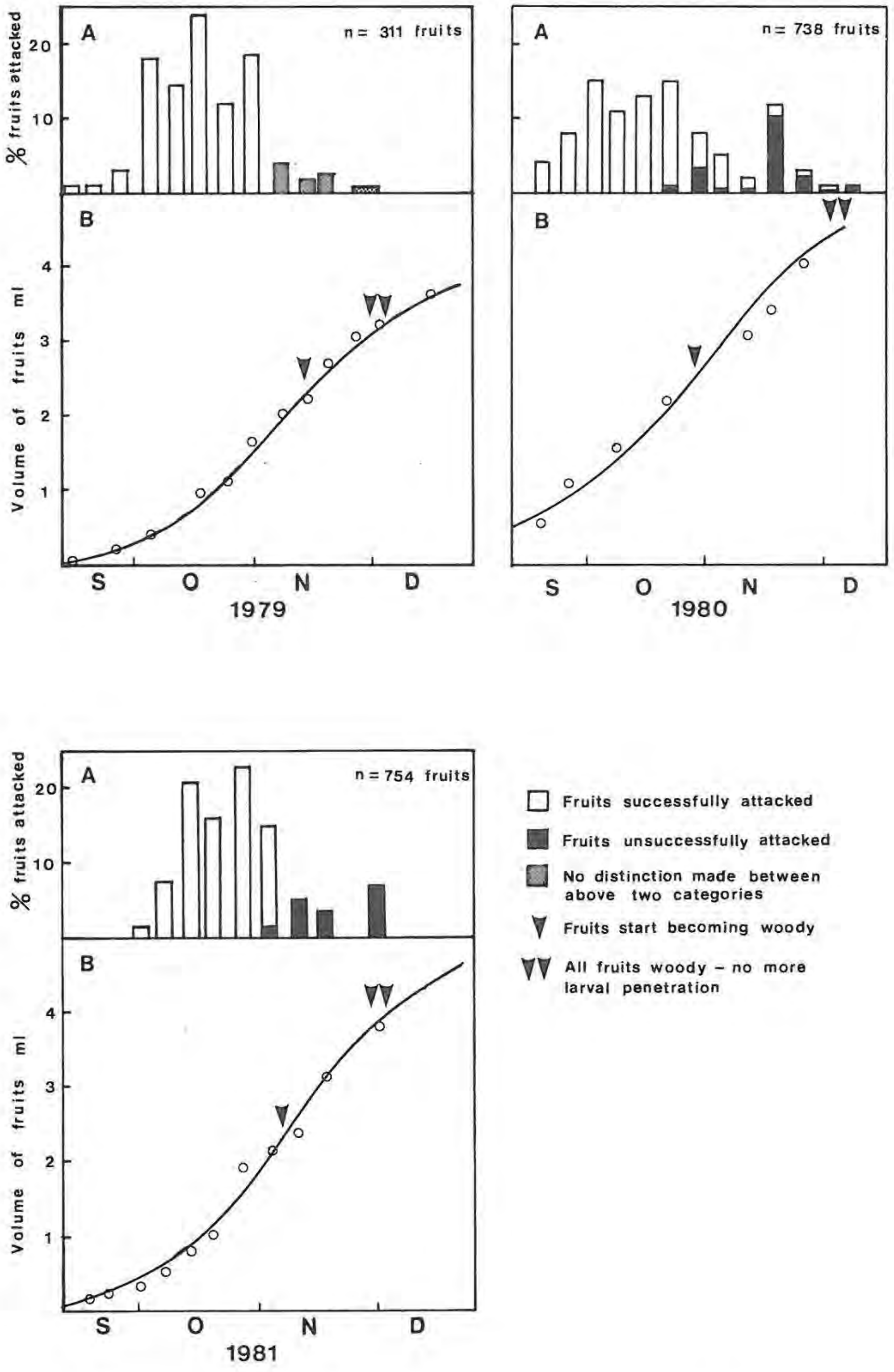


Fig. 12: (A) The seasonal incidence of the larvae of the hakea fruit weevil, Erytenna consputa, in relation to (B) the development of the fruits of its host, Hakea sericea, for three seasons, as shown by the pattern of fruit attack at Goudini. The lines were fitted by eye.

4. PREDICTING THE RATE OF INCREASE OF E. CONSPUTA UNDER SOUTH AFRICAN CONDITIONS

Estimates were made of the adult longevity, and of the mortality of the different stages, and this together with the figures on fecundity from Chapter 3 were used to construct a partial life table for E. consputa under South African conditions. A model using the life table data was then constructed to predict the approximate rate of increase of E. consputa at the release sites.

ADULT LONGEVITY AND MORTALITY

Neser (1968) suspected that E. consputa adults lived for up to three years. By means of the general appearance of the weevils, together with certain characteristics of their physiological condition such as the fat bodies, urate cells, spermatheca and oviducts, he was able to divide field-collected samples of E. consputa adults into "young" (those that have not yet completed an egg-laying season), "old" (those that have completed one egg-laying season), and "very old" adults (those that have completed two egg-laying seasons).

The maximum longevity recorded from the feeding and egg-laying trial in Chapter 3 was approximately 730 days. Similar longevity has been reported for other adult curculionids. Both the plum curculio, Conotrachelius nenuphar (Herbst), and the vegetable weevil, Listroderus costiorostris obliquus Klug are known to live for up to two years (Burk, 1982). It is however likely that the overall longevity of the E. consputa weevils in these trials was reduced because of caging, and regular handling.

As is often the case with adult individuals in the field, it is difficult to determine, with any accuracy, the average mortality of a population over time for use in life tables. Neser (1968) used the relative proportions of the three age-groups of adults in samples that he collected at Wilson's Promontory 5 - 9 months after the last breeding season, to describe the pattern of mortality (Table 7). The three groups approximated to a geometric series and from this Neser concluded that there was a constant rate of mortality throughout the adult life. His conclusion is however only valid if it is assumed that the population sampled was at a stable equilibrium. Based on his figures approximately 40 and 10% of the original adults in a generation survive to the start of the second and third egg-laying seasons respectively.

Sample date	Adults n	Number in each age class		
		Young	Old	Very old
February	52	29	23[a]	–
April	66	40	20	6
June	69	44	18	7

a = No distinction made between old and very old adults

Table 7: The age classification of samples of adults of the hakea fruit weevil, Erytenna consputa, collected by Neser (1968) between February and June, 1968, at Wilson's Promontory, Victoria.

Adult mortality in South Africa during the first two years of adult life appears to be lower than that in Australia, as shown by the pattern of mortality in Figure 13 which is based on the mortality of adults in the feeding (n = 10) and oviposition (n = 28) trials (see Chapter 3), and on observations of mortality made in the field in South Africa.

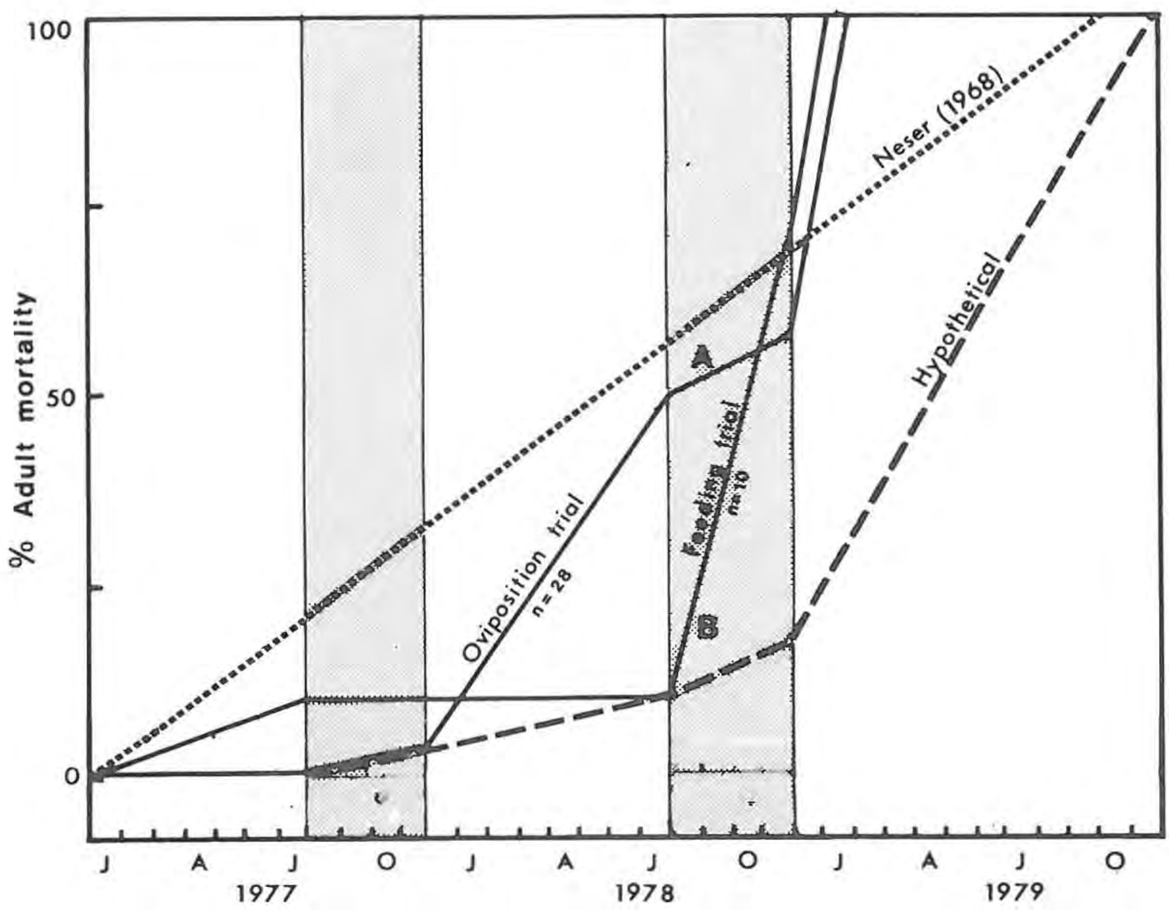


Fig. 13: A simplified hypothetical graph of the suspected pattern of adult mortality of the hakea fruit weevil, Erytenna consputa, in the field in South Africa, as derived from the total mortality between, and during (shaded), egg-laying seasons for two sets of caged adults of known age, and from the pattern of mortality of the adults at Wilson's Promontory in Australia, as concluded from field counts by Neser (1968). (A and B are explained in the text.)

The high mortalities of adults in the oviposition trial following the first egg-laying season, and in the feeding trial during the second egg-laying season (Fig. 13) are ascribed to the effects of caging and frequent handling. In the former case the females were almost certain to have died because of a lack of sufficient succulent, vegetative growth in the field cages during the off-season when the cages were not being moved regularly. After weekly changing of the cages was resumed in July, 1978, the mortality rate dropped dramatically (Fig. 13 - point A).

In the case of the feeding trial the high mortality (Fig. 13 - point B) during the second egg-laying season is attributable to the regular handling to which these adults were subjected. By this time they were showing definite signs of wear; scales had been rubbed off and appendages were missing.

Although the caging could arguably have favoured the adults by for example excluding potential predators, no special care was taken to exclude the predators, so that adults were frequently confined in the sleeves with predators, particularly spiders (see below).

Based therefore on the minimal mortality of the two groups of caged adults, together with the constant rate of mortality suggested by Neser (1968), and assuming a maximum longevity of three years, a hypothetical graph has been constructed to describe the probable pattern of mortality for a generation of E. consputa adults (Fig. 13).

The above data are not totally satisfactory but indicate that, following high survival (over 90%) of young adults, at least 80% of them complete the first two egg-laying seasons. Probably less than 30% survive to the start of the third egg-laying season, and none survive to the fourth season.

The most likely factors responsible for adult weevil mortality in South Africa were considered to be disease, predation, and possibly parasitism by the haemolymph-sucking mite reported by Neser (1968), which may have been introduced with E. consputa. No disease epidemics were apparent, and checks made for microsporidian organisms proved negative.

According to Neser (1968) the haemolymph-sucking mites were found on between 1 - 7% of the adults in samples from Wilson's Promontory. None of these mites have yet been recovered from E. consputa locally.

Predation therefore remains as possibly the most important cause of natural mortality of E. consputa in South Africa. By far the most common predators on the H. sericea trees were spiders. Apart from the orb web spider, Araneus sp. (Argiopidae), all the other spiders belonged to the families Salticidae, Clubionidae, Thomisidae, Sparassidae and Drassidae. According to Dippenaar (in litt., 1977) these are all potential predators of E. consputa adults, although in studies on salticids, Given (1980) found that while all species of Diptera were attacked by salticids (jumping spiders), beetles such as Dermestes sp., which are highly sclerotized, were consumed less readily. Neser (1968) also considered mortality from predation by spiders to be unlikely in Australia. No predation has been recorded in cases where E. consputa adults have been confined with spiders on H. sericea in the field or in cages in the laboratory. Birds have never been seen foraging or perching on H. sericea trees in South Africa.

Thus there is no evidence that disease, predation or parasitoids significantly reduce the populations of E. consputa adults in South Africa, and it seems very likely that the majority of the adults eventually die of old age as is suggested by Fig. 13.

EGG MORTALITY

The viability of eggs tested in the laboratory was high (93 - 94%) (Table 3). This is similar to the results recorded from the release sites in the field (Table 8).

Release site No.	n	% Hatched	% Mortality Not viable	 Parasitism	 Probable predation
13	39	94,9	5,1	0	0
18	140	85,0	7,1	2,9	5,0
69	97	92,3	6,2	0	1,0
73	89	86,5	12,4	1,1	0
113	73	85,7	2,8	1,5	0
Total	438	90,9	6,7	1,1	1,2

Tabel 8: The mortality of eggs of the hakea fruit weevil, Erytenna consputa, as determined from randomly-collected field samples taken at the end of the egg-laying season from a number of release sites (see Appendix 6 for details).

Total egg mortality in the field was slightly higher than in laboratory, mainly because of the disappearance of eggs due to predation probably by ants (Table 9). In many cases the epidermis covering the egg, together with the egg, was missing. (Crematogaster sp. ants have subsequently been seen attempting to remove eggs.) Although chrysopid larvae are frequently seen on the trees, they do not appear to attack E. consputa eggs. A few mymarid egg parasitoids belonging to the genus Potasson sp., have been reared from eggs, but the level of egg parasitism is very low (<2%) (Table 8).

LARVAL MORTALITY

Before considering the factors causing larval mortality in the field, it is necessary to elaborate on the methods used to gather the data.

In this study, E. consputa eggs were placed singly on individual, young H. sericea plants in the field. Each leaf bearing an egg was glued onto a plant near to a group of suitable fruits using "Bostik White Tile Sealer". The subsequent development and fate of each larva was individually recorded up until the time that it left the fruit to pupate.

The study was repeated three times. The first release of eggs was made in September, 1977, at the Coetzenburg study site (Appendix 1). Because of felling operations the 1978 and 1979 releases had to be made at the Florabult site (Appendix 1).

The number of releases, the hatching dates during the season, and the number of eggs that were used in each release, are shown in Appendices 2 - 4. The fate of each egg and larva was recorded at regular intervals during the development of the individual as shown in Figure 14. The stage of development of the larvae in the attacked fruits was determined by measuring the inter-condylar width of the mandibles that were recovered from the frass in the husks. First, second, and third instar mandibles measured 0,1 - 0,13, 0,15 - 0,2 and 0,23 - 0,33 mm (n = 40) respectively. The relative amount of feeding was also indicative of the amount of larval development that had taken place.

The field data from the larval mortality studies are shown in Appendices 2 - 4. The data from these three tables have been summarized in Table 9 which shows that the overall mortality during the early instars was generally higher than in the more advanced instars. The newly-hatched larvae often failed to penetrate despite their mobility (attacks on fruits up to approximately 170 mm from the nearest egg have been recorded), and in spite of the fact that the eggs are almost always laid close to a suitable fruit (Fig. 10).

From the available evidence, the most likely explanation for

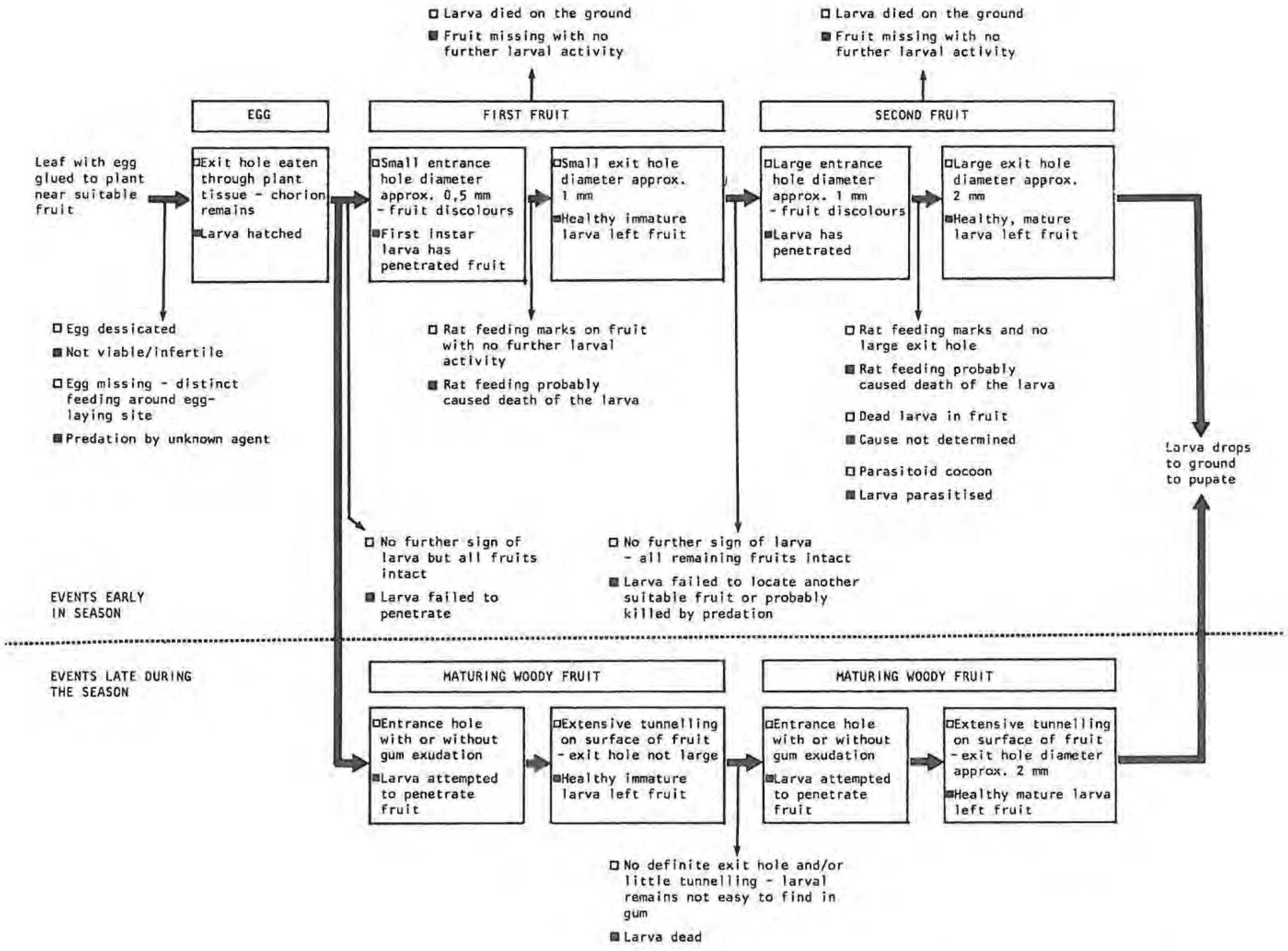


Fig. 14: A diagram showing how mortality data were collected and interpreted in a study on the fate of the eggs and larvae of the hakea fruit weevil, *Erytenna consputa*, in the field. The data shows the most likely sequence of events for *E. consputa* that attack fruit early in the season, and the most probable course of events for *E. consputa* attacking more mature fruit later in the season. Mid-season larvae can switch from feeding on young fruits to mature fruits so that virtually any combination of events is possible. (□ = The observation that was made and/or the circumstantial evidence collected. ■ = The conclusion that followed.)

	Season					
	1977		1978		1979	
Mortality Factor in each Stage	Number Dead	% Mortality	Number Dead	% Mortality	Number Dead	% Mortality
EGG		9,8[a]		11,0		8,4
Not fertile or viable	43[a]		38		14	
Possible Predation/Disappearance			17		2	
EARLY LARVAL INSTARS (I & II)		12,3		38,5		39,0
Failure to penetrate fruit after hatching	20		106		20	
Fruit with larva aborted	14		53		42	
Lost moving between fruits	5		13		2	
Possible rat interference	2		12		9	
Possible *Heliothis* interference	3		0		0	
Dead in fruit - unknown causes	10		9		1	
LATE LARVAL INSTARS (III & IV)		17,3		8,2		15,3
Lost moving between fruits	39		16		14	
Fruit with larva aborted	1		5		3	
Possible interference from other *Erytenna* larvae	3		0		0	
Possible rat interference	4		2		11	
Possible *Heliothis* interference	5		0		0	
Dead in fruit - unknown causes	13		4		1	
Parasitism	11		14		0	
END OF SEASON						
Failure to penetrate woody fruits (all instars)		13,0		25,7		10,5
Percentage of cohort leaving fruit to pupate		47,6		16,6		26,8
Number in cohort	439		501		190	
Number of releases	8		13		8	
Approximate period over which eggs hatched	9 Sept.-4 Nov.		23 Aug.-12 Dec.		20 Sept.-23 Nov.	

Table 9: A summary of the different mortality factors recorded for the immature stages of the hakea fruit weevil, *Erytenna consputa*, following the release of laboratory-collected eggs on *Hakea sericea* in the field over three seasons, together with some details of the releases. For further details see Appendices 2 - 4.

a = Assuming 9,7% egg mortality (i.e. mean for 1978 and 1979) penetration failure is drowning during periods of rain. Rainfall has been implicated as a mortality factor in the population fluctuations of many other insects such as the potato tuber moth (Whiteside, 1978), and Thrips imaginis (Davidson and Andrewartha, 1948). Neser (1968) also recorded that at Wilson's Promontory "there were frequent indications of the disappearance of newly-hatched (E. consputa) larvae, and of older larvae in search of another fruit, and in these adverse weather conditions (rainfall) may have been a contributing factor".

The second important mortality factor acting on the early instar larvae was the abortion of the young fruits containing E. consputa larvae. These larvae either succumbed in the aborted fruit, or they died on the ground. It is not known whether abortion is a response by the plant to E. consputa attack, or whether it was just the normal mass abortion of the young fruits which occurs early in every season. The latter seems more likely since less and less fruits are aborted by the plant as they mature, irrespective of whether they have been attacked by E. consputa larvae or not; the point is discussed more fully in Chapter 6.

The single most important cause of mortality of late-instar E. consputa larvae was the loss of larvae when moving between fruits (Table 9). This is to be expected because most larvae required more than one fruit in which to complete their development (Table 5). The most common pattern was for a larva to complete two instars in the initial fruit attacked. It then leaves as a third instar larva and searches for another fruit. Late instar larvae are mobile: attacks have been recorded by the same larva on fruits up to 610 mm apart. Mortality from this cause can be expected to rise still higher as the population increases, because with an increase in the numbers of larvae they will be forced to spend more time searching for suitable second fruits. Desiccation and predation, particularly by spiders, probably also accounts for the death of many of these larvae.

Although no parasitism was recorded during the 1979 season, parasitism by a Bracon sp. of fourth instar larvae in the preceding two years accounted, respectively, for 4,9 and 3,4% of the total mortality (Table 9).

As the season progresses, larvae in all stages of development succumb because they fail to penetrate the maturing woody fruits. It was often difficult to classify the mortality or the stage of development of such larvae with any degree of certainty, because of the difficulty of finding the larval remains in the gum which was exuded by the fruit at the site where the larva was attempting to penetrate. If the pattern of development of woodiness in the fruits (Fig. 12) is considered together with the seasonal egg-laying patterns in Fig. 8, it is apparent that many larvae only hatch from the eggs once the fruits have already started to harden.

Other mortality factors affecting early and late instar larvae of E. consputa include cannibalism (Neser, 1968), rodents that happen to feed on fruits colonised by E. consputa larvae, and larval mortality from unknown causes. The latter is usually insignificant although it accounted for 12,3% of the mortality during the 1977 season (Table 9).

MORTALITY OF FULLY-DEVELOPED LARVAE AND PUPAE

To determine the mortality of these immature stages in the ground, a comparison was made between the number of adults recaptured from a known number of larvae that had been allowed to pupate in a restricted area in the field at Coetzenburg (Appendix 1), and in the growth-room. Mature E. consputa larvae were collected in H. sericea fruits at the Lebanon release site in the middle of the larval season (27 October). On the same day, these fruits were divided into 18 groups of 20 fruits, and put into 200 x 200 mm 36 gauge, Peiffer-glass gauze bags, through which the larvae could escape. Each bag was tied separately to the lower branch of a H. sericea bush, so that it hung suspended about 100 mm above the ground within the confines of a circular wire frame, which was 500 mm in diameter and 150 mm high. The side of the frame was lined with paper, and the lower rim was sunken into the ground to prevent the larvae from escaping. Fifteen such frames were placed in selected positions which, from past observations, were considered to be suitable for E. consputa pupation.

After five days, the fruits in each gauze bag were removed and checked for large exit holes to see how many larvae had emerged. Two days later the paper sides of the frames were torn off to expose the pupating larvae to the environment and to predators.

A similar procedure was followed in the growth room where the larvae were allowed to pupate in 400 x 300 x 120 mm asbestos trays containing sterilized sand. There were three replicates. The asbestos trays were each kept in 600 x 800 mm 36 gauge, Peiffer-glass gauze sleeves, which were checked regularly for emerging adults. As soon as the first adults emerged in the growth room, gauze sleeves were placed over the frames in the field. These were then checked regularly for adults which were removed and counted. The number of adults collected from each cage was then compared to the number of larvae that had left the fruits to pupate in the frame. By comparing the results for the field and the growth room, it was possible to get some estimate of the survival of pupae in the field.

There was considerable mortality from the time that the mature larva vacated the fruits, and prior to the emergence of the adult. Only 26% (n = 184) of the larvae that dropped to the ground in the field emerged as adults, compared with the 73% (n = 40) recovery of adults in the growth-room. Clearly, from the observations reported in Chapter 3, the mortality at this stage of the life cycle could vary dramatically in the field, depending on the suitability of the substrate for pupation, as well as the occurrence of adverse weather conditions and predators.

The seasonal pattern in overall larval mortality is reflected by the seasonal pattern of the mortality of the larvae up until the time that they leave the fruits to pupate (Fig. 15). Larval mortality (Fig. 15) is generally lowest towards the middle of the fruiting season, usually in October, although this may vary depending on the time of the fruiting season (Fig. 12). The mortality of larvae is always high at the start of the season, because of the abortion of so many of the small fruits containing larvae, and also because of the high failure rate of the larvae to penetrate (Table 9). The latter (due largely to drowning) decreases as the season progresses and the rainfall becomes less frequent. Towards the end of the season larval mortality increases again as the H. sericea fruits start to become woody, and less and less larvae are able to find suitable fruits in which to complete their development (Fig. 15).

A PARTIAL LIFE TABLE

The mortality of E. consputa from egg to adult is summarised in the partial life table in Table 10. Adult mortality is not included. From the table it is concluded that, on average, only 7,9% of the immature stages in each generation emerge as adults.

THE RATE OF INCREASE OF E. CONSPUTA IN SOUTH AFRICA

A prediction of the probable population increase, similar to that made by Hoffmann (1980) for Tucumania tapiacola which was

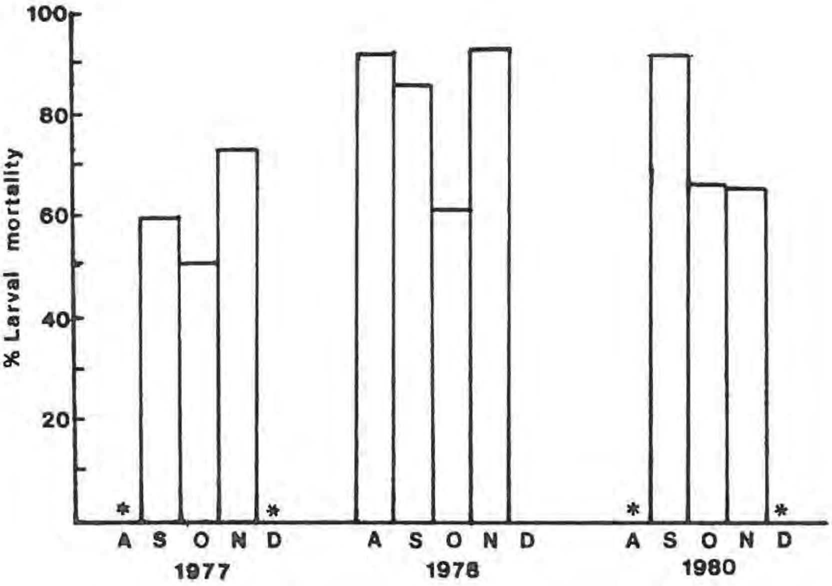


Fig. 15: The seasonal pattern, for three years, of the overall mortality of fixed cohorts of the larvae of the hakea fruit weevil, Erytenna consputa, hatching each month (derived from the field data in Appendices 2 - 4).
* = No data available

released on Opuntia aurantiaca, was made for E. consputa; this was based on the model of May et al. (1974),

$$N_{t+1} = \lambda N_t \qquad (1)$$

Where N_t and N_{t+1} are population numbers in successive generations, and λ is the net rate of increase from generation to generation. In this case

$$\lambda = \frac{AFJ}{2 \times 10^4} \qquad (2)$$

where A is the percentage survival of adults (approximately half of which are females - Chapter 3) during each breeding season, F is the average female fecundity, and J is the average

Stage	Number entering each stage	How this was derived
Egg	114	From total mean fecundity for two years (227,1 eggs per female) determined in Chapter 3
Pupa	34,5	Combined mortality of 1 130 eggs and larvae for Table 9 which, for three years, was 69,7%
Emergent Adults	9	Larval and pupal mortality in the ground from Table 9 which was 73,9%
Total mortality (egg to emergent adults)	92,1%	

Table 10: A partial life table for the hakea fruit weevil, Erytenna consputa, in South Africa, derived from field measurements of its fecundity, and the mortality of the immature stages.

percentage survival of all the immature stages. Survival of both adults and immature stages of E. consputa have been assumed to be density independent, since E. consputa has just been released, its dispersing populations are still at a relatively low level, and presumably it is not yet limited by resources or significantly limited by competition.

The model (1) of May et al. (1974), however, only applies to insects with discrete generations where none of the parents survive to form part of the next generation. Therefore, because of the longevity of the E. consputa adults, the model had to be extended. The extended model, presented diagrammatically in Figure 16, takes into account the fact that an established E. consputa population consists of adults in three age-classes as described at the beginning of this chapter.

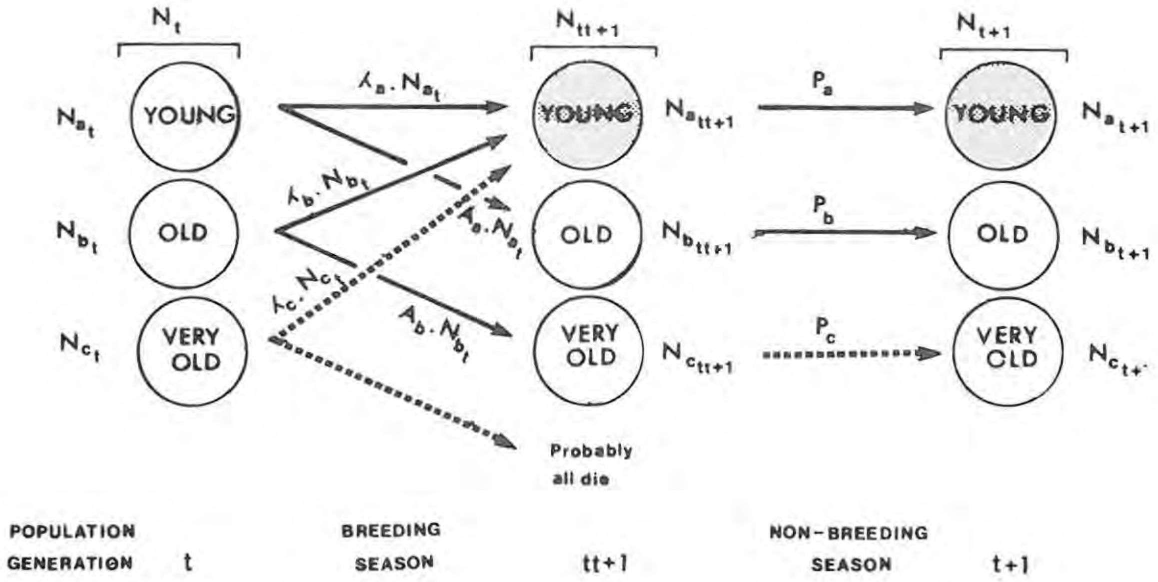


Fig. 16: A diagrammatic model of adult population increase per generation of the hakea fruit weevil, Erytenna consputa, a species that has a reproductive life of two, and possibly three years (no data are available for the latter case, which is shown by dotted lines). At any time t a stable population is composed of "young" adults a, which have not yet completed a breeding season, "old" adults b, which have completed one breeding season, and "very old" adults c, which have completed two or more breeding seasons. These age-classes are shown vertically with N_{a_t} being the number of young adults in their t th generation. In contributing to the next generation t+1, young adults increase at a rate λ_a, whilst a fraction of their number A_a survive to become old adults. The same applies to old adults which increase at a slightly lower rate λ_b. Only a proportion P of the adult population at the end of the breeding season tt+1, survive the non-breeding season, and these constitute the next breeding population N_{t+1}. The shaded circles represent the F_1 generation.

The "young" and "old" adults of any generation both contribute to the next generation, both by reproduction (at approximately equal rates), and survival (at slightly different rates) as is indicated by Figure 16. Although the "very old" adults can possibly still reproduce, they have not been included in the mathematical model because of a lack of data. From Figure 16, and from the counts made by Neser (1968) at Wilson's Promontory, it seems that the contribution of these very old females would not significantly influence the rate of increase of the population.

Following on from the diagrammatic model in Figure 16 and omitting the very old adults, N_{c_t}

$$N_t = N_{a_t} + N_{b_t} \tag{3}$$

and

$$N_{t+1} = N_{a_{t+1}} + N_{b_{t+1}} \tag{4}$$

In the case of E. consputa adults, the generation time, t+1, comprises the breeding period, tt+1, and the non-breeding period (Fig. 13). From (4) it follows that the population at the end of the breeding season will be

$$N_{tt+1} = N_{a_{tt+1}} + N_{b_{tt+1}} \tag{5}$$

As shown in Figure 16, only a proportion, P, of these adults survive the non-breeding season, so that the final number at the end of one generation, t+1, will be

$$N_{t+1} = P_a(N_{a_{tt+1}}) + P_b(N_{b_{tt+1}}) \tag{6}$$

where P_a and P_b is the proportional survival of young and old adults, respectively, at the end of the non-breeding season.

Now

$$N_{a_{tt+1}} = \lambda_a N_{a_t} + \lambda_b N_{b_t} \tag{7}$$

where λ_a and λ_b are the different net rates of increase of young and old adults, and

$$N_{b_{tt+1}} = A_a\ N_{a_t} \tag{8}$$

where A_a is the survival of young adults from the start to the end of the breeding season (Fig. 16).

Substituting (7) and (8) into (6)

$$\begin{aligned} N_{t+1} &= P_a(\lambda_a\ N_{a_t} + \lambda_b\ N_{b_t}) + P_b(A_a\ N_{a_t}) \\ &= N_{a_t}(P_a\ \lambda_a + P_b\ A_a) + P_a\ \lambda_b\ N_{b_t} \qquad (9) \end{aligned}$$

Both λ_a and λ_b were derived from the difference in the survival A of young and old adults. From Figure 16 the value of A_a and A_b, derived from the survival of the 28 females above, is 0,96 and 0,86 respectively (Fig. 13). The values of F (114 eggs) and J (7,9%) are derived from Table 10. The difference in fecundity between young and old females in Chapter 3 is ascribed to a seasonal effect; the overall mean fecundity is therefore used for F. Based on these data $\lambda_a = 4,32$ and $\lambda_b = 3,87$. From Fig. 13, P_a and P_b are estimated to be 1,0 and 0,94 respectively.

Substituting these values into (9)

$$\begin{aligned} N_{t+1} &= N_{a_t}[4,32 + (0,94)(0,96)] + 3,87\ N_{b_t} \\ &= 5,32\ N_{a_t} + 3,87\ N_{b_t} \qquad (10) \end{aligned}$$

where

$$\begin{aligned} N_{b_t} &= A_a\ P_b\ N_{a_t} \\ &= 0,90\ N_{a_t} \qquad (11) \end{aligned}$$

This model (10) was used to predict the populations of E. consputa adults that would develop at a release site following releases of 50 weevils (Fig. 17) (Appendix 5). Although the model is clearly a simplification of mortality in the field, it shows that E. consputa in South Africa has a tremendous capacity for increase. This accounts for the fact that, at release sites where 50 adult E. consputa have been released, significant effects of the weevil have become apparent 4 - 5 year after release.

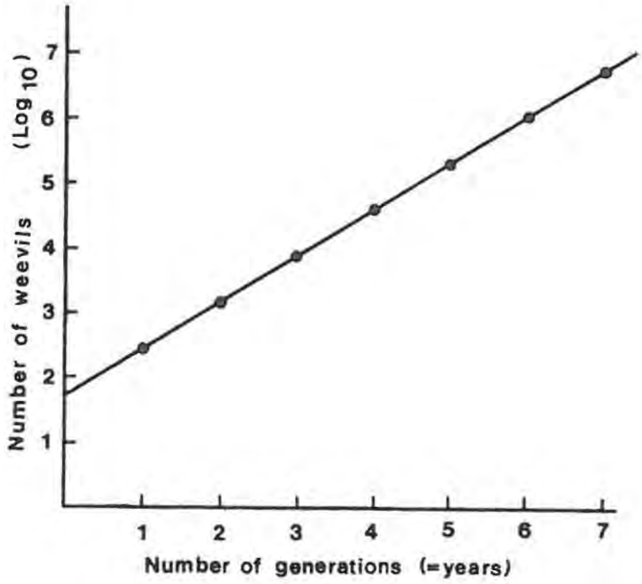


Fig. 17: Populations of the hakea fruit weevil, Erytenna consputa, in subsequent generations in South Africa following the release of 50 adults, when female fecundity for one season is 114 eggs per female, survival of the immature stages is 7,9%, and adult survival over the first two seasons is over 80% (Appendix 5). See the text for the mathematical model.

5. COLONISATION OF H. SERICEA BY E. CONSPUTA

The first large-scale releases of E. consputa were made during August and September, 1975 (Table 1; Fig. 5). These introductions consisted of E. consputa from four localities in three climatically different regions in Australia namely Nerriga and Mittagong in New South Wales, the Grampians and Wilson's Promontory, both of which are in Victoria (Fig. 4).

The intention was that the stocks of E. consputa were to be matched to the different climatic areas in the south and south-western Cape where H. sericea occurred (Fig. 2). The Grampian's climate (Fig. 4) for example, with its very dry summers, is most akin to that of the south-western Cape (Fig. 2) where the most important H. sericea infestations occur, while, according to the classification of Walter & Lieth (1960), the Nerriga climate corresponds most closely with the climatic region around Grahamstown. Emphasis was also put on the need to release from as large a basic stock as possible to maintain genetic diversity (Neser, pers. comm.).

Following the release of E. consputa, the progress of colonisation was followed by measuring the increase in the damage by the weevil as has been done for other biological control agents (Goeden & Ricker, 1978; Kok & Trumble, 1979; Story & Anderson, 1978). Ideally this work should have been combined with the next phase of the study i.e. evaluation, by relating the amount of damage measured to the weed population as Harris (1980a) did in his study on the establishment of the Urophora gall-flies on diffuse and spotted knapweed. Although this approach was considered, the problems associated with the design of a sampling programme for both the insect and the H. sericea fruit populations in the present study made such a quantitative approach unpractical.

The main problems involved in sampling E. consputa were the small size of the colonising population, and the changing dispersion patterns of the weevils both vertically (within the trees), and horizontally (between the trees) from year to year. None of the stages of E. consputa were easy to sample, and destructive sampling could not be considered. The problems were further compounded by the fact that the releases had been made in H. sericea stands of different ages and densities. Accordingly, the shapes of the trees, and the distribution of the fruit in the trees, varied. The terrain on which many of these stands occurred also gave rise to many other practical problems.

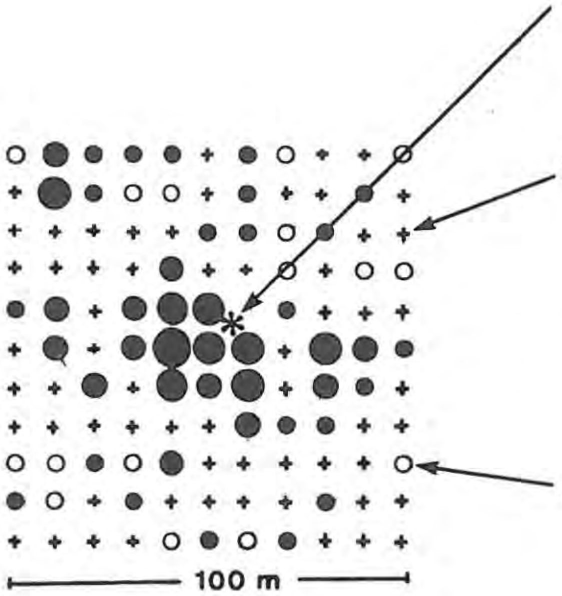
It was therefore decided to revert to less quantitative and more descriptive studies. Firstly, a grid survey method was devised so that the progress of colonisation of the different stocks of E. consputa could be followed more closely at some of the release sites. In addition to this, colonisation at all the sites was assessed by means of a simple rating of E. consputa activity around the release point; this was done at as many of the sites as possible each year.

The results of the grid survey studies, supplemented by a study done at Stettynskloof, also made it possible to draw some conclusions about the pattern and rate of spread of E. consputa around the release point.

GRID SURVEY METHOD

This survey was carried out on a grid around the point at which the E. consputa had originally been released as is shown in Figure 18.

To circumvent the problems of sub-sampling trees, the whole tree, irrespective of size, was taken as a sampling unit. Because most of the trees in a H. sericea stand are of the same age (see Introduction), trees within the same stand were generally of a similar shape and size. Excepting where it is noted, there was always an excess of H. sericea



1. Locate the RELEASE POINT and use this, as the central point of the survey.

2. These 121 SURVEY POINTS (+) are checked on a 10 x 10 metre grid over one hectare around the release point. The tree closest to, and within a three metre radius of each survey point is marked and numbered.

3. Each MARKED TREE is searched for E. consputa activity, and the results are represented as follows:

- ○ No activity
- ● Some sign of activity or up to five husks/tree
- ● 6-15 husks/tree
- ● 16-30 husks/tree
- ● 30+ husks/tree

Fig. 18: An annotated diagram outlining the procedure followed in obtaining data by means of the grid survey method to describe the colonisation of Hakea sericea by the hakea fruit weevil, Erytenna consputa.

fruits for E. consputa to attack at all the sites.

Because of the difficulty of counting any of the stages of E. consputa, the number of husks resulting from larval attack were used as an index of E. consputa activity. The flimsy husks resulting from the small fruits that were attacked were not counted because of their transience on the trees. They were however recorded as indicators of E. consputa activity together with the scarred, sound fruits that had been unsuccessfully attacked.

Plots (grids) of both one, and also of a quarter hectare, were laid out. One hectare plots were used at Doolhof which was the only locality where colonies of E. consputa from the three main climatically different areas in Australia occurred together (Fig. 5). The colony of Mittagong stock at Greyton, although it was some distance away, was included in this study to complete the comparison. For the rest, paired comparisons were made on quarter hectare plots between the colonies of E. consputa from Nerriga (being more abundant they could conveniently be used as controls), and the colonies started with stocks from the other areas in Australia (Fig. 5). Data were collected annually between 1976 and 1978.

In addition to the presentation of data as shown in Figure 18, the progress of colonisation was shown by the change, from year to year, in the percentage of marked trees on which E. consputa activity had been found, and also by the trend in the change of the mean number of husks per marked tree at each site.

The advantages of the grid survey method was that it was very adaptable, and that it made repeated, systematic searching around the release point possible.

In the one hectare grids at Doolhof and Greyton there was a consistent increase, from year to year, in the level of E. consputa activity on all the marked trees around the Nerriga, Mittagong and Grampians release points (Fig. 19). By the end of the three-year study period 79,8, 100 and 84,7 per cent of the marked trees in the respective grids showed E. consputa activity (Table 11). The progress of colonisation at these sites can also be seen from the steady increase in the number of husks per marked tree (Table 11). Because of the many variables involved it is not meaningful to compare directly the absolute success of colonisation between the Nerriga, Mittagong and Grampians populations. The trends, however, are clear.

In contrast to the successful colonisation of these three populations, colonisation by the Wilson's Promontory stock was poor (Fig. 19; Table 11).

Figure 20 and Table 12 show that in the quarter hectare grids there were similar increases in *E. consputa* activity at all the colonies of Nerriga stock excepting the one at Hout Bay (Fig. 20; Table 12). The poor colonisation of both the Nerriga and Mittagong stock there could be attributed to the poor fruiting of the trees; many of the trees failed to set any fruit.

The Nerriga and Wilson's Promontory stocks at Franschhoek occurred about 400 metres apart in the same *H. sericea* stand, so that a direct comparison between these sites was possible. While the colonisation of the Wilson's Promontory *E. consputa* was better here (Fig. 20) than at Doolhof (Fig. 19) (this despite the fact that less adults had been released), both the increase and spread of activity of the adjacent Nerriga colony was still considerably better (Fig. 20; Table 12). The mean number of husks per tree was almost eight times higher by 1978 (Table 12) for Nerriga than Wilson's Promontory stocks.

Although the colonies of Nerriga and Grampians stock at Stettynskloof were originally paired off, the former colonized a stand of *H. sericea* that grew on a moister, south-facing slope, while the latter colonized a stand on a drier, more barren, north-facing slope. It is difficult to interpret the poor result of the colonisation of the Grampians stock under these circumstances because of the possibly overriding importance of the habitat.

ACTIVITY RATING OF *E. CONSPUTA* COLONIES

As many of the 58 *E. consputa* colonies as possible were visited each year. At each site a rating for the *E. consputa*

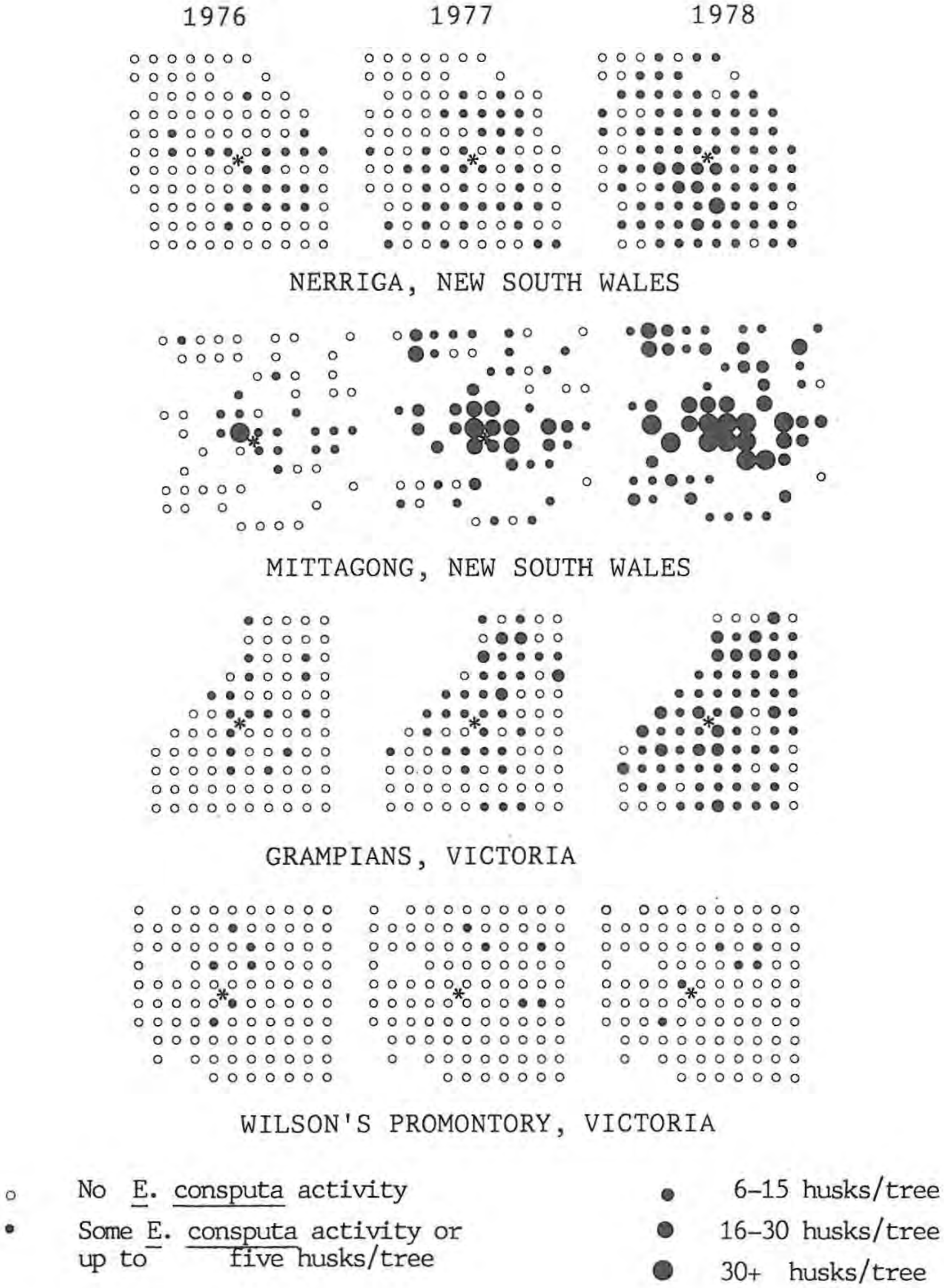


Fig. 19: A comparison of the increase and spread of the hakea fruit weevil, Erytenna consputa, introduced from different areas in Australia (Fig. 4), on marked Hakea sericea trees in a one hectare grid around the release point (*) following the releases made in August and September, 1975, and in the case of the Mittagong stock in August, 1976. The Mittagong stock was released at Greyton and the other stocks at Doolhof near Wellington (Fig. 5; Appendix 6).

Locality of release site	E. consputa releases		Number of trees marked	Number of husks per marked tree			Percentage of marked trees with weevil activity		
	Origin	Number Released		1976	1977	1978	1976	1977	1978
Doolhof "C"	Nerriga, N.S.W.	100	104	0,2	0,5	1,7	21,2	37,5	79,8
Greyton	Mittagong, N.S.W.	69	60	0,6	6,0	12,8	23,3	70,0	100,0
Doolhof "A"	Grampians, Victoria	100	85	0,2	1,1	2,8	18,8	41,2	84,7
Doolhof "B"	Wilson's Promontory, Victoria	100	100	0,1	0,1	0,1	6,0	5,0	5,0

Table 11: A comparison of the rate of colonisation of the hakea fruit weevil, Erytenna consputa, from different regions in Australia (Fig. 4), on Hakea sericea at different release sites in South Africa (Appendix 6) over a three-year period, following the release of the weevils in August and September, 1975.

activity was made, based on the number of husks that could be found around the release point, within 15 minutes; this was scored on a scale from 0 - 4 as shown in Appendix 6. Only those husks of more mature fruits, as mentioned above, were counted. At the end of each year the mean rating for each of the four E. consputa stocks was determined from the ratings of all the respective colonies that had been visited.

Colonies of the Nerriga, and later (by 1977) the Mittagong stock, showed the highest mean activity rating (Fig. 21). While the present results can only be taken to suggest that the Grampians stock was less successful than the New South Wales stocks, it is clear that the overall colonisation by the Wilson's Promontory stock was much poorer (Fig. 21). The slight increase in the mean rating in 1978 for the Wilson's Promontory stock was due to a high rating given to the Franschhoek "C" colony which was probably contaminated with Nerriga

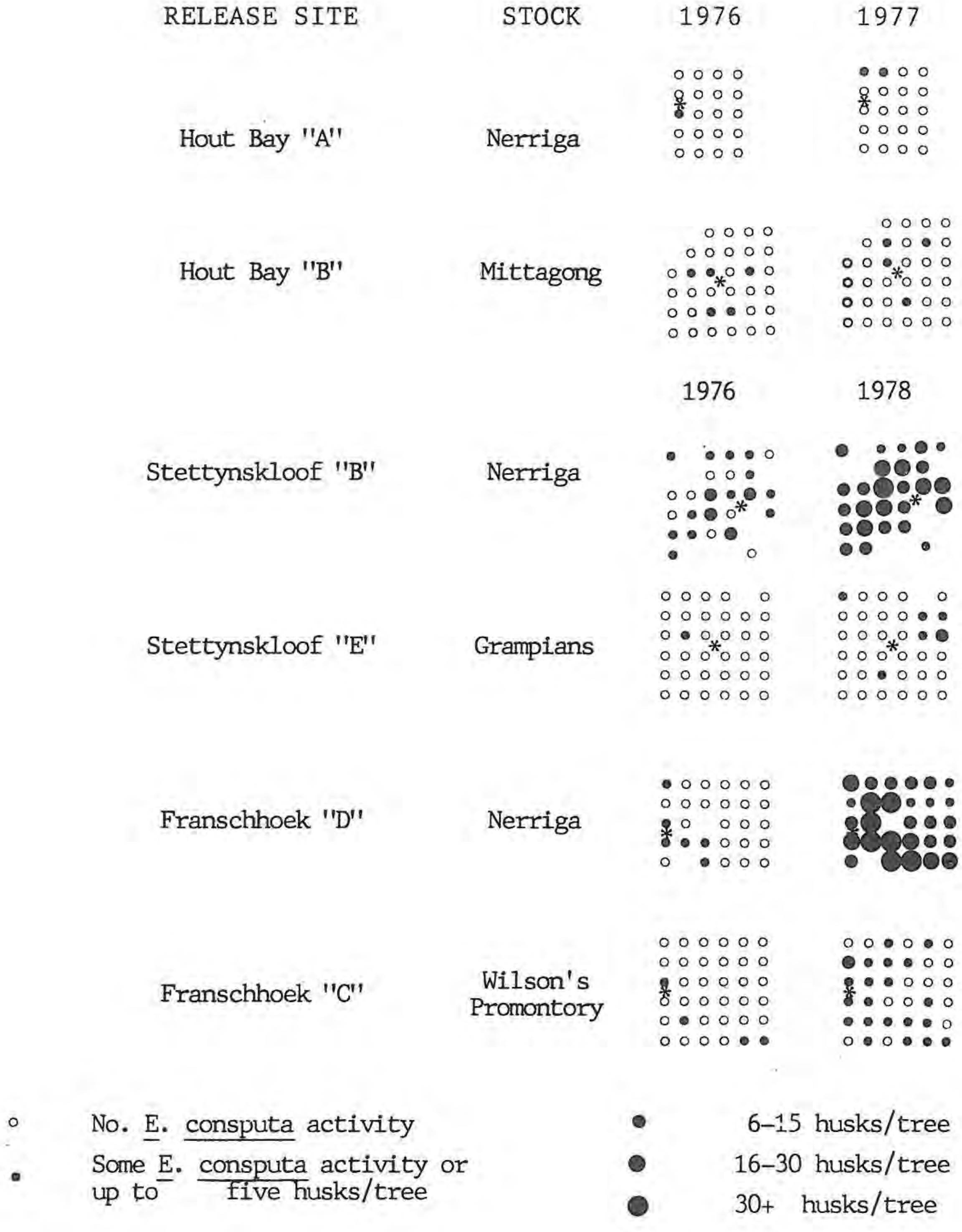


Fig. 20: A comparison, made at three different localities (Appendix 6) in the south-western Cape between 1976 and 1978, of the increase and spread of the hakea fruit weevil, Erytenna consputa, introduced from different areas in Australia (Fig. 4), on marked Hakea sericea trees in paired 0,25 hectare plots around the respective release points (*), following the release of the weevil in August and September, 1975.

Locality of release site	*E. consputa* releases		Number of trees marked	Number of husks per marked tree			Percentage of marked trees with weevil activity		
	Origin	Number released		1976	1977	1978	1976	1977	1978
Hout Bay "A"	Nerriga, N.S.W.	26	20	0,1	0,2	*	5,0	10,0	*
Hout Bay "B"	Mittagong, N.S.W.	38	33	0,1	0,1	*	11,8	7,8	*
Stettynskloof "A"	Nerriga	50	25	1,7	-	12,7	64,0	-	100,0
Stettynskloof "D"	Grampians, Victoria	34	39	0,1	-	0,3	2,6	-	15,4
Franschhoek Pass "B"	Nerriga	50	28	0,4	-	15,9	21,4	-	100,0
Franschhoek Pass "A"	Wilson's Promontory, Victoria	40	30	0,3	-	2,0	16,7	-	70,0

* Destroyed by felling

Table 12: A comparison of the rate of colonisation of the hakea fruit weevil, *Erytenna consputa*, from different regions in Australia (Fig. 4), on *Hakea sericea* at different release sites in South Africa (Appendix 6) over a three year period, following releases made during August and September, 1975.

stock from the nearby Franschhoek "D" colony (Appendix 6).

During the four years of this study only one of each of the respective colonies of the Nerriga, Mittagong and Grampians stock failed to establish. By comparison five colonies stocked with *E. consputa* from Wilson's Promontory failed to establish (Appendix 6).

Accidental felling, fire, excessive natural abortion of fruits, and the effects of the fungal pathogen, *Colletotrichum gloeosporioides* (Morris, 1982), were the main threats that hampered colonisation (Appendix 6). The threat posed by these factors increased with the age of the *H. sericea* stand.

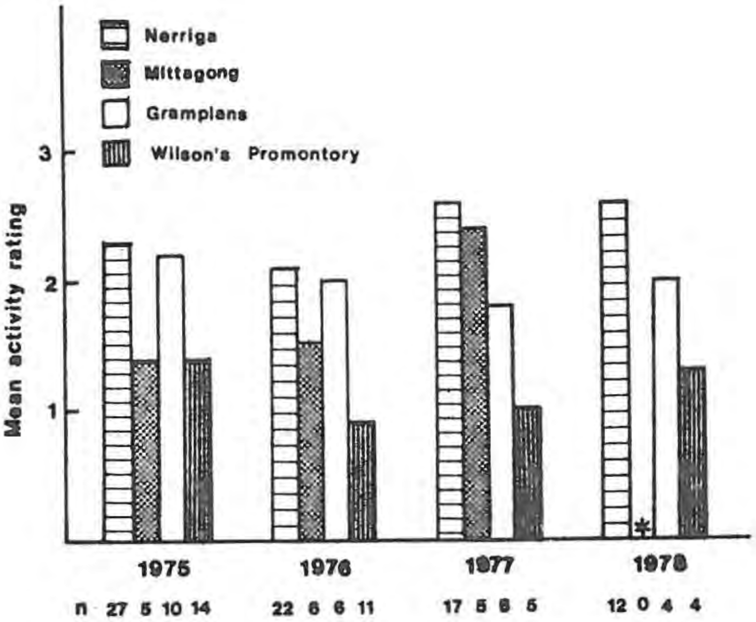


Fig. 21: A comparison of the mean annual activity rating (see Appendix 6) of the hakea fruit weevil, Erytenna consputa, from four different areas in Australia, at the different release sites in the south and south-western Cape over a four-year period following its release in August and September, 1975. The number of release sites rated each year is shown below the x-axis. (* No data.)

A significant result of this study was the fact that the Nerriga and the Mittagong stocks of E. consputa, colonised H. sericea successfully throughout its distribution in the southern, south-western and eastern Cape under all the different climatic conditions (Fig. 2). Some of these areas differ markedly from the climate in southern New South Wales (Fig. 4).

PATTERN AND RATE OF SPREAD

To supplement the observations on the pattern and rate of spread made from the grid survey studies above, a further, similar study was done at Stettynskloof "C" where counts along 100 metre long transects around the central one hectare plot were made. All the husks in the trees touching a rope, which had been strung along each transect as shown in Figure 22, were counted.

The pattern of spread of the Nerriga and Mittagong stocks, as found in the grid survey studies above, is represented by the results of the study done at Stettynskloof "C" (Fig. 22). Here, after the first generation, the E. consputa husks were plentiful in a few trees immediately around the point of release, with less and less activity away from the release point. This pattern persisted in subsequent years with most of the weevil activity always concentrated around the release point (Fig. 22). The pattern of spread did however vary, depending on the density of the fruits. At Doolhof "C" for example, where the H. sericea infestation consisted of a dense stand of small trees, each with only a few fruits, there was a more even spread of E. consputa damage throughout the whole grid (Fig. 19).

In comparison with other colonising weevil species such as Rhinocyllus conicus Froelich on musk thistle, Carduus nutans L. (Hodgson & Rees, 1976), the rate of spread of E. consputa colonies was rather slow. The rate of spread was very much dependent on tree and fruit densities, but generally after the first generation following release, E. consputa activity was found up to 20 metres from the release point. The rate of spread in the subsequent generations at Stettynskloof "C" is shown in Figure 22. While a few adults may have dispersed further, the main body of the colony had spread over 200 metres from the release point by the end of the fourth generation.

There was no evidence of any long-distance dispersal by E. consputa as found, for example, in the pine weevil, Hylobius abietis L., which can migrate up to 80 km in a single migration flight (Solbreck, 1980).

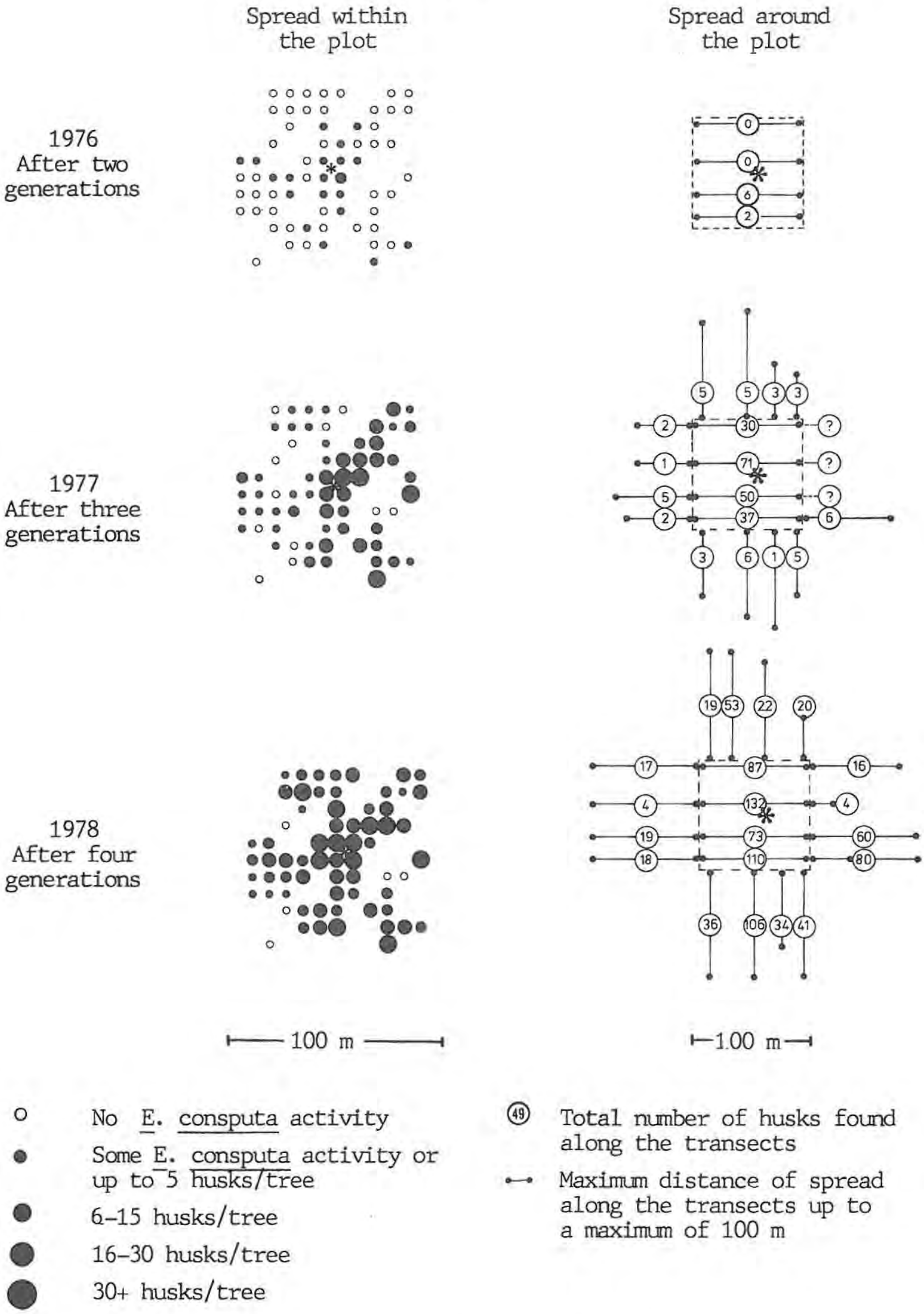


Fig. 22: The pattern of spread of a colony of the hakea fruit weevil, Erytenna consputa, from Nerriga within and around a one hectare grid at Stettynskloff "C" (Appendix 6), following the release (at *) of 50 weevils in September, 1975, as shown by the grid survey method.

CONCLUDING REMARKS

All these results have been confirmed by measures of activity that have been made regularly since 1978 at all the release sites (Appendix 6).

Following the early results of this study, all subsequent introductions of E. consputa were mostly from the Nerriga area (Table 1). As far as can be ascertained all except one of these releases, barring those subjected to felling or burning, have colonised successfully (Appendix 6). Five of the original Grampians colonies are still surviving (Appendix 6).

The only colonies of Wilson's Promontory stock still remaining, four in all, have been contaminated with other E. consputa stocks from adjacent colonies or following accidental releases. A release of 239 E. consputa adults from Wilson's Promontory, the largest single release of E. consputa ever made, was made in July, 1980 in a healthy stand of young H. sericea. Despite some evidence of larval damage found in the fruiting season that followed, no subsequent activity was found (Appendix 6).

The most likely explanation for this variable colonisation of E. consputa from the different areas in Australia is the existence of host-specific strains within the species consputa. The hypothesis is dealt with in more detail in Appendix 7 and is summarized here.

The possible existence of strains of E. consputa is suggested by colour (Fig. 30) and biological differences of the weevils from the different regions in Australia. E. consputa from Wilson's Promontory, for example, pupates both in the husks on the tree and in the ground, while in the Nerriga stocks only the latter habit is found.

The strains of *E. consputa* are most probably a result of the existence of strains of its host plant, *H. sericea*, which consists of geographically different forms occurring in, what from herbarium records (Fig. 30) appear to be, geographically isolated populations (Fig. 4). The distinctiveness in the genotypes of many of these populations was demonstrated by planting seed from the different areas in Australia, together, in a study plot at Stellenbosch (Figs. 31 and 32; Table 19). Strains of *E. consputa* from the different areas in Australia are not equally compatible with the other geographically-isolated strains of *H. sericea*.

A morphological comparison between the *H. sericea* strains from the different areas in Australia and the South African strain, together with historical indications (Neser & Annecke, 1973), strongly suggest that the South African strain originated from New South Wales. This would explain the widespread success in colonisation of the *E. consputa* from New South Wales (Nerriga) in South Africa.

6. THE IMPACT OF E. CONSPUTA ON H. SERICEA FRUIT AND SEED PRODUCTION

Once the establishment of E. consputa had been confirmed and monitored, the weevil's potential in reducing the seed production of H. sericea was investigated by measuring its impact on a population of H. sericea fruits. This was done by means of a more extensive study using fixed transects. In this study only two counts were made each season: one of young fruits at the beginning of the season, and a second at the end of the season, of the surviving fruits. In order to verify that overall fruit loss, i.e. the difference between the two counts was due to E. consputa, a more intensive study was made of the mortality factors responsible for fruit loss. These were related to fruit development which was monitored at the same time. All these studies were done at Goudini (Appendix 1).

MORTALITY FACTORS ACTING ON H. SERICEA FRUITS

Each year approximately 1 000 fruits were marked on randomly selected trees and branches within transects, and the subsequent fate of each of these fruits was followed at weekly intervals. This was made possible by dividing the fruits on the branches into small numbered groups by means of a system using pieces of coloured wool which were tied around the branches at specific points (Fig. 23). Each cause of fruit loss was recorded as soon as it first became apparent (Table 13).

For these studies the term "fruit" had to be defined in practical terms. Strictly speaking an ovary becomes a fruit when the gametes fuse. Obviously this definition could not be applied in the field, and the earliest count was only possible when the fruits had reached a mean volume of approximately 0,1 ml, i.e. approximately 10 mm in length.

The incidence of the various mortalities affecting the fruits was related to fruit development which was measured weekly by means of fruit volume. The volume of a sample of fruits was determined by means of displacement of a 1% Teepol solution in a 50 ml burette. Later in the season when the fruits were larger, a 250 ml measuring cylinder was used. The fruit stalks were trimmed off and the fruits were wetted beforehand to eliminate the problem of air bubbles. Each reading was taken 60 seconds after immersion to allow the fluid level to settle.

Fig. 23: A young Hakea sericea tree divided up into segments by means of coloured wool, so that each segment could be identified. This made it possible to follow the fate of the developing fruits within each segment individually.

The fruit sample was collected randomly along imaginary transects through the H. sericea stand. The tree nearest the tip of the front foot at five metre intervals along these transects was selected for sampling. At the first tree, the nearest fruit above head height was picked. The same procedure was followed at the next two trees along the transect but with the fruits picked at waist height, and at knee height, respectively. The routine was repeated until the required number of fruits had been collected. The fruits, after picking, were kept in plastic bags to prevent desiccation of the fruits before volume determination could be done in the laboratory. The optimal sample size was determined by plotting the standard error of the mean against the number of samples taken randomly from a single large sample (Van Ark, 1982).

Cause	Symptoms
Natural abortion	Fruit starts yellowing. No Damage apparent.
E. consputa adult feeding	Fruit starts yellowing. One or more distinctive feeding punctures on the fruit.
E. consputa larval feeding	Fruit starts yellowing. Larval entrance hole typically covered by a small mound of frass.
Rodents	Fruits hollowed or with parts bitten off. Incisor scars.
Noctuid or psychid larvae	Fruits hollowed through round hole up to 5 mm in diameter.
Heteropteran feeding	Dark blue-green blotches on the fruits.

Table 13: A list of the symptoms and causes of mortality for Hakea sericea fruits recorded in the transect study at Goudini.

E. consputa was the most important cause of fruit loss, and it was responsible for 88,8% of the total fruit loss in 1980 (Table 14). There was, however, large variation between the years. Since each fruit was recorded individually, counting error can be discounted. The variation is probably due to the fact that in 1979 and 1981 more fruits dropped from the tree between counts; these fruits were placed in the "missing" category together with the "other" factors (the latter only constituted between 1 - 2% of the total each year).

In 1981 a sample of fruits (n = 92) collected from under the trees at the beginning of the season showed that 95,6% of these fruits had been attacked by E. consputa larvae. In other words, at least 95,6% of "missing" fruits can be attributed to loss caused by E. consputa.

Mortality factor	% Total mortality		
	1979	1980	1981
Erytenna consputa (larva and adult)	62,8	88,8	75,7
Natural abortion	14,8	7,0	10,9
Missing and other	22,5	4,3	13,4

Table 14: A comparison of the contribution of the most important causes of Hakea sericea fruit loss for three years at Goudini.

If this "missing" category is added to the mortality caused by E. consputa, it is estimated that the weevil was responsible for approximately 85,3, 93,1 and 89,1% of the total fruit loss in the plot in each of the three successive years.

In figure 24 the seasonal incidence of the most important mortality factors is shown together with the pattern of survival and development of the fruits. It is clear from Figure 24 that E. consputa was the main cause of mortality, and that it became more important over the three years of the study.

As could be expected, the pattern of E. consputa larval attack in Figure 24 followed a trend similar to that of the seasonal egg-laying pattern of E. consputa described in Chapter 3 (Fig. 6). Fruits were first attacked when they had reached a volume of approximately 0,3 ml. The intensive larval attack started when the mean fruit size of the population was approximately 0,5 ml. Towards the end of the season the decline in the intensity of larval attack coincided with the first record of woodiness in the fruit sample (Fig. 24). The development of the woodiness in the fruit population was monitored with a Bellauf penetrometer (Cherret, 1968) fitted with a 1 mm diameter tip. The hardness of each fruit in the sample was tested by placing the tip of the penetrometer in the centre of the cheek of a fruit. The fruits were classified into two groups; those that were penetrated by the tip of the penetrometer, and those that withstood the maximum pressure of 1 590 bars. The latter group was no longer vulnerable to E. consputa attack.

Natural abortion of the fruits was highest while the fruits were still small at the start of the season, and decreased gradually as the fruits developed (Fig. 24). There is always a massive natural abortion of flowers and small fruits after flowering (Fugler, 1979). By the time the intensive E. consputa larval attack had started, the level of fruit abortion was comparatively low (Fig. 24).

This raises the question as to what contribution E. consputa was really making to the loss of fruit. Was E. consputa not just removing fruit that would have been aborted in any event? To answer this question a chemical exclusion trial

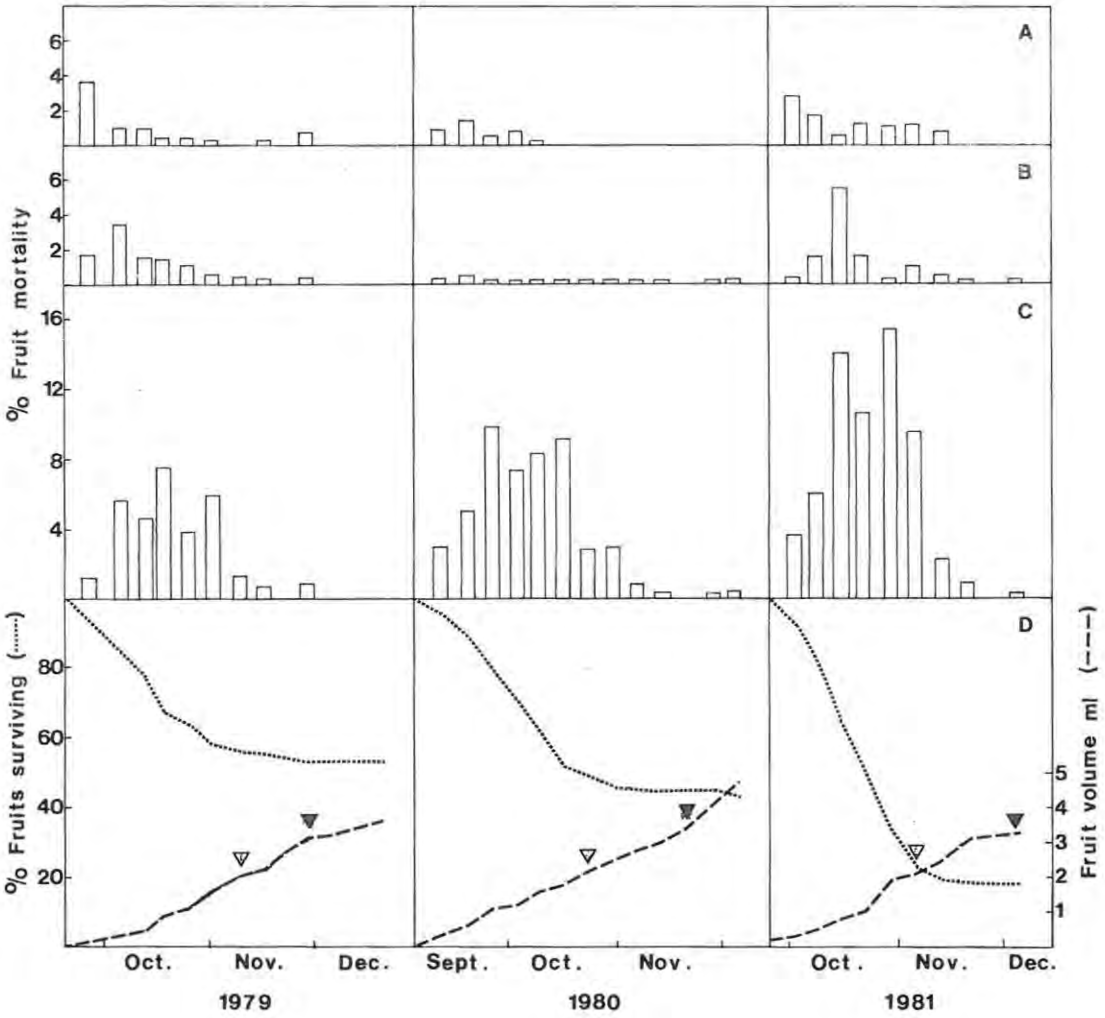


Fig. 24: The seasonal incidence of the most important factors responsible for the loss of Hakea sericea fruits namely, (A) natural abortion, (B) "missing", and (C) the hakea fruit weevil, Erytenna consputa, in relation to (D) the development of the fruit, and also their combined effect on the survival of the fruits. (▼ = Fruits start becoming woody; ▼▼ = All fruits woody and no longer vulnerable to E. consputa attack.)

was carried out. Sixteen H. sericea trees were paired off, one branch on each tree was selected, and the fruits on it were counted. The paired trees, and also the respective branches on these trees were selected to be as similar to each other as possible. One randomly selected branch from each pair was sprayed at three weekly intervals with

Sumicidin (1,5 ml/10 l) to the point of run-off. Sumicidin is a contact insecticide registered for the control of weevils in orchards (Bot & Hollings, 1982). Its efficacy in killing E. consputa adults and larvae was verified beforehand in the laboratory. The fate of the fruits on all the branches was recorded in the same way as that described above.

Table 15 shows that natural abortion in the absence of E. consputa i.e. on the sprayed branches, was only marginally higher than when the weevils were present. This table also emphasizes the contribution of E. consputa as an important mortality factor affecting H. sericea fruits.

Treatment	Fruits n	% contribution of each mortality factor					% Fruits surviving
		Natural abortion	Erytenna larvae	Missing	Erytenna adults	Other	
Sprayed	1 269	40,3	0	5,0	0,3	0,2	54,1
Unsprayed	1 153	34,6	44,2	5,6	2,3	0,7	12,6

Table 15: A comparison of mortality factors affecting Hakea sericea fruits and the survival of fruits on eight sprayed and unsprayed branches in a chemical exclusion trial at Goudini.

THE IMPACT OF E. CONSPUTA ON FRUIT PRODUCTION

Eleven, one-metre-wide transects were laid out five metres apart in the six-year old H. sericea stand, next to old H. sericea trees in which E. consputa had originally been released (Fig. 25). The transects were divided up into 50 one metre quadrats.

All the H. sericea trees in each quadrat were marked and numbered. The potential fruit production within the transects was determined by counting all the developing fruits on the

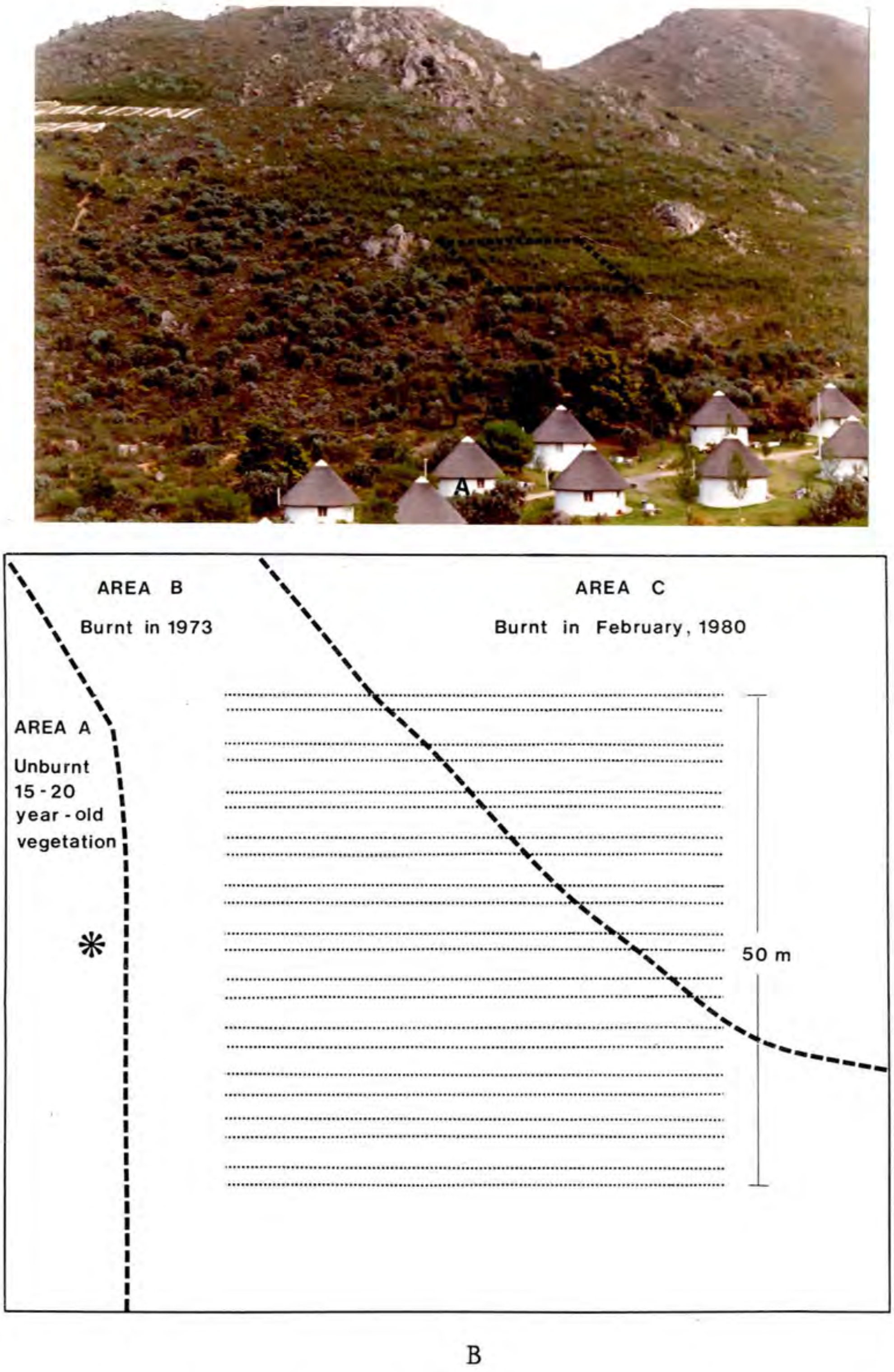


Fig. 25: (A) The study plot at Goudini in September, 1979 and, (B) a diagram of the lay-out of the eleven 1 x 50 m fixed transects (not drawn to scale) in relation to the release point (*) of the hakea fruit weevil, Erytenna consputa, and showing also the history of fires at the site. Twenty adult weevils were released there in August, 1975.

marked trees at the start of each fruiting season. These counts were done when the mean volume of the fruit population was approximately 0,3 ml, after the bulk of the fruits had naturally aborted as shown in Figure 24. The entire tree was used as a sampling unit.

A second count was made during February of each year of the mature, surviving H. sericea fruits. By subtracting the two counts the overall fruit loss could be determined. From these counts fruit production and fruit loss could be expressed either per tree or per m^2.

Counts were repeated on randomly selected trees to determine the amount of error inherent in the method. As shown in Appendix 8 there was always a tendency to undercount. The highest mean error ever incurred as 3,3%.

Fruit loss, attributable mostly to E. consputa as shown above, increased dramatically over the three year period, 1979 - 1981, from 38,8 to 81,0% (Fig. 26; Appendix 9). This increase is even more dramatic considering the fact that the potential fruit production of the trees, which were entering the reproductive phase (Fig. 1), increased, over the same period, by almost 500% from 23,4 fruits per m^2 to 134,5 fruits per m^2.

A closer estimate of the level of E. consputa activity was possible from counts made each year, in four randomly selected transects, of the number of scarred fruits (Fig. 11E) that were unsuccessfully attacked by E.consputa. This also reflected the increasing role of E. consputa as a mortality factor and by 1982, 95,6% of the surviving H. sericea fruits were scarred as a result of unsuccessful E. consputa attack (Table 16; Fig. 26 - shaded portion).

By combining the counts of scarred and successfully attacked fruits, it can be seen from Table 16 that only 0,8% of 17 769 fruits in these four transects escaped E. consputa attack in 1981 (Fig. 26).

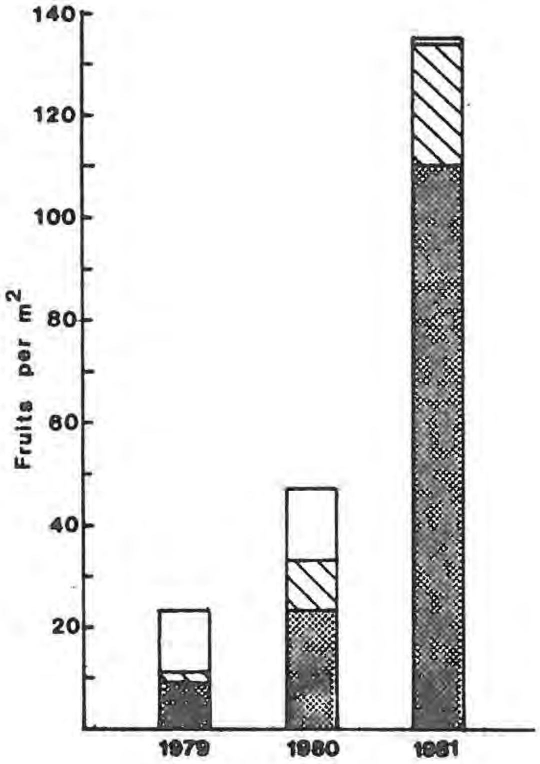


Fig. 26: Potential fruit production of six-year-old Hakea sericea trees at Goudini between 1979 and 1981, showing the fruit loss each year caused mainly by the hakea fruit weevil, Erytenna consputa (dots). The shaded portions of the histograms show the proportion of scarred fruits that were unsuccessfully attacked by E. consputa, and the clear portions represent the remainder of the surviving fruits that escaped E. consputa attack.

PATTERNS OF COLONISATION OF H. SERICEA BY E. CONSPUTA

As explained in Chapter 5, larval damage, as an index of weevil activity, is one of the easiest ways of monitoring an E. consputa population. It gives a good indication of the

Year	% Scarred fruits (n in brackets)	% Scarred & successfully attacked fruits (n in brackets)
1979	10,0 (281)	39,4 (2 211)
1980	43,0 (1 009)	78,3 (5 735)
1981	95,6 (3 373)	99,2 (17 769)

Table 16: The level of activity of the hakea fruit weevil, Erytenna consputa, as shown by counts of scarred fruits that were unsuccessfully attacked by E. consputa, and the combined counts of scarred and successfully attacked fruits in four randomly selected transects at Goudini between 1979 - 1981.

distribution of the adult population, firstly because the eggs are laid singly, and secondly because movement of the larvae relative to the size of the trees and the plot is negligible.

To determine the distribution of E. consputa activity within the plot, the percentage fruit loss in the quadrats along each transect (Fig. 25) was mapped using the (LSTATS) SYMAP Computer programme (Version 5.20 altered for execution on the B-6700, University of Delaware, June, 1976, from the Programme Library of the Division of Biometrical and Datametrical Services, Department of Agriculture, Pretoria).

Figure 27 shows that in 1979 the fruit attack, at all densities, was highest nearest the release point, decreasing with distance away from it. E. consputa was clearly still actively dispersing through the plot. In 1980 damage levels between 34 - 66% occurred throughout the plot. Islands of damage exceeding 66% were still more prevalent nearer the release point. By 1981 the colonisation of the plot was complete

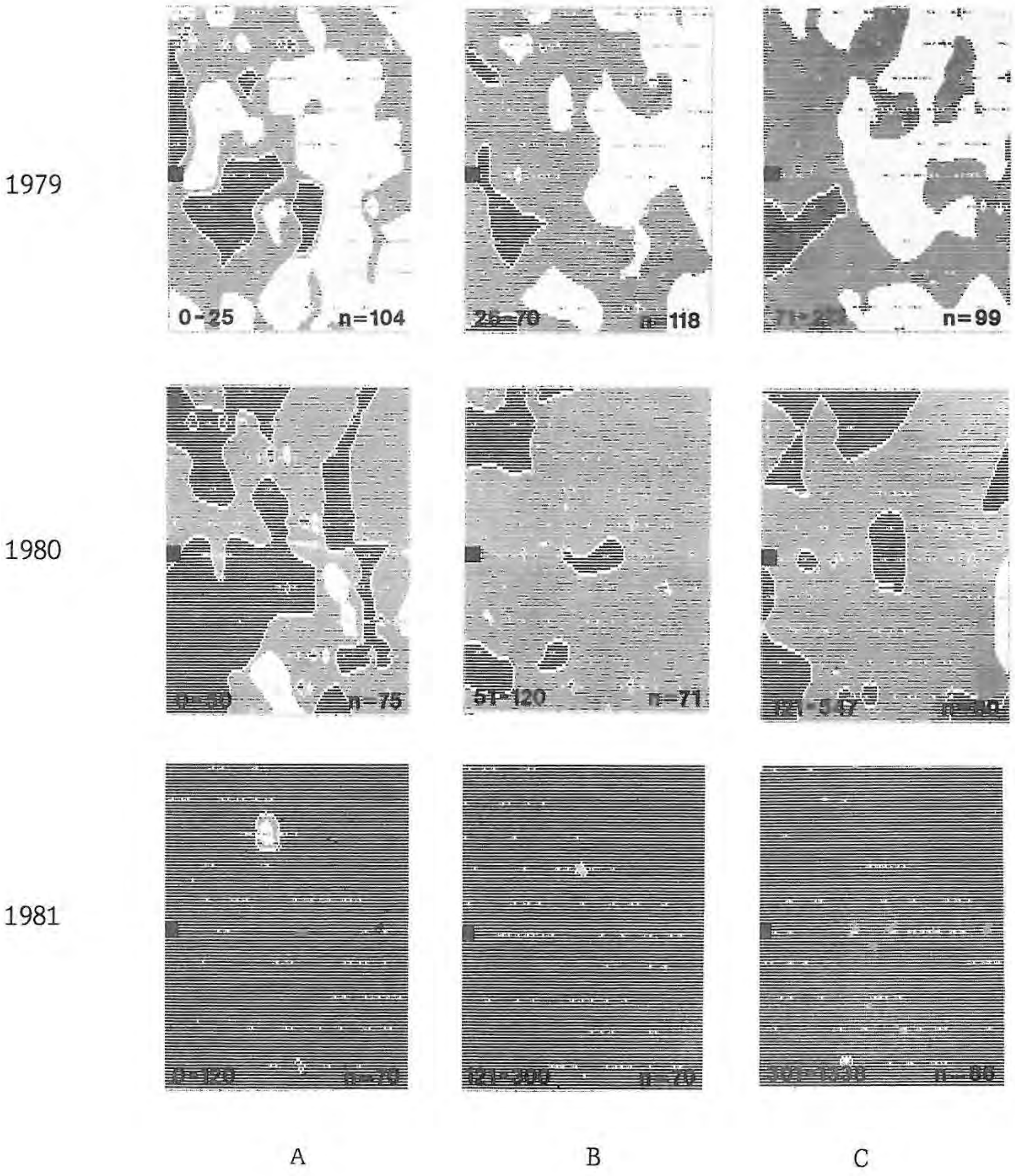


Fig. 27: The pattern of spread of the hakea fruit weevil, Erytenna consputa, into a 50 x 50 m plot infested with Hakea sericea (Fig. 25), as shown by the distribution pattern of fruit loss at three different intensities in the plot (light = 0-33%; darker = 34-66% and darkest = 67-100%), plotted with the SYMAP computer programme for three different fruit densities A, B and C (class intervals per m^2 given in the lower left hand corner), for three consecutive years.

■ = point where 20 E. consputa adults (approximately 10 females) were released in August, 1975 at Goudini.

n = total number of data points (m^2 quadrats) along 11 transects.

with fruit loss exceeding 66% in all three density classes, spread evenly over the whole plot.

The pattern of colonisation observed in this plot, is similar to that described by the more extensive grid survey method in Chapter 5. It suggests that the colonising population spreads as a cohesive body, with the individuals either walking from one tree canopy to the next or making only short flights.

THE INFLUENCE OF TREE AND FRUIT DISTRIBUTION ON E. CONSPUTA ACTIVITY

Using SYMAP the spatial distribution of H. sericea trees, young fruits at the start of the fruiting season (from the first count), and fruit loss in each quadrat were mapped.

As demonstrated by Fugler (1979) the trees are non-randomly distributed; both the trees and the fruits show a clumping in their distribution (Fig. 28). The sudden absence of trees and fruits in the upper right-hand corner of the plot in 1980 and 1981 are as a result of the fire which destroyed 617 trees and 116 quadrats (Table 17).

The tree and fruit distributions show little correlation; this is because of the variation in tree size which is dependent on density. There is a strong negative correlation between tree size (stem circumference measured 150 mm above the ground) and tree density (n = 50; r = -0,65). Since trees at lower densities tend to be larger, and since Fugler (1979) showed that there was a positive relationship between stem circumference and fruit number, trees at low densities produce relatively more and not less fruits.

The pattern of fruit loss (Fig. 28) in all three years, was very closely related to the distribution of the healthy fruits.

Fig. 28: The distribution of Hakea sericea (A) trees, (B) young fruits, and (C) fruit loss (the latter attributable mainly to the hakea fruit weevil, Erytenna consputa) in three density classes (upper class limits per m^2 given in the lower left hand corner) in a 50 x 50 metre plot at Goudini between 1979 and 1981, as plotted with the SYMAP computer programme from 550 data points (m^2 quadrats) along 11 transects (Fig. 25). A fire at the beginning of 1980 destroyed all the trees in the top right-hand corner of the plot.

■ = point where 20 E. consputa adults were released in August, 1975.

	Quadrats		Tree population		Potential fruit population^{d}			Fruit loss^{b}		Fruits^{c} surviving	
Year	Total	Number with trees	Total	m^{-2}	Total	m^{-2}	Per tree	Total	%	Total	Cumulative m^{-2}
Prior to 1979	-	-	-	-	-	-	-	-	-	828	24,1
1979	550	327	1 146	2,1	12 877	23,4	11,2	4 996	38,8	7 881	37,2
1980	434^{a}	226	529^{a}	1,2	24 569	56,6	46,4	14 275	58,1	10 294	61,0
1981	434	226	529	1,2	58 505	134,8	110,6	47 376	81,0	11 129	86,6

a = Decrease as a result of the fire (Fig. 28)
b = Due mainly to Erytenna consputa
c = To convert to number of seeds, multiply by two
d = Based on a count of developing fruits at the start of the season when the mean fruit volume is approximately 0,3 ml.

Table 17: A summary of the main data collected from the study of Hakea sericea fruit loss at Goudini (Fig. 25).

Correlation with the distribution of the trees was poor. It is concluded that E. consputa shows a strong aggregative response to the distribution of vulnerable fruits, even at lower levels of E. consputa activity as in 1979. In predator-prey models this would strongly imply non-randomness in the searching behaviour of the "predator" (Hassell, 1979), in this case E. consputa, and this topic is amplified in the discussion. This type of behaviour may explain the pattern of spread of E. consputa which suggests that as long as the female is successful in finding enough suitable fruits for egg-laying within a critical time, she tends to remain on a tree or within a "patch" in a way similar to that of parasitoids parasitizing their hosts.

Finally the percentage fruit loss due to E. consputa at the various fruit densities (Table 18) was compared. The fruit density classes used in the comparison were arbitrarily chosen each year to constitute three equal classes (Fig. 27).

There was no significant difference in the mean level of attack between the different densities in any of the years, although variation (S.D.) in the attack rates was always highest at low fruit densities, decreasing together with an increase in fruit density (Table 18). The consistency of E. consputa attack at high fruit densities follows from the aggregative response discussed above. At the lower fruit densities the consistency of attack corresponds more to a random type of searching, although the overall effect of attack, i.e. the mean rate of attack, is the same, and this is what is ultimately important.

Year	Fruit density m^2	n	$\bar{x}$ % fruit loss	S.D.	C.V.
1979	0 - 25	104	36,2	27,7	76,5
	26 - 70	118	38,0	16,2	42,6
	71 - 271	99	34,6	11,6	33,5
TOTAL		327	38,8	4,1	10,5
1980	0 - 50	75	58,6	26,2	30,6
	51 - 120	71	57,4	11,2	19,5
	121 - 547	80	58,1	11,0	18,9
TOTAL		226	58,0	3,0	5,2
1981	0 - 120	70	87,2	17,1	19,6
	121 - 300	70	82,6	8,4	10,2
	301 - 1338	86	80,5	6,4	8,0
TOTAL		226	83,4	3,4	4,1

Table 18: The mean fruit loss, due mainly to the hakea fruit weevil, Erytenna consputa, at different fruit class densities in 11 transects at Goudini between 1979 - 1981.

7. DISCUSSION

Seed predators have been used with limited success in biological control. From the world-list of biological control agents (Julien, 1982) it appears that about 39 species and/or strains of seed predators have been used in biological control programmes to date. Most of these were successfully established and 59% of them "substantially" reduced the seed production (>60%) of their hosts, but only about a quarter of them had any significant effect on population densities of the target weed; in many of these cases, this was only achieved in combination with a second agent.

In the following discussion the efficacy of seed-attacking insects in biological control is discussed in the light of predictions on the success of *E. consputa*. Key questions are:

(a) what is the maximum level of seed loss that can be expected as a result of attack by *E. consputa*?

(b) how consistently will this level of attack be maintained in the long-term?

(c) how consistent will this level of attack be throughout the distribution of *H. sericea*? and

(d) what will the effect of this seed loss be on *H. sericea* populations?

Finally, the future of *E. consputa* in the integrated control of *H. sericea*, is discussed in the context of the use of seed predators in biological control generally.

WHAT IS THE MAXIMUM LEVEL OF DAMAGE THAT CAN BE EXPECTED FROM E. CONSPUTA?

This will depend largely on the carrying capacity of the plant i.e. the number of adult E. consputa which each H. sericea tree can support throughout the year. Although there are no data to determine the carrying capacity for E. consputa, seed predators, in their native environments where their own populations are suppressed by natural enemies, achieve very high levels of seed predation. Janzen (1969) gives many examples of seed predation over 90% and approaching 100% in various Central American tree species that he studied. Neser (1968) estimated that in Australia E. consputa itself was responsible for approximately 70% destruction of H. sericea fruits. Levels of seed loss well over 90% have also been measured for many of the established seed-attacking insects used in biological control programmes (Julien, 1982). In the successful biological control programmes on plumeless thistle, Carduus acanthoides, and musk thistle, Carduus nutans, levels of seed reduction between 70 - 80% by the weevil Rhinocyllus conicus were recorded (Kok & Surles, 1975).

Barring the possible effects of density dependent factors at higher E. consputa population densities (such as a higher larval mortality resulting from increased interspecific competition for the available fruits), and based on the recorded increase in damage at Goudini from year to year, together with the fact that only 0,5% of the fruits escaped E. consputa larval attack in 1981 (Fig. 26), it is probable that E. consputa will attain almost 100% fruit predation on H. sericea in South Africa.

HOW CONSISTENTLY WILL THIS LEVEL OF ATTACK BE MAINTAINED IN THE LONG-TERM?

Despite the expected high level of seed attack, it is equally important to consider whether *E. consputa* can sustain this level of damage over a long period because the effective seed production of an *H. sericea* tree is the sum total of the fruits that it has accumulated from both good and bad fruiting seasons throughout its life-time (Fig. 1).

The consistency of *E. consputa* attack will depend largely on the nature of the equilibrium maintained by the weevil populations at, or near, the carrying capacity of the habitat. The effect of various mechanisms known in other plants to prevent consistent seed loss, may also be relevant. Important considerations with regard to the nature of the equilibrium of populations are the stability of the habitat (Southwood *et al.*, 1974; Southwood, 1977), and conditions affecting the oscillations of the populations about the carrying capacity of the habitat (May *et al.*, 1974).

Reproduction of *E. consputa* is favoured because the habitat seems to be both stable and predictable. *H. sericea* is generally long-lived (Fig. 1), and the average incidence of fires in the mountain fynbos according to Kruger (1979) varies at random between 6 - 40 years; under the present management practices burns will be done at 12 year intervals. The length of time that the habitat remains suitable for breeding (H) is therefore much greater than the generation time (T) (Southwood, 1977) of *E. consputa*. Habitat stability is therefore high. No variable fruiting (see below) has been detected in *H. sericea*, and *E. consputa* is not affected by the slight variations in flowering and fruiting times from year to year (see Fig. 12), so that there is little variation in the favourableness of the habitat each year i.e. the habitat is also predictable.

To maintain effective attack rates consistently, any fluctuations in the populations of seed predators such as *E. consputa* should be small. Monotonic damping, as discussed by Hassell *et al.* (1976), where there is an immediate return to equilibrium, or damped oscillations with a small amplitude, would be most conducive to consistent attack. Patterns or fluctuations tending towards large cyclic patterns or chaotic fluctuations, typical of insects such as Leptinotarsa decemlineata (Say) would be unfavourable because of the seed produced in years when seed predator populations were low. Although there are not data concerning density dependent mortality in E. consputa, it is most likely that with a value of $\lambda = 5{,}32$ for the finite rate of increase, E. consputa populations will always tend to remain near equilibrium (Hassell et al., 1976).

The possible long-term success of E. consputa can also be gauged by drawing an analogy between the E. consputa - H. sericea interaction and the parasitoid - host interaction. E. consputa appears to have nearly all the attributes of a successful parasitoid with a low q value (q = host population after control ÷ host population before control) as discussed by Beddington et al. (1978) namely:

a. high aggregative responses to host patches (see Chapter 6; Fig. 28);

b. high effective searching efficiencies (see Chapter 6; Table 18);

c. high degree of monophagy (Neser, 1968);

d. high degrees of synchrony with the host (see Chapter 3; Fig. 12);

e. effective attack rates (see Chapter 6; Fig. 26);

f. high egg complement (this is applicable to E. consputa under South African conditions where there is low egg parasitism - see Chapters 3 and 4);

g. low handling time;

h. high powers of dispersal between patches.

Apart from the last two characteristics which have not yet been studied, E. consputa compares favourably with all the other criteria, which indicates that it is likely to be a very effective biological control agent.

The likelihood of consistently high levels of attack is also made greater by the fact that H. sericea, for its part, does not appear to have any of the active defense mechanisms usually found in plants to overcome predispersal predation. The phenomenon of "mast" years is particularly strongly developed in woody perennials, especially in temperate regions. In these "mast" years seed production is very high, and such a year is then followed by a group of years of poor seed production (Harper, 1977). Similarly De Steven (1981) found that variable fruiting occurred in the witchhazel, Hamomelis virginiana L., which she interpreted as a mechanism of the plant to escape excessive fruit predation by the seed-infesting weevil, Pseudanthonomus hamamelidis Pierce. (The weevil has a phenology very similar to that of E. consputa.)

According to Figure 1, and from the results at Goudini (Chapter 6), it seems that once H. sericea is in the reproductive phase, it increases and maintains a high level of fruit production each year until it becomes moribund. H. sericea therefore appears to use the strategy of predator satiation. Here, because of a lack of time, the seed predator population is not able to make the maximum numerical response to the mass of fruits produced by the host plant; this allows a supernumerary portion of fruits to go free (Janzen, 1969).

The second flush of flowers produced by H. sericea later in the season (Fugler, 1979) has been considered as a possible compensatory or "defense" mechanism of the plant to supplement, if necessary, a poor fruit set of the main first flush.

This, however, seems unlikely because flowering occurs mainly on new growth and the plant is limited in time by the amount of new shoots that it can produce in the short period (three months) after the first flush. For H. sericea there has not been any evidence that the size of the second flush, which has up until now been negligible compared to that of the first flush, has increased despite the increase in E. consputa damage to the fruits of the first flush. In any event, from the egg-laying pattern in Figure 6 it can be seen that any fruits produced in the second flush will still be vulnerable to attack by E. consputa.

Therefore, information on the relative stability and predictability of the habitat, the expectations for E. consputa population fluctuations, and the apparent absence of any effective defensive mechanisms by the plant, suggests that E. consputa will maintain a consistent level of attack over a long period of time.

HOW CONSISTENT WILL THIS LEVEL OF ATTACK BE THROUGHOUT THE DISTRIBUTION OF H. SERICEA?

In contrast to the considerable geographic variation of H. sericea in south-eastern Australia (Appendix 7), H. sericea in South Africa is remarkably homogeneous and only two forms have been recognized. Both forms are equally susceptible to attack by E. consputa (Appendix 6). There is therefore no problem with variable resistance of the different taxa as found in some plants such as Lantana camara L. (Cilliers, 1982).

Apart from climatic variations from west to east throughout the distribution of H. sericea (Fig. 2) local variations in the climate may also influence flower and fruiting times of the plant. Because E. consputa development is synchronized with that of the host plant, and not with climate (see Chapter

3), maximum destructiveness by the E. consputa population is always ensured. With gorse this was one of the main failings of the seed weevil, Exapion ulicis (Forster), because during winter the weevil was in "semi-dispause" at the base of the gorse spines and it therefore did not attack the pods from the winter flowering (MacCarter & Gaynor, 1980).

Variation in the habitat itself might also be important in influencing the effectiveness of E. consputa. In the case of crofton weed, Eupatorium adenophorum Sprengel, under attack by the tephritids Praecidochares utilis Stone and Xanthacuira connexionis Benjamin, good control of infestation was achieved in the drier areas where the weed occurred, but in the wetter lowlands and highlands the weed densities for the most part remained unchanged (Julien, 1982).

Although more information is needed, two very important considerations regarding the habitat of E. consputa, namely, the homogeneity of its host plant in South Africa,and the effective synchronisation of E. consputa with H. sericea, make it likely that E. consputa attack will be consistently high in the many differing habitats throughout the distribution of H. sericea.

WHAT WILL THE EFFECT OF THIS SEED LOSS BE ON H. SERICEA POPULATIONS?

Initially the "prodigal parent" type theories, as they have been labelled by Janzen (1969), suggested that "a plant produces so much seed that variation in seed mortality is unimportant, since only one seed has to survive to produce another plant". Furthermore this argument emphasizes that every individual on death must only, on average, leave one descendent, otherwise there would be a continual increase in the number of individuals. Salisbury (1942) has countered this by pointing out that these theorists stray by placing undue stress on the average considered over a long period, and therefore, by emphasizing the average, they are led to neglect those fluctuations from which the mean is derived, and which biologically may be of far greater importance. More recently Janzen (1969) and Harper (1977), taking the view that seeds are juvenile plants and not just "plant products" (Slobodkin et al., 1967) have also argued against this, saying that seed predators, acting both before and after seed dispersal, may have a significant effect on plant populations. This also includes the influence of seed predators acting as a selective pressure for plant attributes such as seed size, number and dispersal (Janzen, 1969). In this discussion the concern is mainly with the effect of E. consputa on plant density, and on the rate of spread of the H. sericea populations.

Observations made by Janzen (1969) in Central America and successful biological control programmes using only seed-attacking insects like the weevil Rhinocyllus conicus on plumeless thistle, C. acanthoides, and musk thistle, C. nutans (Kok & Surles, 1975), have shown beyond all doubt that seed predators can influence the population density of plants. On the other hand, notable failures such as the attempt to control gorse by E. ulicis (MacCarter & Gaynor, 1980) make it clear that generalisations are not helpful.

According to Harper (1977), seed predation is only relevant in the control of a population if it carries seed density below that to which the plant population will be reduced by later density-dependent processes. Although the present study has shown that pre-dispersal predation by E. consputa is "high", it seems unlikely that E. consputa will ever, on its own, hold the accumulated seed production down to 3 - 4 seeds per m^2 which is about the maximum supportable H. sericea plant density. In 1981, alone, at Goudini, even with 81% fruit loss, 1,3 seeds per m^2 survived the season (Table 17), and accumulations over the years must eventually exceed 4 seeds per m^2. The status of H. sericea as a weed will thus be maintained if all these seeds survive.

However those seeds that survive E. consputa attack still have to contend with post-dispersal mortality which would appear to be high. In independent trials, Kluge (in litt., 1982) and Richardson (pers. comm.) estimated that only 3 - 5% of a H. sericea seed "rain " produces seedlings. Two of the main components of post-dispersal mortality are predation and the inability of the seeds to find "safe" sites for germination (Harper, 1977). Both are density-dependent. However, while in the former instance there is likely to be a positive relationship between seed mortality and predation, mortality and the availability of "safe" sites are inversely related.

In a heterogeneous habitat such as that of the fynbos the limitation of suitable "safe" sites could be especially important in the case of H. sericea seeds because these have thin testae and no true dormancy. There is no H. sericea seed bank in the soil. H. sericea seeds therefore have to germinate as quickly as possible or perish from exposure, or have a greater chance of being eaten. In the case of long-lived seeds like those of gorse, on the other hand, they have 40 years in which to find a "safe" site for germination.

By reducing the seed "rain", and therefore increasing the probability of post-dispersal mortality, E. consputa is likely to have a significant effect on plant density. Reduction of the seed "rain" by E. consputa will also limit the rate of spread of H. sericea. Seed density after dispersal typically decreases with distance from the source (Fig. 29). According to Harper (1977), a reduction in the seed crop of 50% will halve the number of seeds reaching any point in the dispersal range, thereby altering the distance from the seed crop at which any particular density of seeds will land.

From the above discussion a very important conclusion regarding the effect of seed predators on a colonising population can be clearly stated; this is, as can be deduced from

Figure 29, that while there is a threshold level for seed destruction that must be attained before there is any effect on plant density, any reduction in the seed rain is likely to reduce the speed of colonisation of a given plant population.

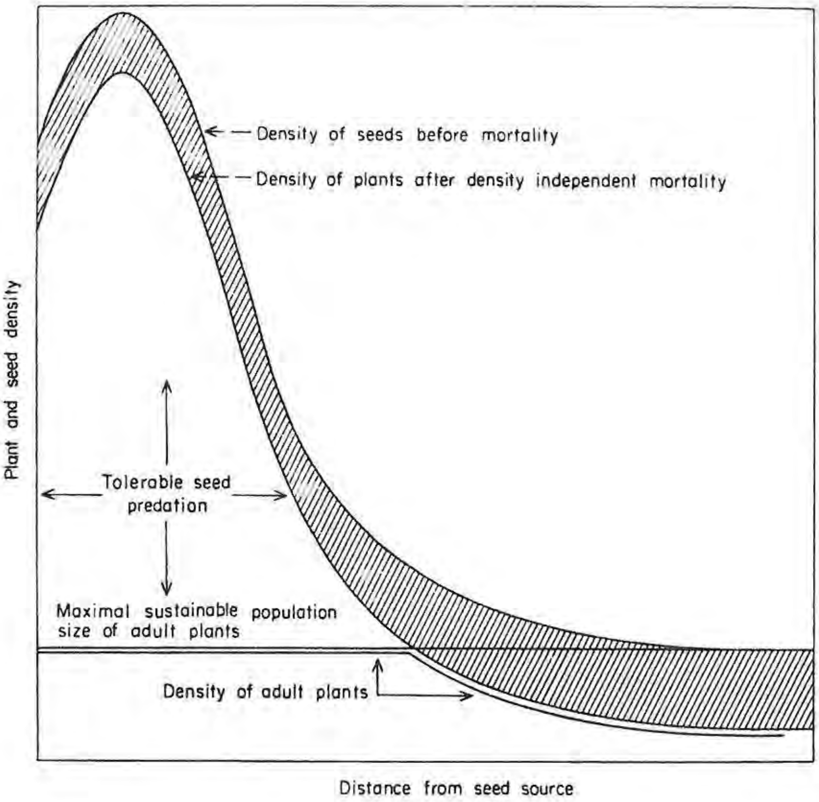


Fig. 29: An idealized relationship between seed dispersal with distance and the density of adult plants showing the level of predation that is tolerable without affecting the size of populations of adult plants. In effect seed predation is tolerable if it takes what is doomed to die through density dependent causes. (Taken from Harper, J.L. 1977. Population biology of plants. 3rd Edition. Academic Press, London).

This duscussion therefore suggests that the observed destruction of over 80% by E. consputa will drastically reduce the rate of spread of H. sericea. Although the threshold level of destruction by E. consputa for an effect on plant density has not been demonstrated, the high effective attack-rates of E. consputa, together with the potentially important post-dispersal mortality of the plant, indicate that a reduction in density of the target weed can also be expected.

SEED PREDATORS AND THE FUTURE OF E. CONSPUTA AND BIOLOGICAL CONTROL IN THE INTEGRATED CONTROL OF H. SERICEA

The following generalisations can therefore be drawn about the host plant - insect interaction that may be expected to enhance the chances of successful biological control (reduction of spread and/or plant density of the weed) using a seed-attacking insect.

a. The host plant should be short-lived, e.g. an annual.

b. The seeds of the host plant should not have dormancy; the seed bank must be minimal.

c. The host plant should not reproduce vegetatively.

d. The host plant should not have effective defence mechanisms against the seed predators such as "mast" years.

e. The plant population should be as homogeneous as possible.

f. The insect must maintain a high level of attack (at least $>60\%$). (Insect - host plant compatability as discussed in Chapter 5 and Appendix 7 is important here if maximum attack-rates are to be achieved.)

g. The attack must be consistently high over the whole distribution of the plant.

h. The attack must be consistently high in the long-term i.e. the seed predator must be well-synchronized with its host.

i. The habitat must be stable.

Apart from being a perennial, and apart from the consistency of attack of *E. consputa* throughout its distribution, which must still be confirmed, all the other attributes apply to either *H. sericea* or *E. consputa*. This, together with the results of this study and the predictions above, show that there is good reason to be optimistic about the potential for success of *E. consputa*, and that other agents apart from the hakea seed moth, *Carposina autologa*, and the hakea leaf weevil, *Cydmaea binotata*, which have already been established, may prove unnecessary, especially in view of the progress being made with mechanical clearing (Fig. 3) and the increasing importance of the fungus *C. gloeosporeoides*.

In order to verify these predictions the most pressing need at the moment is for the complete integration of biological control with all other methods of control. This means that the contribution of *E. consputa* should be maximized as quickly as possible by way of an intensive distribution programme.

The further distribution of *E. consputa* can take place from the approximately 90 colonies that have survived from the release listed in Appendix 6. Many of these are now being protected as so-called hakea "reserves". These reserves are 5 - 10 ha blocks of *H. sericea* around the respective release points; the reserves are recognized by the forestry officials and are mapped as such on their conservation plans. Where possible, precautions have been taken to protect the reserves against fires. The reserves, which are strategically placed throughout the *H. sericea*-infested areas, serve as permanent breeding centres for *E. consputa*. Apart from the normal dispersal of *E. consputa* that occurs from these reserves, an intensive campaign must now be launched to fill the gaps in the present distribution of *E. consputa* between the various reserves. This can be done quite easily by picking and distributing husks in the non-breeding season when the weevils are mainly sheltering. Unskilled labour can be used for this purpose. It is estimated that 20 man-days collecting at a thriving colony, could yield up to 3 000 weevils which would be sufficient to ensure the effective distribution of *E. consputa* at most of the forest stations; this is about half the total number of weevils that were originally imported from Australia to establish *E. consputa* throughout the Cape (Table 1). Because of the ease with which *E. consputa* can be spread, approaches can also be made to other interested parties, such as the Mountain Club of South Africa, to encourage its members to assist with this phase of the work.

Although most of the research required has been completed, two matters still need immediate attention. Firstly, levels of *E. consputa* attack must be determined at a number of release sites or reserves throughout the distribution of *H. sericea* to verify the consistency of attack. Secondly, the build-up and spread of *E. consputa* populations in young *H. sericea* stands after fire must be determined. This is a critical period with regard to the control of seed production, because if there is a time-lag between the regeneration and spread of the *E. consputa* populations and production of seed by the young plants, this will result in low initial attack rates; any subsequent effect of *E. consputa* therefore, no matter how spectacular, will be obliterated by the seed store already accumulated.

This information will also be useful in deciding how successful *E. consputa* would be in suppressing the threat posed by odd, scattered plants that regenerate from seed following the initial clearing and burning operation of mechanical control. If biological control is successful in controlling seed production on these plants it would save the need for costly follow-up work which is the major problem associated with mechanical clearing.

It is therefore suggested that, apart from the limited research outlined above, an all-out effort should now be made to maximize the effect of E. consputa together with the other two biological control agents over the next three years, and that at the end of this period further requirements for biological control should be reconsidered, based on the overall performance of the established agents and the progress of other methods of control. It is also important for the biological control of weeds in South Africa and in the rest of the world that the success obtained with E. consputa should be widely publicized.

8. SUMMARY

Hakea sericea is a shrub, introduced into South Africa from south-eastern Australia, that is now invading the indigenous "fynbos" vegetation in the Cape mountains. Presently an area of 480 000 hectares is affected. One of the main factors contributing to the success of H. sericea as a weed is its copious seed production. The seeds are accumulated on the plant throughout its life-time. When the plant eventually dies, usually after a fire, the fruits dehisce and all the seeds are released within the space of a few days, resulting in seed densities of up to 7 500 seeds per m^2. Dense, impenetrable stands of H. sericea develop which suppress the indigenous vegetation. Apart from the labour intensive mechanical clearing of H. sericea, biological control appears to be the only other means of control.

This study deals with the post-release evaluation of the effectiveness of the first successfully-established, biological control agent, the hakea fruit weevil, Erytenna consputa. Most of the damage is done by the larval stage of the weevil which attacks the young developing fruits, thereby reducing seed production.

Some additional basic biological and ecological information pertinent to the post-release studies was collected. Although adult feeding by E. consputa decreases towards winter, the adults keep feeding on buds and succulent growth throughout the year. At breeding time flowers, and to a very limited degree, small fruits, are also included in the diet. The mean fecundity for two egg-laying seasons was 227,1 ± 16,1 eggs per female with more eggs being laid during the second season. Egg-laying started towards the end of July or during August, and built up to a mean daily egg-laying rate of 1,5 eggs per female per day during October. Despite variations in the H. sericea fruiting season from year to year, larval attack was always well-synchronized with fruiting on the plant which ensured high effective attack rates. Each larva destroyed

1 - 3 fruits.

Mortality of E. consputa was highest in the larval and pupal stages. Larval mortality, mostly plant-related, was highest at the beginning and at the end of the season. Adult mortality over the first two years appeared to be low. Despite an overall mortality of 92,1% for all the immature stages, it was calculated that the E. consputa populations have a high finite, annual rate of increase in South Africa ($\lambda = 5{,}32$). Populations of E. consputa, capable of causing significant damage, can be expected at release sites 4 - 5 years after release.

Variable success was achieved with the establishment of E. consputa from the different climatic areas in Australia. This was attributed mainly to the incompatability of certain identifiable strains of E. consputa (from those different areas) with the particular strain of H. sericea in South Africa. The E. consputa from the Nerriga area south of Sydney, New South Wales, established most readily on H. sericea throughout its distribution in South Africa. The colonies of E. consputa spread slowly around the release points (up to nine hectares around the release point after four generations) with little indication of any active dispersal.

E. consputa was shown to be the most important mortality factor affecting the developing H. sericea fruits; it accounted for more than 80% of the overall mortality of the potential fruit crop following the "normal" mass abortion of flowers and developing ovaries. At the main study site fruit loss, attributable mainly to E. consputa, increased from 38,8 to 81,0% over three years despite an increase of almost 500% in the potential fruit production of the growing H. sericea trees. The pattern of fruit loss within the study plot showed that E. consputa had a high aggregative response, and that the overall E. consputa attack rate was the same at both high and low fruit densities in a given year.

Finally the potential of *E. consputa*, and seed predators in biological control generally, was assessed using the results from this study, together with information from the literature. Attributes of both the target plant (e.g. seed dormancy) and the seed predators (e.g. level and consistency of attack rates), that were conducive to the effective control of the plant populations, were considered. From this it is predicted that *E. consputa* will drastically reduce the rate of spread (or colonisation) of *H. sericea* in South Africa, and that it will most likely also reduce the plant density of subsequent *H. sericea* generations.

Only limited further research on *E. consputa* is proposed. The main emphasis now should be to distribute *E. consputa* (and the two other biological control agents) as quickly and as widely as possible to maximize their effects. The overall progress of these insects together with that of the mechanical clearing programme should then be reviewed in three years time to decide if any new biological control initiatives are needed.

Appendix 1. Details of the main study sites.

Name of site	Situation	Description of *Hakea sericea* stand
Florabult 18°53'E 33°58'S	Lower, western-facing slope of Stellenbosch Mountain	Medium dense stand of trees established after a fire in 1976
Coetzenburg 18°53'E 33°58'S	Lower, northern-facing slope of Stellenbosch Mountain	Medium dense stand of trees that established after a fire in 1975. Gumosis disease absent
Goudini 19°15'E 33°40'S	Eastern-facing slope of Badsberg Mountain	Various aged plant populations as shown in Fig. 25

Appendix 2 - 4. A summary of the field data on egg and larval mortality of the hakea fruit weevil *Erytenna consputa* at Coetzenburg in 1977 (Appendix 2), and Florabult in 1978 and 1979 respectively (Appendices 3 and 4). The table shows instances of mortality in the different stages.

Appendix 3 and 4 show that a high proportion of the field data was discarded. Most of that recorded as "Eggs missing" was as a result of leaves with eggs that dropped off. If no larva was found it was assumed that the egg had fallen off before it had hatched. "Data lost" referred mostly to cases where the original release tree could not be found, material taken to the laboratory was mislaid or where field notes made it impossible to make any reasonable conclusion.

The only proportion of the discarded results that could have meaningfully influenced the results was the "Missing fruits" category. In 1978 this constituted a significant proportion of the total mortality (11%), and comprised mostly those cases where the egg had hatched, and where a nearby fruit was missing. Most of these fruits probably contained larvae (see text). Some of the older fruits could possibly have been dislodged by rats.

Appendix 2 - Mortalities 1977

			Mortalities																							Data discarded				
						Approximate larval instars																								
			Eggs			I				II					III					IV										
Release number	n	Date from which eggs started hatching	Either infertile or not viable	Possible predation	Total	Fail to penetrate	Fruit with larva aborted	Possibly due to rats	Total	Lost searching for "new" fruit	Fruit with larva aborted	Possibly due to rats	Dead in fruit	Total	Lost searching for "new" fruit	Fruit with larva aborted	Possibly due to rats	Dead in fruit	Total	Parasitism	Total	Larvae failing to penetrate hardening fruits (all instars)	Total	Number of larvae to pupate	Total number of larvae used for data	Eggs missing or damaged	Fruits accidentally picked	Data lost	Fruit with larva missing	Total
1	No data	Sept. 9	No data								11		2	13	2				2				15	15	30	No data				
2		25				7			7	2	1			3	8		1	1	10	4	4		24	25	49					
3		Oct. 1				2			2	1	1		2	4	3		2	5d	10				16	32	48					
4		9				5			5	2		1	1	4	4		1	4e	9	1	1		19	39	58					
5		17				3			3			2b	4	6	12		4c	2	18	2	2		29	22	51					
6		23				2	1	1a	5				1	1	8	1		5	14	3	3		23	30	53					
7		28				1			1						2				2	1	1	17	21	31	52					
8		Nov. 4																				40	40	15	55					
Total						20	1	2	23	5	13	3	10	31	39	1	8	17	65	11	11	57	187	209	396					

a = 1 from Heliothis competition; b = 2 from Heliothis competition; c = 4 from Heliothis competition; d = 1 from competition between two E. consputa larvae; e = 2 from competition between two E. consputa larvae and from Heliothis competition.

Appendix 3 - Mortalities 1978

Release number	n	Date from which eggs started hatching	Mortalities																					Number of larvae to pupate	Total larvae used for data	Data discarded				
			Eggs			Approximate larval instars																Larvae failing to penetrate hardening fruits (all instars)	Total							
						I				II					III					IV										
			Either infertile or not viable	Possible predation	Total	Fail to penetrate	Fruit with larva aborted	Possibly due to rats	Total	Lost searching for "new" fruit	Fruit with larva aborted	Possibly due to rats	Dead in fruit	Total	Lost searching for "new" fruit	Fruit with larva aborted	Possibly due to rats	Dead in fruit	Total	Parasitism	Total					Eggs missing or damaged	Fruits accidentally picked	Data lost	Fruit with larva missing	Total
1	55	Aug. 23	3	2	5	5			5	1	19			20	1	1		1	3				33	5	38	12	4	1		17
2	62	29	10		10	21			21		3	2	3	8									39	1	40	12	1	6	3	22
3	61	Sep. 5	2		2	6		2	8		23			23		2			2				35		35	13	2	1	10	26
4	59	12	1		1	16			16	5	2	3		10			1		1				28	4	32	8	2	7	10	27
5	49	19	1		1	16			16	1			1	2	1				1				20	3	23	15		10	1	26
6	50	28	1		1		1	1	2	3	2		2	7	5			3	8	1	1	1	20	10	30	14			6	20
7	60	Okt. 5	4	2	6	4		2	6	2	2		2	6	2	1			3				21	15	36	4		1	19	24
8	63	17	5	1	6	5			5	1	1	2		4	4	1			5	2	2	5	27	21	48	11	1	3		15
9	66	29	2	1	3	10			10						2				2	3	3	13	31	14	45	11		8	2	21
10	67	Nov. 2	1	2	3	9			9				1	1	1				1	1	1	28	43	6	49	18				18
11	56	10	5	2	7	3			3													34	44	3	47	3		5	1	9
12	61	28	2	6	8	3			3											6	6	34	51	1	52	5		4		9
13	28	Dec. 12	1	1	2	8			8								1		1	1	1	14	26		26	3				3
Total	737		38	17	55	106	1	5	112	13	52	7	9	81	16	5	2	4	27	14	14	129	418	83	501	129	10	46	52	237

Appendix 4 - Mortalities 1979

			Mortalities																							Data discarded				
						Approximate larval instars																								
			Eggs			I				II					III					IV										
Release number	n	Date from when eggs started hatching	Either infertile or not viable	Possible predation	Total	Fail to penetrate	Fruit with larva aborted	Possibly due to rats	Total	Lost searching for "new" fruit	Fruit with larva aborted	Possibly due to rats	Dead in fruit	Total	Lost searching for "new" fruit	Fruit with larva aborted	Possibly due to rats	Dead in fruit	Total	Parasitism	Total	Larvae failing to penetrate hardening fruits (all instars)	Total	Number of larvae to pupate	Total larvae used for data	Eggs missing or damaged	Fruits accidentally picked	Data lost	Fruit with larva missing	Total
1	25	Sep. 20	2		2	3			3		15		1[a]	16									21	0	21	2	1	1	1	4
2	37	25	2		2	5			5	2	16	1		19									26	4	30	6		1		7
3	51	Okt. 1	6		6	4			4		9	1		10	4				4				24	8	32	3		16		19
4	24	9				5			5		2			2	3	1			4				11	6	17	4	1	1	1	7
5	32	17													3		4		7			5	12	9	21	11				11
6	32	23				1			1			1		1	4		3	1	8			3	13	6	19	9		4		13
7	43	28	3	1	4							4		4		2	3		5			4	17	10	27	5		11		16
8	29	Nov. 23	1	1	2	2		1	3			1		1			1		1			8	15	8	23	3		3		6
Total	273		14	2	16	20		1	21	2	42	8	1	53	14	3	11	1	29	0	0	20	139	51	190	43	2	37	1	83

a = Heliothis sp. interference

Appendix 5. The calculation of the hakea fruit weevil, Erytenna consputa, populations after successive generations, based on the equation $N_{t+1} = 5,32\ N_{a_t} + 3,87\ N_{b_t}$ in Chapter 4, following the release of 50 adults.

Field generation	Equation Parameters					
	From (10) $5,32\ N_{a_t}$	From (11) N_{b_t}	From (10) $3,87\ N_{b_t}$	From (10) N_{t+1}	Log N_{t+1}	From (1)
0 (1975)	50			50	1,70	–
1	216		45	261	2,42	5,22
2	1 149	194	174	1 323	3,12	5,07
3	6 113	1 034	752	6 865	3,84	5,19
4	32 522	5 501	4 002	36 525	4,56	5,32
5	173 021	29 270	21 292	194 314	5,29	5,32
6	920 475	155 719	113 277	1 033 752	6,01	5,32
7 (1982)	4 896 927	828 427	602 634	5 499 561	6,74	5,32

Appendix 6 The activity and fate of colonies of the hakea fruit weevil, *Erytenna consputa*, from the different areas in Australia at all the release sites in southern, south-western and eastern Cape.

Activity rating for *E. consputa* colonies.

3 - High 50+husks/man/15 min.
2 - Medium 26 - 50 husks/man/15 min.
1 - Low 1 - 25 husks/man/15 min.
0 - No activity

Fate of *E. consputa* colonies.

C - *Hakea sericea* felled.
B - Site burnt.
D - *H. sericea* decimated by disease.

Factors influencing activity of *E. consputa*

F - Fruiting severely restricted by the fungal disease, *Colletotrichum gloeosporioides*.

M - Colony contaminated by weevils of another stock, either accidentally or from a nearby release site. Subsequent ratings in parenthesis.

N - A new release made at the site.

A - *H. sericea* setting fruit poorly.

Erytenna consputa			Location of release site		State or fate of release after successive generations following release						
Site number	Number released	Release date	Mountain range	Locality	1	2	3	4	5	6	7
A. NERRIGA / BRAIDWOOD / OALLEN / NOWRA DISTRICTS, NEW SOUTH WALES											
2	76	Sept 1975	Jonkershoek	Banhoek "B"	2	C					
4	54		Jonkershoek	Botmaskop	2		3		3		
6	40		Simonsberg	Rhodes Fruit Farm "B"	2				2		
7	25		Stellenbosch	Jonkershoek	2	C					
17	100		Hottentotsholland	Sir Lowry's Pass	2	2		3		B	
18	20		Groenland	Lebanon Forest Res.	3	3		3		3	3
22	120		Kleinriviers	Witteklip	2	2A	2A	1		1	1
25	50		Du Toitskloof	Elandspad	2	2	3			3	
26	50		Du Toitskloof	Stettynskloof "A"	3	3			3		
27	50		Du Toitskloof	Stettynskloof "B"	2	3		3	3		
28	50		Du Toitskloof	Stettynskloof "C"	3	3	3	3	3		
30	50		Du Toitskloof	Stettynskloof "D"	3		3	3		C	
33	100		Limiet	Doolhof "C"	2A	3A	3	3	3		
37	26		Constantia	Hout Bay "A"	1A	1	1	C			
40	50		Franschhoek	Franschhoek Pass "B"	2	1		B		2	
42	20		Franschhoek	Purgatory "B"	2	3F	3F	3	3	3	
44	40		Franschhoek	Purgatory "C"	2	3	3	3	3	3	
46	40		Franschhoek	Franschhoek Pass "D"	2	3		3		3	
48	40		Stettyns	Bundu Farm "B"	2		3	C			
49	100		Elandskloof	Mooiplaas	1		B			2	3
50	60		Slanghoek	Witelsrivier	3	3	3	3		3	3
51	80		Badsberg	Ruigtevlei	3	1	B	0	0	0	
52	20		Badsberg	Goudini	3	3	3	3	3	3	3
55	60		Attakwaskloof	Voortrekker Monument "A"	2	1A	3M		B		
58	20		Outeniqua	Waboomskraal "B"	3	3	3		3	3	
59	67		Outeniqua	Montagu Pass	3	1D	0				
66	40		Signal Hill	Grahamstown	2	1A	3	B	3	3	
69	200		Du Toitskloof	Wemmershoek "C"	3		3		3	3	3
76	50	Aug 1977	Klein Swartberg	Waterkloof "A"	3		C				
77	50		Klein Swartberg	Waterkloof "B"			C				
78	50		Outeniqua	Ruitersbos	3		2A	1			
79	50		Outeniqua	Teewaterberg	1D						
80	50		Outeniqua	Brookesbosberg	3				1D		
81	100		Outeniqua	Keurboomsrivier	3						
82	50		-	Grahamstown Distr.	2	2	2	3			
83	50		Elandsberg	Longmore	B						
84	100		Tsitsikamma	Jagersbos	3A		3		2A		
85	41		Tsitsikamma	Joubertina	3		3				
86	47		Outeniqua	Afgunstrivier	3			3	3		
87	50		Outeniqua	Croxden	3		3	3			
88	50	Sept 1977	Kleinriviers	Walsh Acres				3	3		
89	50		Kleinriviers	Good Luck	3			3	3		
90	100		Swartberg	Caledon Garden	3	B					
91	50		Swartberg	Swartrivier					B		
92	50		Swartberg	Dieprivier					N		
93	50		Swartberg	Middleton	3			3			
94	100		Franschhoek	Franschhoek "A"	2	3		3			
95	50		Groenland	Welgegund	3		3				

Erytenna consputa			Location of release site		State or fate of release after successive generations following release						
Site number	Number released	Release date	Mountain range	Locality	1	2	3	4	5	6	7
96	50	Sept 1977	Hottentotsholland	Knorhoek	1A			0			
97	50		Hottentotsholland	Vergelegen	2	3		3			
98	50		Helderberg	Nature Reserve	3		C			2	
99	50		Stettyn	Stettyn		3			3		
100	50		Stettyn	Twistniet		2			1		
101	50		Riviersonderend	Kykuit		1		2			
102	50		Stettyn	Brandvlei "A"			2	3	3		
103	50		Stettyn	Brandvlei "B"		2		2			
104	50		Stettyn	Brandvlei "C"		3		3			
105	50		Stettyn	High Noon							
106	50		Riviersonderend	Villiersdorp				3			
107	50		Riviersonderend	Helderstroom		3					
108	50		Riviersonderend	Genadendal		3	B				
109	50		Riviersonderend	Oubos		3		B			
110	50		Riviersonderend	Soetmelksvlei		3		B			
111	72 & 20		Constantia	Peterhof	3	3		3	3		
112	50		Stettyn	Aasvoëlberg	3			3			
113	21		-	Devon Valley		2	3	3	3		
114	2		Outeniqua	Ruitersbos	C						
115	100		Outeniqua	Molenrivier "D"	3		3				
122	50	July 1978	Tsitsikamma	Karreedouw Pass		1F	1F	C			
123	50		Tsitsikamma	Krakeel		B					
124	50		Vleitjies se Berg	Die Vlugt		3		3			
125	15		Vleitjies se Berg	Uitvlug		3		3			
127	45		Outeniqua	Onbedacht		3					
137	33	July 1979	Franschhoek	Franschhoek "B"	3	3					
142	25	June 1981	Hottentotsholland	Vergelegen							
144	105		Swartberg	Caledon							
145	99		Swartberg	Caledon							
146	91		Kleinriviers	Jaswinda	2						
147	56		Riviersonderend	Middelplaas							
148	130		Outeniqua	North Station	2						
149	130		Outeniqua	Elandsrivier	3						
150	130		Outeniqua	Schoonberg	2						
151	130		Outeniqua	V.d. Merwe	1						
152	130		Outeniqua	Bergplaas	1						
B. MITTAGONG, NEW SOUTH WALES											
35	40	Sept 1975	Kalkbaai	Silvermine	1	1	2		2		
36	38		Constantia	Houtbay "B"	1A	1A	1A	C			
53	96		Klein Swartberg	Peak Plaats	1	3	3				
56	40		Attakwaskloof	Voortrekker Monument "B"	2	1A	3M		B		
62	48		Outeniqua	Molenrivier "C"	2	3	3		3	3	
63	47		Tsitsikamma	Kareedouw	C	0A	0				
71	75	Aug 1976	Swartberg	Speelmansrivier		3		2B			
72	69		Riviersonderend	Greyton	2	3	3		3		
74	68		Hottentotsholland	Vergelegen	3						
121	58	Aug 1978	Outeniqua	Kleinplaat			0A		B		
126	60		Vleitjies se Berg	Onbedag		3					

Erytenna consputa Site number	Number released	Release date	Location of release site: Mountain Range	Locality	State or fate of release after successive generation following release: 1	2	3	4	5	6	7
C. GRAMPIANS, VICTORIA											
1	68	Sept 1975	Jonkershoek	Banhoek "B"	3	C					
8	50		Stellenbosch	Coetzenburg "B"	3				2	2	
11	50		Helderberg	Alto "B"	2	3	2F	1F	1D		1D
12	210		Helderberg	Blyhoek "A"	2		2F	3		3	
15	50		Hottentotsholland	Vergelegen "B"	2	2B					
29	34(30)		Du Toitskloof	Stettynskloof "E"	2	1		1N	C		
31	100		Limiet	Doolhof "A"	3	3	3	3	3		
54	100		Klein Swartberg	Peak Plaats	2	2	2		C		
57	20		Outeniqua	Waboomskraal "A"	1A	1A	0		0		
70	80		Du Toitskloof	Wemmerhoek "D"	2		2				
D. CANN RIVER, VICTORIA											
13	120	Aug 1974	Helderberg	Blyhoek "B"			3		3	3	3
73	84	Sept 1976	Stellenbosch	Paradyskloof	2	2	M	(3)	(3)	(3)	
154	79	Aug 1978	Tsitsikamma	Stormsriver		2					
E. WILSON'S PROMONTORY, VICTORIA					5	6	7	8	9	10	11
9	74	Mar 1971	Stellenbosch	Coetzenburg "A"	2	M	(3)	(3)	(3)	(3)	(3)
67	200		Du Toitskloof	Wemmerhoek "A"		M	(3)	(3)	(3)	(3)	(3)
					1	2	3	4	5	6	7
60	20(48)	Jul? 1974	Outeniqua	Molenrivier "A"		1N	1C				
3	50	Jun 1975	Groot Drakenstein	Banhoek	1	B					
5	32	Sept 1975	Simonsberg	Rhodes Fruit Farm "A"	1	C					
10	50		Helderberg	Alto "A"	2	1	1D	1D		0	
14	50		Hottentotsholland	Vergelegen "A"	1		B	0			
16	8?		Helderberg	Lourensford	2	0C	0				
32	100		Limiet	Doolhof "B"	2	2	2	1		0	
39	50		Franschhoek	Franschhoek Pass "A"	0	0				B	
41	50		Franschhoek	Purgatory "A"	2	1F	0D	0			
45	40		Franschhoek	Franschhoek Pass "C"	1	2		3M		(3)	
47	40		Aasvoëlberg	Bundu Farm	2	1	1	B			
61	44		Outeniqua	Molenrivier "B"	1	0	0				
64	30		Outeniqua	Goudveld	1	0F	0				
65	60		Tsitsikamma	Stormsrivier	1	0	0				
68	180		Du Toitskloof	Wemmershoek "B"	1	2		C	3		
153	239	Jul 1980	Groot Drakenstein	Groot Drakenstein	1	0					

Appendix 7. STRAINS OF *E. CONSPUTA*

The difference between the colonising success of the stocks from the different areas in Australia, may be explained by the existence of different strains of *E. consputa*.

The existence of sub-specific entities is well established (Mayr, 1958), and in biological control the importance of the selection of the best strain of a particular biological control agent for maximum effectiveness is widely accepted (Goeden, 1978; Marshall *et al.*, 1980; Room, 1980; Winder & Harley, 1978). Ecological races of the thistle seed weevil, *Rhinocyllus conicus*, were recognized when *R. conicus*, which had been collected on musk thistle, *Carduus nutans*, colonised poorly on milk thistle, *Silybum marianum*, although this was a 'known' host of *R. conicus* (Goeden, 1978). Harris (1980b) also suggests that the failure of leafy spurge insects in Canada was due to the occurrence of host races.

The existence of strains of *E. consputa* is suggested by the fact that colour and biological differences between populations from the different areas in New South Wales and Victoria are known and that there is good reason to believe that the host plant species, *H. sericea*, itself, may comprise a number of strains.

All *E. consputa* adults reared from *H. sericea* fruits at Wilson's Promontory (Fig. 30 - middle) are more red-brown than *E. consputa* from the Nerriga area (Fig. 30 - top). There is some confusion in the accessions with Wilson's Promontory material which came from collections made of the adult weevils sheltering in husks on *H. sericea*.

In these series there are both "true" Wilson's Promontory type *E. consputa*, and a colour form closer to that of the Nerriga stock. The fact that the one series of 30 mounted *E. consputa* reared from *H. sericea* fruits at Wilson's Promontory are

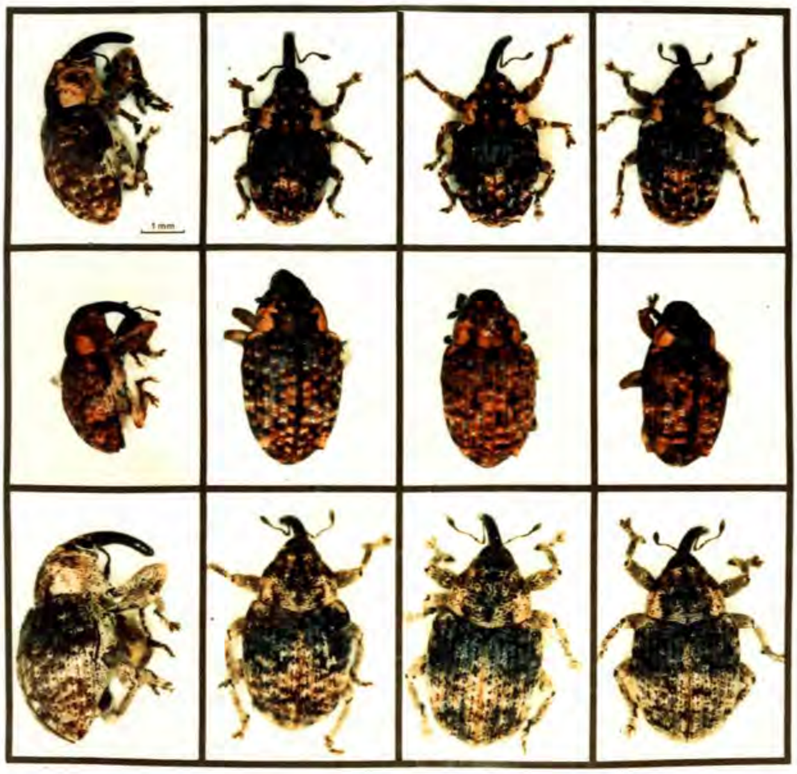


Fig. 30: Pinned specimens of *Erytenna consputa* collected on *Hakea sericea* near Nerriga, New South Wales (top row), *Erytenna consputa* reared from larvae collected in fruits of *Hakea sericea* at Wilson's Promontory, Victoria (middle row) and *Erytenna* sp. collected on *H. sericea* near Nerriga, but probably from *Hakea dactyloides* (bottom row). These are all specimens of young adults.

all of the "true" red-brown type suggest that these are from some other host plant and were just "tourists" (Moran & Southwood, 1982) at the time of collection, or that some accidental mixing of the stocks occurred when the weevils were all brought together for shipment. With age the scales rub off, making it more difficult to distinguish between the different colour forms in the older adults. No "red-brown" individuals have ever been collected from husks in the Nerriga area. The specimens from the Grampians are also different from the "true" Wilson's Promontory stocks although they are less easily distinguishable from the Nerriga weevils.

The biological significance of these colour forms is suggested by the presence of another colour variant closely resembling *E. consputa* which was frequently collected from husks on *H. sericea* together with *E. consputa* (Fig. 30 - bottom). This form is generally slightly larger and more "grey-brown" in colour than the typical Nerriga type *E. consputa*. Zimmerman (*in litt.*, 1979) subsequently found minute differences in the male genitalia of this form and the *E. consputa* from Nerriga, which led him to suspect "that two closely allied, confusingly closely similar species are involved."

A possible clue to the host-relationships of the "grey-brown" form is that Zimmerman's identification was made from a series of 12 adults which had been collected sheltering in a cluster of *Hakea dactyloides* fruits. No other colour forms were present. The significance of this is that while the fruits of *H. dactyloides* are attacked in the same way as those of *H. sericea*, the resulting husks crumble and do not last as long on the tree as do those of *H. sericea*. Shelter on *H. dactyloides* is therefore limited. Since *H. dactyloides* is sympatric with *H. sericea*, it may be that the "grey-brown" form is the homologue of *E. consputa* on *H. dactyloides*, which by necessity is often forced to shelter on *H. sericea*. This is a similar case to that reported by Sands and Fenner (1978) who found that the two sub-species of the moth *Hypochrysops ignitis* differed only slightly in morphology, while their plant hosts and physiology differed considerably.

There are also biological differences between the Nerriga and Wilson's Promontory strains of *E. consputa*. In the former group the mature larvae always leave the fruit to pupate in the ground, while in the latter a certain proportion of the larvae pupate in the husks (Neser, *pers. comm.*). From observations made by Neser (1968) it also seems possible that the Nerriga stock lay a greater proportion of their eggs in leaf tips, than do the *E. consputa* from the other regions.

Mating experiments done in South Africa are precluded at this stage because of the possible impurity of the Wilson's Promontory stock. Offspring were however produced by virgin females from a Wilson's Promontory colony in South Africa that had been crossed with Nerriga males. The larvae from this cross pupated in both the husks and in the soil. *E. consputa* from the different areas can therefore interbreed.

This confusing situation is further compounded by the fact that the host plant genus *Hakea* is in urgent need of revision. *H. sericea* varies morphologically throughout its distribution (Fig. 31) and the exact status of these geographically different forms is not known. *Hakea decurrens* R. Br., which, for example, differs notably from *H. sericea* in that it coppices from the lateral roots was, until recently, still included in the species "*sericea*". Webb (1965) also mentions a form of *H. sericea*, known as *H. sericea* var. *lissosperma*, which was to be redescribed as a distinct species.

To test the constancy of the different genotypes, *H. sericea* seed from many localities in the main collecting areas in Australia was planted in a study plot near Stellenbosch. Unfortunately many of these plants grew poorly or died, but the few from each region which survived, retained many of the differences seen in herbarium specimens from Australia, confirming the distinctiveness of each genotype (Fig. 32; Table 19). Initial studies have also shown that differences in the morphology of the pollen similar to those between species of *Hakea*, also occur in the pollen of the different strains (Fig. 33).

Neser (1968) was aware of these local differences in the allopatric populations of *H. sericea* (Fig. 31), and suspected that the differences in fruit structure as well as other characteristics, e.g. shape and size, were apparently not entirely a result of local conditions, as they also occurred

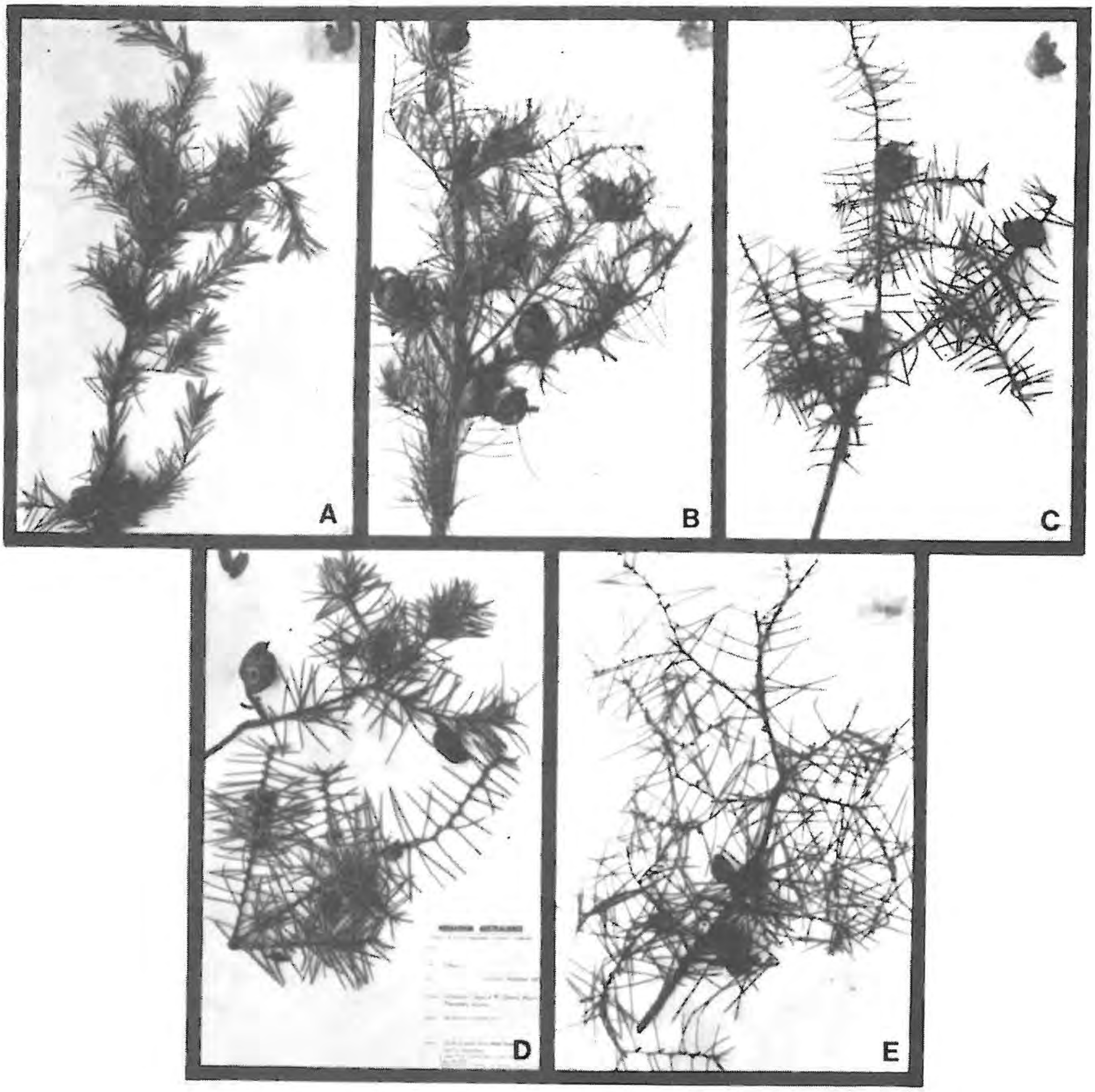


Fig. 31: Variability within the species *Hakea sericea* in Australia, as shown by herbarium specimens from (A) Sydney and (B) the Nerriga area, New South Wales, (C) the Cann River area, Victoria, (D) Wilson's Promontory, Victoria, and (E) the Grampians, Victoria.

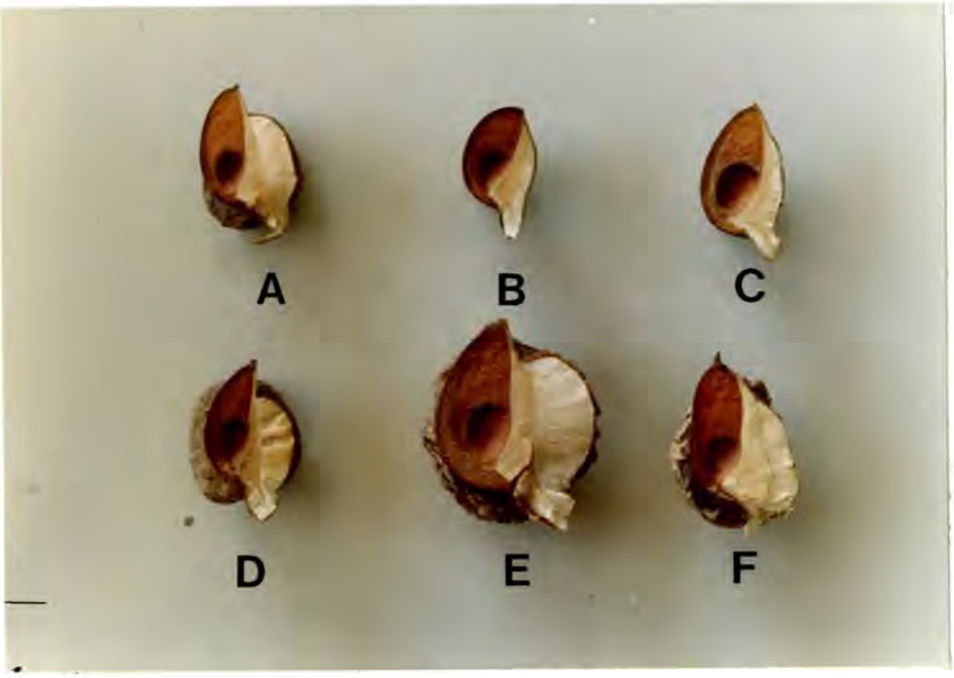


Fig. 32: Dehisced fruits (one half only) which were collected from Hakea sericea plants growing together in an experimental plot at Stellenbosch from seed which was originally collected (A) near Nerriga, New South Wales, (B) in the Cann River area, Victoria, (C) in the Grampians, Victoria, (D) between Nerriga and Nowra, New South Wales, (E) at Wilson's Promontory, Victoria, and (F) at Stellenbosch.

in cultivated plants. The significance of these differences was however overlooked, because of the emphasis then on finding populations of weevils to match the different climatic regions in the south-western and southern Cape (Webb, 1965; Neser, 1968).

H. sericea in South Africa, on the other hand, is morphologically homogeneous almost throughout its distribution, except for the H. sericea at Grahamstown. In addition to slight morphological differences Lubke (1980) has confirmed differences between the growth of the two strains under the same conditions, and the Grahamstown strain is also known

	Origin of plants					
		Nerriga area				
Characteristic	South Africa (S.A.)	near Oallen Ford	near Nowra	Cann river	Wilson's Promontory	Grampians
MORPHOLOGICAL						
Leaf						
Leaf-base - point of attachment to the stem		Same as S.A.	Same as S.A.		Similar to Cann River	Similar to Cann River
	Base of leaf not well-defined			Attached onto a raised portion of the stem. Base of leaf well-defined.		
Flower						
Colour	Cream	Same as S.A.	Same as S.A.	Cream & pink	Same as S.A.	Same as S.A.
Proportion of stalk to style	Almost equal	Same as S.A.	Same as S.A.	Much shorter than style	Much shorter than style	Much shorter than style
Fruit (Fig. 32)						
Approx. max. size (size variable depending on growth of plant)	See Fig. 32	Slightly smaller than S.A.	Slightly smaller than S.A.	Much smaller than S.A. (plants growing very poorly)	Much larger than S.A.	Smaller than S.A. (plants growing poorly)
Width of granular layer along suture indicated by the arrow in Fig.	See Fig. 32	Similar to S.A.	Similar to S.A.	Similar to S.A.	Much wider than S.A.	Similar to S.A.
PHENOLOGICAL						
Flowering time 1982 season	June - August	About 3 weeks after S.A.	About 3 weeks after S.A.	About 1 week after S.A.	About 4 weeks before S.A.	Same as S.A.

Table 19: A comparison of a few reliable morphological characters, and one phenological character of Hakea sericea plants from different areas in Australia and the H. sericea from South Africa. The plants have all been grown together in an experimental plot at Stellenbosch from seed originally collected at the different localities in Australia.

to be resistant to the pathogen, Colletotrichum gloeosporioides (Morris, pers. comm.). The H. sericea at Grahamstown has however been well colonised by the Nerriga stock of E. consputa (Appendix 6).

In highly-developed insect-host plant associations, the development of strains in the latter may give rise to the co-evolution of co-adapted strains of the specialized insect species that feed on them. Available evidence would suggest that the genus Erytenna, together with two other genera, namely Cydmaea and Dicomada, are closely associated with the genus Hakea. E. consputa as it is presently known, belongs to the Erytenna/Cydmaea/Dicomada complex of the sub-family Erirhininae. The three genera are "closely similar and have similar host associations" (Zimmerman, in litt., 1980), and

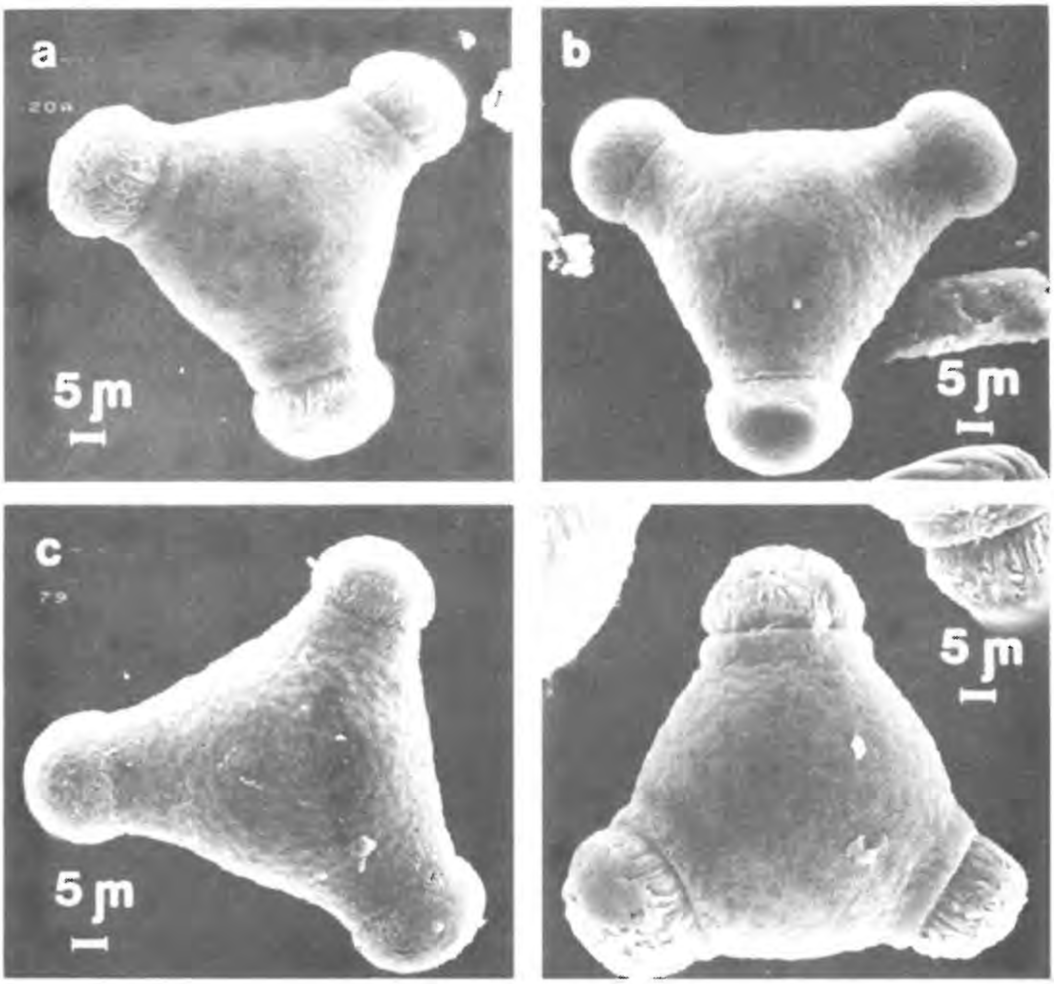


Fig. 33: Pollen grains which were collected from different regions of south-eastern Australia namely (a) Nerriga area, New South Wales, (b) Wilson's Promontory, Victoria, and (c) The Grampians, Victoria, and from (d) an unidentified Western Australian species of Hakea. The pollen was collected from plants growing together in an experimental plot at Stellenbosch.

on the limited knowledge available they have only been reared from, and mainly collected on, plants in the genus *Hakea* (Moore, 1964; Neser, 1968; Zimmerman, *in litt*., 1980).

The genus *Erytenna* contains two species namely *consputa* and *dispersa* described from "south Australia" and "western Australia" respectively (Pascoe, 1870). Zimmerman (*in litt*., 1976) originally believed these to be synonyms and if this is the case *E. consputa* has, to date, according to Neser (*in litt*., 1976), been collected from *H. sericea*, *H. gibbosa* and and *H. dactyloides* in eastern Australia, and from *Hakea nitida*, *Hakea cucullata* and *Hakea oleifolia* in Western Australia. The apparent lack of species specificity suggested by the above host records is probably due in part to the poor state of the taxonomy of the genus, as can be seen from the account in Neser (1968), and from the fact that some specimens may merely have been collected as tourists on these other *Hakea* species. This view is supported by the fact that *E. consputa*, collected on *H. sericea* in Australia, has failed to establish on another *Hakea* weed in South Africa, namely *Hakea gibbosa*. What is important here, however, is the restriction of the genus *Erytenna* to the genus *Hakea*.

The known list of *Cydmaea* species with their host records is shown in Table 20. The confusing and conflicting situation at the species level is again attributable largely to the neglected state of the taxonomy, and should not detract from the apparent specificity of *Cydmaea* within the genus *Hakea*. An explanatory note by Zimmerman (*in litt*., 1980) says that "although Lea originally stated that *Cydmaea eucalypti* was taken on *Eucalyptus*, it is possible that the host association was cited in error" (Table 20).

Little is known about the third genus, *Dicomada*. *Dicomada rufa* Blackburn larvae develop in the buds of *H. sericea* (Kluge, *in litt*., 1980).

There is also a suggestion of speciation of Erytenna on plants in the genus Hakea. After suggesting Erytenna to be a monotypic genus (see above) Zimmerman (in litt., 1979) subsequently has been of the opinion that there are several species. Specimens collected from Hakea obliqua and Hakea flabellifolia, recently appear,to be two new species. The present E. consputa was for a time known as E. sp. near consputa (Neser, 1968).

Cydmaea species	Locality	Host and additional biological data	Reference
binotata Lea	1) Sydney Area N.S.W.	1) Feeding on buds, foliage and flowers of Hakea gibbosa.	Moore (1964)
	2) Nerriga Area N.S.W.	1) Collected from husks on Hakea sericea. Tested and released for biological control of H. sericea in South Africa.	Kluge (1978)
bimaculata Pascoe	–	1) Adults taken from H. sericea trees.	Neser (1968)
crassirostris Blackburn	1) Sydney Area N.S.W.	1) Larvae destroy developing fruits of Hakea teretifolia.	Moore (1964)
	2) Sydney Area N.S.W.	2) Emerged from H. gibbosa husks.	Neser (1968)
	3) Sydney Area N.S.W.	3) Emerged from H. gibbosa husks.	Kluge (1980 in litt.)
diversa Lea	1) Sydney Area N.S.W.	1) Feeding on flowers, foliage and buds of H. teretifolia.	Moore (1964)
	2) –	2) Taken from H. sericea tree.	Neser (1968)
diversa Lea	Sydney Area N.S.W.	1) Severe damage to flowers of Hakea leucoptera.	Moore (1964)
eucalypti Lea	1) Sydney Area N.S.W.	1) Feeds on buds, shoots and foliage of H. sericea.	Moore (1964)
	2) –	2) Taken from Hakea oleifolia. (Note - Host association of specific name with Eucalytus probably an error (Zimmerman, in litt.).)	Kluge (1980 in litt.)
luctuosa Pascoe	1) Sydney Area N.S.W.	1) Severe damage by larvae to foliage of H. teretifolia.	Moore (1964)
	2) –	2) Emerged from husks on H. sericea.	Kluge (1980 in litt.)
major Blackburn	Sydney Area N.S.W.	1) Fruits destroyed by larvae; adults feed on buds of H. gibbosa.	Moore (1964)
major var.	Sydney Area N.S.W.	1) Collected on H. gibbosa - uniformly grey colour.	Moore (1964)

Table 20: A summary of data on the distribution and host-plant associations of the hakea fruit weevil, Cydmaea binotata, collected from various sources.

From a comparison of a few reliable characteristics of the *H. sericea* plants growing together at Stellenbosch (Table 19), it appears that the Nerriga strain of *E. consputa* from New South Wales is most likely that of the South African *H. sericea*. According to Neser & Annecke (1973) it is also very likely that the South African *H. sericea* was introduced from somewhere in New South Wales, probably from around Sydney together with other such weeds as *Hakea gibbosa* (which is endemic to a limited area around Sydney) and *Acacia longifolia*. This would account for the superior colonisation achieved by the Nerriga stock of *E. consputa*.

Based on these results, the variable colonisation of *H. sericea* by *E. consputa* in South Africa can be attributed to the existence of different strains of *E. consputa* from the different areas in Australia.

Appendix 8: A summary of the counts that were repeated on randomly selected trees following each of the two main counts of young fruits and surviving fruits between 1979 - 1981, showing the degree of error incurred on these counts.

Count	Year	Sample size		Error		
					Range	
		Trees	Fruits	Mean %	Overcount	Undercount
Young fruits at the start of the season (Sept. - Oct.)	1979	43	1 392	-2,3	50 vs 38	51 vs 63
	1980	29	1 282	-1,4	68 vs 59	55 vs 77
	1981	16	1 959	-3,3	197 vs 182	192 vs 227
Surviving fruits at the end of the season (Feb.)	1979	329	4 924	-2,8	-	-
	1980		No data			
	1981	33	648	0	19 vs 17	34 vs 38

Appendix 9. The level of activity of the hakea fruit weevil, Erytenna consputa, as shown by counts of scarred fruits, and the combined counts of scarred and successfully attacked fruits in four randomly selected transects at Goudini between 1979 - 1981.

Year	Transect Number	Number of scarred fruits		Total number of scarred and successfully attacked fruits	
		Total	%[a]	Total	%[b]
1979	1	64	15,2	315	35,9
	14	62	8,4	946	35,5
	18	57	7,9	417	53,1
	20	98	8,3	533	33,0
1980	1	247	51,8	1 177	83,7
	3	117	41,2	553	80,2
	7	484	45,0	1 819	69,8
	12	161	33,9	2 186	79,3
1981	3	148	94,3	1 073	99,2
	5	1 130	93,5	6 468	99,0
	18	935	98,9	5 439	99,8
	20	1 160	95,6	4 789	98,9

a = Expressed as a percentage of the surviving fruits

b = Expressed as a percentage of the total number of young fruits in the first count at the start of the season.

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